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Influence of ocean deoxygenation on demersal fish communities: Lessons from upwelling margins and oxygen minimum zones

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Influence of ocean deoxygenation on demersal fish communities: Lessons from upwelling margins and oxygen minimum zones

A dissertation submitted in partial satisfaction of the requirements for the degree Doctor of Philosophy

in

Oceanography

by

Natalya D. Gallo

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The Dissertation of Natalya D. Gallo is approved, and it is acceptable in quality and in form for publication on microfilm and electronically:

Chair

University of California San Diego

2018

DEDICATION

To Cody Gallo, for your continuous love and support. To Evie, for giving me perspective – may the natural world inspire you the way it does me.

EPIGRAPH

“The sea itself is our laboratory”

- Walter Munk

“In the end we will conserve only what we love. We will love only what we understand. We will understand only what we are taught.”

- Baba Dioum, 1968

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Chapter 4, in full, has been accepted for publication in *Ecology*. **Gallo, N.D.**, Levin, L.A., Beckwith, M., Barry, J.P. Home sweet suboxic home: Remarkable hypoxia tolerance in two demersal fish species in the Gulf of California. The dissertation author was the primary investigator and author of this paper.

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Chapter 7, in full, is a reprint of the material as it appears in **Gallo, N.D.,** Victor, D.G., and Levin, L.A. (2017) Ocean commitments under the Paris Agreement. *Nature Climate Change* 7, 833-838. The dissertation author was the primary investigator and author of this material.

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Gallo, ND, Levin, LA, Beckwith, M, Barry, JP (accepted) Home sweet suboxic home: Remarkable hypoxia tolerance in two demersal fish species in the Gulf of California. *Ecology*.

Gerringer, ME, Andrews, AH, Huss, GR, Nagashima, K, Popp, BN, Linley, TD, **Gallo, ND**, Clark, MR, Jamieson, AJ, Drazen, JC (2018) Life history of abyssal and hadal fishes from otolith growth zones and oxygen isotopic compositions. *Deep-Sea Research I* 132, 37-50.

Gallo, ND, Victor, DG, Levin, LA (2017) Ocean commitments under the Paris Agreement. *Nature Climate Change* 7, 833-838.

Januchowski-Hartley, S, Selkoe, K, **Gallo, N**, Bird, C, Hogan, J (2017) Knowledge sharing about deep-sea ecosystems to inform conservation and research decisions. *FACETS* 2, 984-997.

Gallo, ND, Levin, LA (2016) Fish ecology and evolution in the world's oxygen minimum zones and implications of ocean deoxygenation. *Advances in Marine Biology* 74, 117-198.

Levin, LA, Mengerinck, K, Gjerde, KM, Rowden, AA, Van Dover, CL, Clark, MR, Ramirez-Llodra, E, Currie, B, Smith, CR, Sato, KN, **Gallo, ND**, Sweetman, AK, Lily, H, Armstrong, CW, Brider, J (2016) Defining "serious harm" to the marine environment in the context of deep-seabed mining. *Marine Policy* 74, 245-259.

Levin, LA, Girguis, P, German, CR, Brennan, ML, Tüzün, S, Wagner, J, Smart, C, Kruger, A, Inderbitzen, K, Le, J, Martinez, M, Martinez, C, Kappel, E, **Gallo, N**, Grupe, BM (2016) Exploration and discovery of methane seeps and associated communities in the California Borderland. *Oceanography* 29(1) Supp., 40-43.

Eddebbar, YA, **Gallo, ND**, Linsmayer, LB (2015) The oceans and the UN Framework Convention on Climate Change. *ASLO Bulletin* 24(3), 69-72.

Gallo, ND, Cameron, J, Hardy, K, Fryer, P, Bartlett, DH, Levin, LA (2015) Submersible- and lander-observed community patterns in the Mariana and New Britain trenches:

Influence of productivity and depth on epibenthic and scavenging communities. *Deep-Sea Research I* 99, 119-133.

Lehnert, EM, Mouchka, ME, Burriesci, MS, **Gallo, ND**, Pringle, JR (2014) Extensive differences in gene expression between symbiotic and aposymbiotic cnidarians. *G3: Genes, Genomes, Genetics* 4, 277-295.

Gallo, ND, Certner, RH, Parikh, N, Cho, H, Gibbons, A, Kim, C, Liu, T, Miller, H, Throwe, T, Wooten, M, Vanko, DA, Sellner, KG (2014) Efficacy of *Microcystis aeruginosa* removal in deionized and brackish water. *Proceedings for the 15th International Conference on Harmful Algae.*

Gallo, ND, Jeffery, WR (2012) Evolution of space dependent growth in the teleost *Astyanax mexicanus*. *PLoS ONE* 7(8), e41443.

ABSTRACT OF THE DISSERTATION

Influence of ocean deoxygenation on demersal fish communities: Lessons from upwelling margins and oxygen minimum zones

by

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Professor Lisa A. Levin, Chair

As oceans warm due to anthropogenic climate change, the global ocean oxygen inventory decreases in a process known as ocean deoxygenation. Since oxygen is fundamental for aerobic life, ocean deoxygenation can impact marine organisms across multiple levels of biological organization. This research used the steep gradients in oxygen characteristic of upwelling margins with oxygen minimum zones (OMZs), as a natural experiment to study how hypoxia affects the composition, diversity, trophic structure and dynamics of demersal fish communities. Despite the severely hypoxic conditions ($[O_2] < 22$ µmol kg^{-1}), demersal fish are shown to be present in OMZ systems around the world; several species exhibit remarkable hypoxia tolerance in the Gulf of California ($[O_2] < 2\ \mu mol\ kg^{-1}$). Demersal fish diversity is sensitive to hypoxia, and diversity shows a non-linear response to low oxygen conditions, decreasing rapidly below a region-specific oxygen threshold. Density patterns are less predictable in relation to oxygen levels. Paired video and environmental samples, taken using an autonomous nanolander, show that seafloor communities on the upper margin (100-400 m) in the Southern California Bight (SCB) experience substantial natural oxygen variability at daily and weekly timescales, but communities do not respond to low-oxygen events at these timescales. Feeding relationships are also altered by hypoxia. At the upper OMZ boundary in the SCB a transition occurs from primarily pelagic-feeding to benthic-feeding fishes, which contrasts with the pattern on non-upwelling margins. The expansion of low-oxygen conditions in the E. Pacific may lead to a shift in community composition as intolerant species are excluded and hypoxia-tolerant species become competitive, an overall decrease in diversity, a reduction in bentho-pelagic coupling, and a lengthening of the food chain as demersal fish shift to utilizing benthic resources. Considering the natural variation of oxygen conditions across different timescales is important as existing modes of variability determine exposure histories of animals and likely influence sensitivity of communities to deoxygenation. Despite major ecological consequences of ocean deoxygenation, an analysis of Nationally Determined Contributions submitted under the Paris Agreement indicate that oxygen loss remains an under acknowledged topic by policy-makers in the international climate community.

CHAPTER 1

Introduction

Chapter 1. Introduction

Climate Change and Ocean Deoxygenation

Climate change due to anthropogenic greenhouse gas emissions is fundamentally altering the ocean. Warming, acidification, deoxygenation, and changes in primary productivity are the primary impacts of climate change for marine ecosystems (Bopp et al. 2013, Pörtner et al. 2014). These impacts change the amount of habitable environment and food supply for marine organisms and affect shallow (Doney et al. 2012) to deep-sea ecosystems (Levin and LeBris 2015, Sweetman et al. 2017).

As oceans warm due to anthropogenic climate change, the global ocean oxygen inventory decreases in a process known as ocean deoxygenation, which is driven by changes in gas solubility, ocean ventilation, and biological consumption (Keeling et al. 2010, Schmidtko et al. 2017, Oschlies et al. 2018). The Intergovernmental Panel on Climate Change predicts a 3-6% decrease in the ocean oxygen content during the 21st century in response to surface warming (IPCC 2013). However, long-term ocean monitoring shows that deoxygenation is occurring faster than predicted. Since 1960, the ocean has lost 2% of its oxygen (Schmidtko et al. 2017, Figure 1.1 A). Ocean deoxygenation does not proceed uniformly across the ocean (Long et al. 2016, Levin 2018); certain regions (e.g. tropical and North Pacific, Whitney et al. 2007) and depths (eg. 100-300 m, Bograd et al. 2008, Figure 1.1 B) have experienced much more substantial oxygen losses than the global mean.

Areas of the ocean that are already low in oxygen are particularly vulnerable to deoxygenation. For example, a 1°C warming throughout the upper ocean, is predicted to increase the volume of hypoxic areas by 10% and triple the volume of suboxic waters (Deutsch et al. 2011). Oxygen minimum zones (OMZs) typically occur at depths between

100-1500 m along eastern boundary currents and are naturally low in oxygen due to the combined processes of high oxygen consumption at depth and limited ventilation (Wyrtki 1962). The volume and spatial extent of OMZs is predicted to increase with anthropogenic ocean warming and related changes to oceanic circulation (Keeling et al. 2010), and OMZ expansion has already been observed in the eastern tropical Atlantic and the equatorial Pacific (Stramma et al. 2008). In coastal areas, eutrophication-driven hypoxic conditions will be further exacerbated by oxygen loss from climate change (Breitburg et al. 2018).

Ocean deoxygenation has high potential to impact marine communities. Past changes in global ocean oxygen conditions have been associated with marine extinctions and diversity loss (White 1988, Moffitt et al. 2015). For most animals, oxygen is a fundamental requirement for metabolism. At the cellular level, oxygen limitation below a critical threshold (P_{crit}) impacts the ability of an animal to produce energy required to sustain essential cell function including protein synthesis and acid-base regulation (Seibel 2011). Since oxygen is so fundamental for aerobic life, oxygen limitation impacts organisms across multiple levels of biological organization, from the molecular to the ecological. Molecular and cellular responses influence the physiological functioning of an animal, affecting behavior, growth, reproductive output, and longevity of individual organisms, leading to population-level changes and ultimately community and ecosystem-level changes mediated through ecological interactions (Pörtner and Peck 2010).

Demersal Fish Communities and Fisheries

Fish and crustaceans are two of the groups most sensitive to hypoxia (Vaquer-Sunyer and Duarte 2008) and hypoxia-driven mortality events of fish have been reported in the scientific literature (Grantham et al. 2004) and in the media. However, fishes differ greatly in their hypoxia tolerances (Chu and Tunnicliffe 2015, Chu and Gale 2017) and an assortment of demersal bony fish species are known from OMZs around the world (Hunter et al. 2011, Stein et al. 2006). Some of these include commercially important fisheries species, such as the short and longspine thornyheads, the dover sole, and the sablefish (Vetter et al. 1994, Vetter 1996, Norse et al. 2012). However, other commercially important species, such as rockfish (*Sebastes spp.*), are largely intolerant of OMZ conditions (McClatchie et al. 2010). The sensitivity of demersal fisheries species to hypoxia exposure is one of the biggest questions facing sustainable fisheries management in a warming world (Keller et al. 2009, Keller et al. 2015).

In this thesis, I have chosen to focus on the demersal fish community for the following reasons: demersal fish are ecologically important as benthic and demersal predators; they support commercially-important fisheries in many parts of the world; many species are intolerant to hypoxia and may be vulnerable to ocean deoxygenation; and a few species have high hypoxia tolerance and may expand their ranges in the future.

Oxygen Minimum Zones as Natural Experimental Systems

There is a critical need to understand organismal and ecosystem sensitivities to deoxygenation, and its synergistic impacts with warming and acidification. While carefully-controlled manipulative laboratory experiments provide important insight into the physiological sensitivities of animals, they have several limitations. Specifically, experiments are usually short relative to the life of the animal, represent an acute change, and focus only on the physiological responses while de-coupling ecological relationships that play an important role in fitness. Deep-sea animals present an additional challenge, due to the difficulties of recovering healthy animals from depth and performing experiments under appropriate pressures.

OMZs represent fascinating places to study the physiological and ecological consequences of oxygen-limiting environments, and can be used as natural laboratories to gain insight into the effects of ocean deoxygenation on marine communities. OMZs are severely hypoxic systems, defined as having a dissolved oxygen concentration <0.5 ml l^{-1} (Levin 2003) or <22.5 µmol kg^{-1}. Along with being low in oxygen, these areas are also high in CO_2 and low in pH, with pCO_2 values of >1200 µatm and pH <7.7 (Feely et al. 2008). These low oxygen waters impact the pelagic community (Gilly et al. 2013), as well as the seafloor community in areas where OMZ waters intersect the continental margins (Levin 2003). Globally, OMZs make up over 1 million km^2 of permanently hypoxic continental shelf and bathyal sea floor (Helly and Levin 2004).

Regional and temporal differences in oxygen conditions in the marine environment affect the evolution of species and communities through time (Chu and Gale 2017). The first goal of the dissertation was to examine if similar characteristics (e.g. adaptations, representative families, density and diversity trends) emerged in demersal fish communities when comparing across regions with OMZs. Chapter 2, published as Gallo and Levin (2016), utilizes a comparative approach to review what is known about demersal fish communities in OMZs. Knowledge gaps and challenges identified during the writing of this chapter inspired the subsequent chapters of my thesis.

On continental margins with OMZs, steep natural gradients in climate-relevant variables exist with depth (Sperling et al. 2016). Sampling communities across spatial and vertical physicochemical gradients allows an examination of how environmental conditions correlate with differences in the structure and function of marine communities. This approach, termed the “natural laboratory” approach, can identify important thresholds, both for community metrics and for individual species, which can later be applied to predictive climate change models (Sperling et al. 2016). In this thesis, I use the steep environmental gradients in OMZ systems as natural laboratories to study how low oxygen environments affect the structure and function of demersal fish communities, and how ocean deoxygenation may impact these communities.

One of the challenges of utilizing the natural laboratory approach is that oxygen gradients frequently co-vary with other important environmental parameters, such as temperature and pH, with depth. In the Gulf of California, the unique oceanographic conditions decouple environmental covariance across relatively short spatial (i.e. latitudinal) and vertical (i.e. depth) scales. Chapter 3 makes use of the strong hydrographic gradients in the Gulf of California to study how environmental conditions correlate with trends in deep-sea demersal fish community structure and considers climate change vulnerability for these communities. Chapter 3, in full, has been reviewed and is in revision for publication.

The southern Gulf of California is one of the most extreme OMZ environments in the world, due to the suboxic conditions present throughout an extensive portion of the water column (Hendrickx and Serrano 2014). Consequently, it provides the opportunity to assess if extreme low oxygen environments exclude demersal fish. Chapter 4 describes observations of two demersal fish species from the Gulf of California that represent some of the world’s most hypoxia-tolerant fish species known. These observations invite reconsideration of the capacity for hypoxia tolerance in fish. Chapter 4, in full, has been accepted for publication in *Ecology*.

The Role of Natural Spatial and Temporal Environmental Variability

Recently, there has been an acknowledgement in the scientific community of the role of natural environmental variability in influencing the ability of communities to tolerate environmental changes induced by climate change. Stochastic environments produce communities and species that are more tolerant of extreme conditions than communities from environmentally constant areas (Bay and Palumbi 2014). Variability of environmental parameters (temperature, oxygen, pH) is therefore an important environmental factor to consider when studying the impacts of hydrographic gradients in the environment on communities.

While data on shallow-water environmental variability have proven valuable (Frieder et al. 2012, Hofmann et al. 2011, Levin et al. 2015), high-frequency deep-water oxygen measurements are rare. In Southern California, quarterly data from the California Cooperative Oceanic Fisheries Investigations (CalCOFI) show large oxygen losses at depths between 100-400 m, especially nearshore (Bograd et al. 2008, Figure 1.1 B), highlighting the sensitivity and variability of these regions at longer timescales. CalCOFI provides important quarterly measurements, but misses daily, weekly and even seasonal extreme events (Send and Nam 2012). The natural variability in environmental parameters that organisms experience may be much greater than the mean change. Understanding how communities respond to natural variability of climate parameters can help inform our understanding of community vulnerabilities to ocean deoxygenation.

Datasets that couple community responses with the natural variability of oxygen in near-shore deep-sea ecosystems are rare but informative (Matabos et al. 2012, Matabos et al.

2014). Chapter 5 focuses on developing an autonomous lander to collect paired video and high-frequency environmental data for examining deep-water oxygen variability and demersal fish community responses at depths between 100-400 m in the Southern California Bight (SCB).

Effects of Hypoxia on Ecological Interactions

Previous studies have shown that dissolved oxygen levels play a critical role in influencing megafaunal composition and community structure along the continental margins (Quiroga et al. 2009, Gooday et al. 2010) and within submarine canyons (De Leo et al. 2012). Due to their sensitivity to hypoxia (Vaquer-Sunyer and Duarte 2008), demersal fish may experience mortality, sublethal impacts, and habitat compression in response to ocean deoxygenation. Habitat compression due to OMZ expansion has already been documented for pelagic billfish in the tropical northeast Atlantic (Stramma et al. 2011) and in the Pacific (Prince and Goodyear 2006), but has not yet been documented for demersal fish species in the published literature. Demersal fish occupy high trophic positions within the benthic food web (Merrett and Haedrich 1997), so the exclusion of intolerant demersal fish species in OMZs can have functional implications for the continental margin food web.

While climate-related alterations in species distributions have received a lot of attention, food web changes have been less explored to date. The few studies that have looked at the relationship between trophic ecology and environmental oxygen conditions suggest that low oxygen conditions can impact food web structure by lengthening food chains (Norris et al. 2013), altering predatory-prey interactions (Breitburg et al. 1997), and affecting feeding modes (Sperling et al. 2013). Chapter 6 focuses on how the presence of the OMZ in the

Southern California Bight affects the trophic ecology of the demersal fish community and what the implications of deoxygenation may be for continental margin trophic relationships and predator-prey dynamics.

Connecting Science to Policy: Challenges and Opportunities

Excellent research on the science and impacts of climate change is produced by the academic community every day, however translating and communicating those findings to the policy-making community presents additional obstacles. There is growing recognition of the ineffective transfer of knowledge between the scientific community and the community of decision-makers and managers, partially driven by the traditional reliance of scientists on the "knowledge deficit model" of science communication (Simis et al. 2016). Priorities, timelines, vocabularies, and culture differ between these two communities, making effective communication challenging. However, the central environmental challenges of our time will require scientists and policy-makers to work effectively to ensure that policy decisions are informed by robust science.

The oceans cover 71% of the planet and are essential to the climate regulation of the planet. They have absorbed over 93% of the additional heat trapped in the climate system, and have taken up ~30% of anthropogenic CO_2, resulting in widespread impacts to marine ecosystems (Pörtner et al. 2014). Globally, ~ 1 billion people rely on fish as their primary source of animal protein and these people largely live in developing countries (FAO 2014). In 2010, fish provided more than half of the world's population with 15% of their animal protein (FAO 2014). Physical changes from climate change including warming, acidification, deoxygenation, and altered productivity patterns, compound the effects of other stressors on coastal communities and impact food security and fisheries sustainability (Mora et al. 2013, DOALOS 2010).

Despite our reliance on the ocean for climate regulation and food security, and the clear scientific evidence for the adverse impacts of climate change on the oceans, the ocean is under acknowledged within the international climate policy process (Galland et al. 2012, Eddebbar et al. 2015). In Chapter 7, I explore how countries include ocean and marine topics in their national climate plans, called Nationally Determined Contributions (NDCs), under the Paris Agreement. Chapter 7 has been published, in full, as Gallo et al. (2017).

The Thesis: Introductory Remarks

When I began my dissertation in 2012, ocean deoxygenation was just beginning to gain attention in the scientific community as an important impact of climate change (Keeling et al. 2010). Within the international climate policy community, knowledge was even more limited, and even the IPCC's Summary for Policymakers for the AR5 WG1 report (IPCC 2013) did not include deoxygenation. There was also a paucity of scientifically-credible information available to the public about ocean deoxygenation, which contrasted strongly with a powerful information campaign about ocean acidification. My undergraduate research days had been spent thinking about eutrophication-driven hypoxia in marine coastal systems (Gallo et al. 2014) and how different environmental conditions give rise to different evolutionary trajectories for fish (Gallo and Jeffery 2012). These experiences naturally primed my dissertation interests in studying how oxygen minimum zones influence the ecology of demersal fish communities, and how these low oxygen systems could provide insight into the ecological impacts of ocean deoxygenation. The final chapter, Chapter 8, summarizes and integrates the findings of this dissertation and their implications for demersal fish communities in a warming world.

Literature Cited

Bay, R.A., Palumbi, S.R. 2014. Multilocus adaptation associated with heat resistance in reef-building corals. Current Biology 24, 2952-2956.

Bograd, S.J., Castro, C.G., Lorenzo, E.D., Palacios, D.M., Bailey, H., Gilly, W., Chavez, F.P. 2008. Oxygen declines and the shoaling of the hypoxic boundary in the California Current. Geophys. Res. Lett. 35, L12607.

Bopp, L., Resplandy, L., Orr, J.C., Doney, S.C., Dunne, J.P., Gehlen, M., Halloran, P., Heinze, C., Ilyina, T., Séférian, R., Tjiputra, J., Vichi, M. 2013. Multiple stressors of ocean ecosystems in the 21st century: projections with CMIP5 models. Biogeosciences 10, 6225-6245.

Breitburg, D., Levin, L.A., Oschlies, A., Grégoire, M., Chavez, F.P., Conley, D.J., Garçon, V., Gilbert, D., Gutiérrez, D., Isensee, K., Jacinto, G.S., Limburg, K.E., Montes, I., Navqi, S.W.A., Pitcher, G.C., Rabalais, N.N., Roman, M.R., Rose, K.A., Seibel, B.A., Telszewski, M., Yasuhara, M., Zhang, J. (2018) Declining oxygen in the global ocean and coastal waters. *Science* 359(6371), eaam7240.

Breitburg, D.L., Loher, T., Pacey, C.A., Gerstein, A. 1997. Varying effects of low dissolved oxygen on trophic interactions in an estuarine food web. Ecol. Monogr. 67, 489–507.

Chu, J.W.F., Gale, K.S.P. 2016. Ecophysiological limits to aerobic metabolism in hypoxia determine epibenthic distributions and energy sequestration in the northeast Pacific ocean. Limnol. Oceanogr. 62, 59-74.

Chu, J.W.F., Tunnicliffe, V. 2015. Oxygen limitations on marine animal distributions and the collapse of epibenthic community structure during shoaling hypoxia. Global Change Biology. doi: 10.1111/gcb.12898

De Leo, F.C., Drazen, J.C., Vetter, E.W., Rowden, A.A., Smith, C.R. 2012. The effects of submarine canyons and the oxygen minimum zone on deep-sea fish assemblages off Hawai'i. *Deep-Sea Res. I* 64, 54-70.

Deutsch, C., Brix, H., Ito, T., Frenzel, H., Thompson, L. 2011. Climate-forced variability of ocean hypoxia. *Science* 333, 336–339.

DOALOS. 2010. Oceans and climate change. Prepared by the Division for Ocean Affairs and the Law of the Sea, Office of Legal Affairs. http://www.un.org/depts/los/oceans_climate_change/oceans_climate_change_7_september_2010.pdf

Doney, S.C., Ruckelshaus, M., Duffy, J.E., Barry, J.P., Chan, F., English, C.A., Galindo, H.M., Grebmeier, J.M., Hollowed, A.B., Knowlton, N., Polovina, J., Rabalais, N.N., Sydeman, W.J., Talley, L.D. 2012. Climate change impacts on marine ecosystems. Ann. Rev. Mar. Sci. 4, 11-37.

Eddebbar, Y.A., Gallo, N.D., Linsmayer, L.B. 2015. The oceans and the UN Framework Convention on Climate Change. *ASLO Bulletin* 24(3), 69-72.

FAO. 2014. FAO and the post-2105 development agenda: Fisheries, aquaculture, oceans, and seas. http://www.fao.org/fileadmin/user_upload/post-2015/14_themes_Issue_Papers/EN/14 _themes__december_2014_/fisheries-09.pdf

Feely, R.A., Sabine, C.L., Hernandez-Ayon, J.M., Ianson, D., Hales, B. 2008. Evidence for upwelling of corrosive “acidified” water onto the continental shelf. Science 320, 1490-1492.

Frieder, C.A., Nam, S.H., Martz, T.R., and Levin, L.A. 2012. High temporal and spatial variability of dissolved oxygen and pH in a nearshore California kelp forest. Biogeosciences 9, 3917-3930.

Galland, G., Harrould-Kolieb, E., Herr, D. 2012. The ocean and climate change policy. Climate Policy, DOI: 10.1080/14693062.2012.692207.

Gallo, N.D., Certner, R.H., Parikh, N., Cho, H., Gibbons, A., Kim, C., Liu, T., Miller, H., Throwe, T., Wooten, M., Vanko, D.A., Sellner, K.G. 2014. Efficacy of *Microcystis aeruginosa* removal in deionized and brackish water. *Proceedings for the 15th International Conference on Harmful Algae.*

Gallo, N.D., Levin, L.A. 2016. Fish ecology and evolution in the world’s oxygen minimum zones and implications of ocean deoxygenation. Advances in Marine Biology 74, 117-198.

Gallo, N.D., Jeffery, W.R. 2012. Evolution of space dependent growth in the teleost *Astyanax mexicanus*. *PLoS ONE* 7(8), e41443.

Gallo, N.D., Victor, D.G., Levin, L.A. 2017. Ocean commitments under the Paris Agreement. Nature Climate Change 7: 833-838.

Gilly, W.F., Beman, J.M., Litvin, S.Y., Robison, B.H. 2013. Oceanographic and biological effects of shoaling of the oxygen minimum zone. Annu. Rev. Mar. Sci. 5, 393–420.

Gooday, A.J., Bett, B.J., Escobar, E., Ingole, B., Levin, L.A., Neira, C., Raman, A.V., Sellanes, J. 2010. Habitat heterogeneity and its influence on benthic biodiversity in oxygen minimum zones. Marine Ecology 31, 125-147.

Grantham, B.A., Chan, F., Nielsen, K.J., Fox, D.S., Barth, J.A., Huyer, A., Lubchenko, J., Menge, B.A. 2004. Upwelling-driven nearshore hypoxia signals ecosystem and oceanographic changes in the northeast Pacific. Nature 429, 749-754.

Helly, J.J., Levin, L.A. 2004. Global distribution of naturally occurring marine hypoxia on continental margins. Deep-Sea Res. I 51, 1159-1168.

Hendrickx, M.E., Serrano, D. 2014. Effects of the oxygen minimum zone on squat lobster distributions in the Gulf of California, Mexico. Cent. Eur. J. Biol. 9(1), 92-103.

Hofmann, G.E., Smith, J.E., Johnson, K.S., Send, U., Levin, L.A., Micheli, F., Paytan, A., Price, N.N., Peterson, B., Takeshita, Y., Matson, P.G., Crook, E.D., Kroeker, K.J., Gambi, M.C., Rivest, E.B., Frieder, C.A., Yu, P.C., Martz, T.R. 2011. High-frequency dynamics of ocean pH: A multi-ecosystem comparison. PLoS ONE 6(12), e28983.

Hunter, W.R., Oguri, K., Kitazato, H., Ansari, Z.A., Witte, U. 2011. Epi-benthic megafaunal zonation across an oxygen minimum zone at the Indian continental margin. Deep-Sea Res. I 58, 699-710.

IPCC. 2013. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y.V., Bex, Midgley, P.M. (eds.). Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 1535 pp, doi:10.1017/CBO9781107415324.

Keeling, R.F., Kortzinger, A., Gruber, N. 2010. Ocean deoxygenation in a warming world. Annu. Rev. Mar. Sci. 2, 199–229.

Keller, A.A., Simon, V., Chan, F., Wakefield, W.W., Clarke, M.E., Barth, J.A., Kamikawa, D., Fruh, E.L. 2009. Demersal and invertebrate biomass in relation to an offshore hypoxic zone along the US West Coast. Fisheries Oceanography 19(1), 76-87.

Keller, A.A., Ciannelli, L., Wakefield, W.W., Simon, V., Barth, J.A., Pierce, S.D. 2015. Occurrence of demersal fishes in relation to near-bottom oxygen levels within the California Current large marine ecosystem. Fish. Oceanogr. 24(2), 162–176.

Levin, L.A. 2003. Oxygen minimum zone benthos: adaptation and community response to hypoxia. Ocean. Mar. Biol. Ann. Rev. 41:1-45.

Levin, L.A. 2018. Manifestation, drivers, and emergence of open ocean deoxygenation. Annu. Rev. Mar. Sci 10, 229–260.

Levin, L.A., Le Bris, N. 2015. The deep ocean under climate change. Science 350(6262), 766-768.

Long, M.C., Deutsch, C., Ito, T. 2016. Finding forced trends in oceanic oxygen. *Global Biogeochem. Cycles* 30, 381–397.

Matabos, M., Bui, A.O.V., Mihaly, S., Aguzzi, J., Juniper, S.K., Ajayamohan, R.S. 2014. High-frequency study of epibenthic megafaunal community dynamics in Barkley Canyon: A multi-disciplinary approach using the NEPTUNE Canada network. Journal of Marine Systems 130, 56-68.

Matabos, M., Tunnicliffe, V., Juniper, S.K., Dean, C. 2012. A year in hypoxia: epibenthic community responses to severe oxygen deficit at a subsea observatory in a coastal inlet. PloS One 7, e45626.

McClatchie, S., Goericke, R., Cosgrove, R., Auad, G., Vetter, R. 2010. Oxygen in the Southern California Bight: Multidecadal trends and implications for demersal fisheries. Geophysical Research Letters 37, L19602.

Merrett, N.R., Haedrich, R.L. 1997. Deep-Sea Demersal Fish and Fisheries, first ed. Chapman and Hall, London.

Moffitt, S.E., Moffitt, R.A., Sauthoff, W., Davis, C.V., Hewett, K., Hill, T.M. 2015. Paleoceanographic insights on recent oxygen minimum zone expansion: lessons for modern oceanography. PLoS ONE 10(1), e0115246.

Mora, C., Wei, C.-L., Rollo, A., Amaro, T., Baco, A.R., Billett, D., Bopp, L., Chen, Q., Collier, M., Danovar, R., Gooday, A.J., Grupe, B.M., Halloran, P.R., Ingels, J., Jones, D.O.B., Levin, L.A., Nakano, H., Norling, K., Ramirez-Llodra, E., Rex, M., Ruhl, H.A., Smith, C.R., Sweetman, A.K., Thurber, A.R., Tjiputra, J.F., Usseglio, P., Watling, L., Wu, T., Yasuhara, M. 2013. Biotic and human vulnerability to projected changes in ocean biogeochemistry over the 21st Century. *PLoS Biol* 11(10), e1001682.

Norris, R.D., Turner, S.K., Hull, P.M., Ridgwell, A. 2013. Marine ecosystem responses to Cenozoic global change. Science 341, 492–498.

Norse, E.A., Brooke, S., Cheung, W.W.L., Clark, M.R., Ekeland, E., Froese, R., Gjerde, K.M., Haedrich, R.L., Heppell, S.S., Morato, T., Morgan, L.E., Pauly, D., Sumaila, R., Watson, R. 2012. Sustainability of deep-sea fisheries. Mar. Pol. 36, 307–320.

Oschlies, A., Brandt, P., Stramma, L., Schmidtko, S. 2018. Drivers and mechanisms of ocean deoxygenation. Nature Geoscience 11, 476-473.

Pörtner, H.-O., Karl, D.M., Boyd, P.W., Cheung, W.W.L., Lluch-Cota, S.E., Nojiri, Y., Schmidt, D.N., Zavialov, P.O. 2014. Ocean systems. In: Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Field, C.B., V.R. Barros, D.J. Dokken, K.J. Mach, M.D. Mastrandrea, T.E. Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, B. Girma, E.S. Kissel, A.N. Levy, S. MacCracken, P.R. Mastrandrea, and L.L. White (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 411-484.

Pörtner, H.O., Peck, M.A., 2010. Climate change effects on fish and fisheries: towards a cause- and -effect understanding. J. Fish Biol. 77, 1745–1779.

Prince, E.D., Goodyear, C.P. 2006. Hypoxia-based habitat compression of tropical pelagic fishes. Fish. Oceanogr. 15, 451–464.

Quiroga, E., Sellanes, J., Arntz, W.E., Gerdes, D., Gallardo, V.A., Hebbeln, D. 2009. Benthic megafaunal and demersal fish assemblages on the Chilean continental margin: the influence of the oxygen minimum zone on bathymetric distribution. Deep-Sea Res. II 56, 1112–1123.

Schmidtko, S., Stramma, L., Visbeck, M. 2017. Decline in global oceanic oxygen content during the past five decades. Nature 542, 335-339.

Seibel, B.A. 2011. Critical oxygen levels and metabolic suppression in oceanic oxygen minimum zones. J. Exp. Biol. 214, 326–336.

Send, U., Nam, S. 2012. Relaxation from upwelling: the effect on dissolved oxygen on the continental shelf. J. Geophys. Res. 117, C04024.

Simis, M.J., Madden, H., Cacciatore, M.A., Yeo, S.K. 2016. The lure of rationality: Why does the deficit model persist in science communication? Public Understanding of Science 25(4), 400-414.

Sperling, E.A., Frieder C.A., Levin, L.A. 2016. Biodiversity response to natural gradients of multiple stressors on continental margins. *Proc. R. Soc. B* 283: 20160637.

Sperling, E.A., Frieder, C.F., Raman, A.V., Girguis, P.R., Levin, L.A., Knoll, A.H. 2013. Oxygen, ecology, and the Cambrian radiation of animals. PNAS 110 (33), 13446–13451.

Stein, D.L., Drazen, J.C., Schlining, K.L., Barry, J.P., Kuhnz, L. 2006. Snailfishes of the central California coast: video, photographic and morphological observations. J. Fish Biol. 69, 970– 986.

Stramma, L., Johnson, G.C., Sprintall, J., Mohrholz, V. 2008. Expanding oxygen-minimum zones in the tropical oceans. Science 320, 655–658.

Stramma, L., Prince, E.D., Schmidtko, S., Luo, J., Hoolihan, J.P., Visbeck, M., Wallace, D.W.R., Brandt, P., Kortzinger, A. 2011. Expansion of oxygen minimum zones may reduce available habitat for tropical pelagic fishes. Nat. Clim. Change 2, 33–37.

Sweetman, A.K., Thurber, A.R., Smith, C.R., Levin, L.A., Mora, C., Wei, C.-L., Gooday, A.J., Jones, D.O.B., Rex, M., Yasuhara, M., Ingels, J., Ruhl, H.A., Frieder, C.A., Danovaro, R., Wurzberg, L., Baco, A., Grupe, B.M., Pasulka, A., Meyer, K.S., Dunlop, K.M., Henry, L.-A., Roberts, J.M. 2017. Major impacts of climate change on deep-sea benthic ecosystems. Elem Sci Anth. 5: 4.

Vaquer-Sunyer, R., Duarte, C.M. 2008. Thresholds of hypoxia for marine biodiversity. *Proc. Natl. Acad. Sci.* 105, 15452–15457.

Vetter, R.D. 1996. Bathymetric demography and niche separation of thornyhead rockfish: *Sebastolobus alascanus* and *Sebastolobus altivelis*. Can. J. Fish. Aquat. Sci. 53, 600–609.

Vetter, R.D., Lynn, E.A., Garza, M., Costa, A.S. 1994. Depth zonation and metabolic adaptation in Dover sole, *Microstomus pacificus* and other deep-living flatfishes: factors that affect the sole. Mar. Biol. 120, 145–159.

White, B.N. 1988. Oceanic anoxic events and allopatric speciation in the deep sea. Biol. Oceanogr. 5, 243–259.

Whitney, F.A., Freeland, H.J., Robert, M. 2007. Persistently declining oxygen levels in the interior waters of the eastern subarctic Pacific. Prog. Oceanogr. 75, 179–199.

Wyrtki, K. 1962. The oxygen minima in relation to ocean circulation. Deep-Sea Res. I 9, 11–23.

Figures

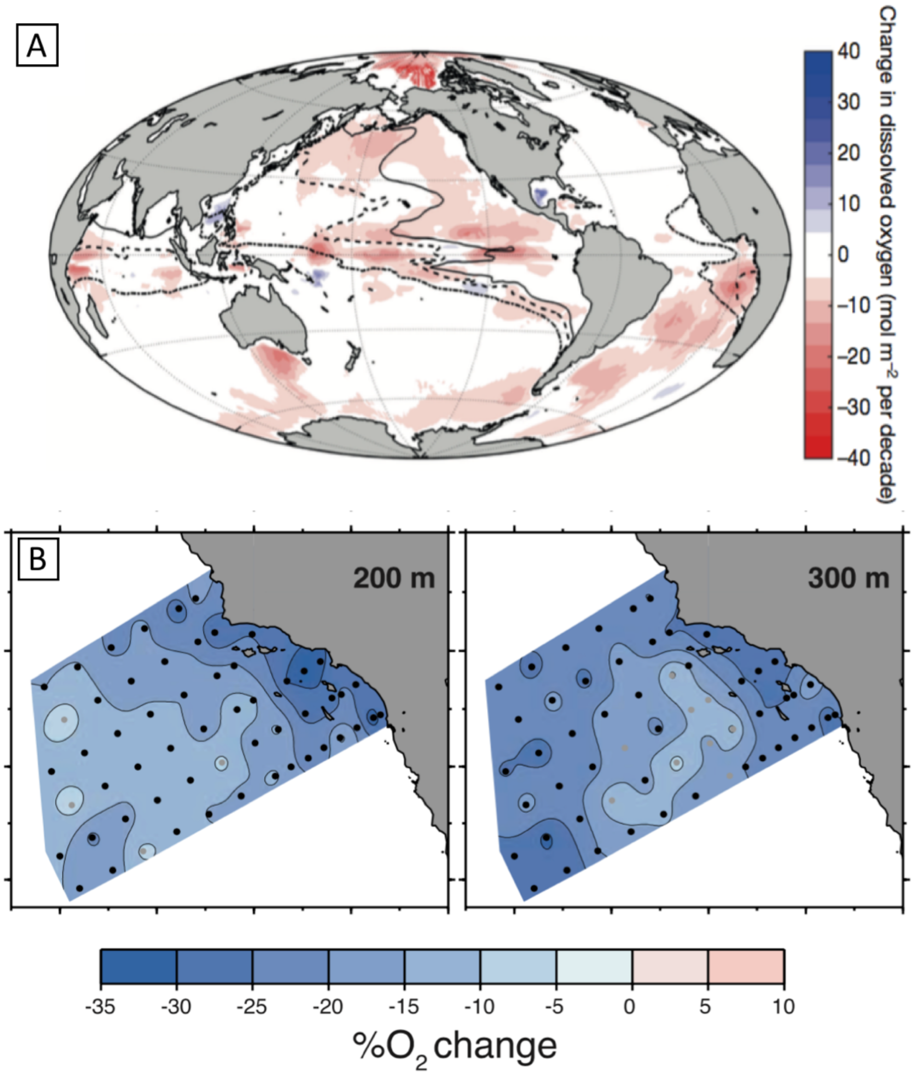

Figure 1.1. Global and regional trends in ocean oxygen loss. A. Global trends in observed oxygen loss over the last five decades, reproduced from Schmidtko et al. (2017). Colors represent change in dissolved oxygen in mol m^{-2} per decade, and all areas in red have lost oxygen. B. Regional trends in oxygen loss in the Southern California Bight from 1984-2006, reproduced from Bograd et al. (2008), showing large oxygen decreases at upper slope depths. Colors represent percent oxygen change and all areas in blue have lost oxygen.

CHAPTER 2

Fish ecology and evolution in the world's oxygen minimum zones and implications for ocean deoxygenation

Synopsis

This chapter is a comparative review that analyzes how oxygen minimum zones have influenced the ecology of demersal fish communities around the world. Evolutionary patterns and mechanisms of hypoxia adaptation in oxygen minimum zone-dwelling fish species are examined, as well as the relationship between oxygen and fish community density and diversity trends. These findings are considered in light of the projected expansion of low oxygen zones with climate change.

This chapter is presented as a paper. "Fish Ecology and Evolution in the World's Oxygen Minimum Zones and Implications of Ocean Deoxygenation," was published as a review paper in *Advances in Marine Biology* in 2016.

Fish Ecology and Evolution in the World's Oxygen Minimum Zones and Implications of Ocean Deoxygenation

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Abstract

Oxygen minimum zones (OMZs) and oxygen limited zones (OLZs) are important oceanographic features in the Pacific, Atlantic, and Indian Ocean, and are characterized by hypoxic conditions that are physiologically challenging for demersal fish. Thickness, depth of the upper boundary, minimum oxygen levels, local temperatures, and diurnal, seasonal, and interannual oxycline variability differ regionally, with the thickest and shallowest OMZs occurring in the subtropics and tropics. Although most fish are not hypoxia-tolerant, at least 77 demersal fish species from 16 orders have evolved physiological, behavioural, and morphological adaptations that allow them to live under the severely hypoxic, hypercapnic, and at times sulphidic conditions found in OMZs. Tolerance to OMZ conditions has evolved multiple times in multiple groups with no single fish family or genus exploiting all OMZs globally. Severely hypoxic conditions in OMZs lead to decreased demersal fish diversity, but fish density trends are variable and dependent on region-specific thresholds. Some OMZ-adapted fish species are more hypoxia-tolerant than most megafaunal invertebrates and are present even when most invertebrates are excluded. Expansions and contractions of OMZs in the past have affected fish evolution and diversity. Current patterns of ocean warming are leading to ocean deoxygenation, causing the expansion and shoaling of OMZs, which is expected to decrease demersal fish diversity and alter trophic pathways on affected margins. Habitat compression is expected for hypoxia-intolerant species, causing increased susceptibility to overfishing for fisheries species. Demersal fisheries are likely to be negatively impacted overall by the expansion of OMZs in a warming world.

1. INTRODUCTION

Fish have been identified as one of the marine groups most sensitive to hypoxia (Vaquer-Sunyer and Duarte, 2008), however, tolerances can vary significantly across species based on evolutionary and environmental history. Oxygen minimum zones (OMZs) have been defined as areas where the dissolved oxygen content of the water drops below 0.5 mL L^{-1} or 22 μmol kg^{-1} or 7.5% saturation (Kamykowski and Zentara, 1990; Levin, 2003; Rogers, 2000) and conditions are considered severely hypoxic

(Hofmann et al., 2011). OMZs are typically treated as lacking demersal fish communities, however most OMZs have certain fish species that have evolved to tolerate the physiologically extreme conditions. For the fish community, these severely hypoxic conditions can give rise to physiological impairment, altered behaviour, reduced feeding, and habitat compression of nontolerant species, while generating food-rich settings that provide refuge from predators for tolerant species, leading to changes in community composition and altered predator–prey relationships along the margins (Keller et al., 2015; Koslow et al., 2011; Levin, 2003). In this way, oxygen gradients interact with other factors on continental margins to generate habitat heterogeneity (Gooday et al., 2010; Sellanes et al., 2010). To date, several studies have looked at megafaunal communities as a whole in specific OMZs. However, it is valuable to focus specifically on the role of OMZs in structuring fish communities and to examine generalities and differences across regions. This review focuses on studies from different OMZs (US West Coast, Namibia, Chile, Peru, Indian Ocean), with further exploration of unpublished and gray literature (Mexico, Central America, Chile) to extract available information about the presence, identity, abundance, and diversity of demersal fish in OMZs. In addition, this review will consider which fish live in OMZs, how they are able to do this through physiological and molecular adaptations, and how these adaptations have arisen through evolutionary time.

Section 2 of the review will focus on characteristics of OMZs that can give rise to different ecological responses in the demersal fish community. Section 3 of the review focuses on what is known regionally about fish communities in different OMZs and explores tolerant and intolerant species, changes in community composition, and changes in abundance and diversity across oxygen gradients. Section 4 of the review investigates the physiology and adaptations of fish species in hypoxic environments to look at which adaptations occur most commonly, whether certain orders or families appear to have greater ability to tolerate low-oxygen conditions, and if physiological adaptations of fish to low oxygen have arisen independently or share common origins. In Section 5, these previous sections are synthesized and discussed within the context of predicted climate-change driven decreases in global oxygen levels and the implications these changes may have for the demersal fish communities of continental margins that have OMZs. This review examines the OMZ as an interacting ecological zone within the continental margin ecosystem and provides an important foundation for understanding how demersal fish communities on the continental margins are currently affected by OMZ conditions and how these communities may respond as OMZs expand with climate change.

2. GLOBAL FISH EXPOSURE TO OXYGEN MINIMUM ZONES

In the modern ocean, OMZ waters typically occur in the bathyal zone (100–1800 m) (Fig. 1) in areas with highly productive surface waters and poor midwater circulation (Wyrtki, 1962). OMZ waters underlie productive eastern boundary current regions including the Humboldt Current off Peru–Chile, the California Current off the US and Mexican West Coast, and the Benguela Current off southwestern Africa (Arntz et al., 2006). OMZ waters are also found in the Arabian Sea and Bay of Bengal in the Indian Ocean with monsoon-driven upwelling, in the eastern tropical Pacific, and in the North Pacific in the West Bering Sea and Gulf of Alaska (Helly and Levin, 2004; Kamykowski and Zentara, 1990; Paulmier and Ruiz-Pino, 2009). Severely hypoxic waters are also found in enclosed bodies of water such as the Baltic Sea, Black Sea, the Gulf of Aden, and the Red Sea (Kamykowski and Zentara, 1990), and in estuarine environments (Diaz and Rosenberg, 1995). Shallow-sill topographical depressions such as the Santa Barbara Basin and the Cariaco Trench can also have lower oxygen conditions than surrounding waters and can be anoxic or near anoxic at the bottom (Kamykowski and Zentara, 1990; Mead, 1963; Moffitt et al., 2014). While oxygen conditions are not low enough to be categorized as an OMZ, the shallow sills surrounding the Sulu Sea also give rise to unique low-oxygen conditions (~39 μmol kg^{-1}) at abyssal depths (3000–5000 m) (Gordon et al., 2011), whereas OMZs typically occur at bathyal depths (Helly and Levin, 2004). Definitions and locations of hypoxic zones in different parts of the world have been thoroughly reviewed (Hofmann et al., 2011).

The total surface area of permanent OMZs in the world's oceans is ~8% of the total oceanic area and the calculated volume of OMZ waters is 10.3 million km^3 (Paulmier and Ruiz-Pino, 2009). Due to global circulation patterns, the northern hemisphere contains the greatest volume of the world's severely hypoxic water (Kamykowski and Zentara, 1990; Wyrtki, 1966) and 95% of the world's suboxic water (<5 μmol kg^{-1}) is in the eastern tropical North Pacific (Deutsch et al., 2011). OMZs are composed of an upper boundary that is sensitive to seasonal fluctuations (Helly and Levin, 2004; Nam et al., 2015), followed by a low-oxygen core, and a more stable lower

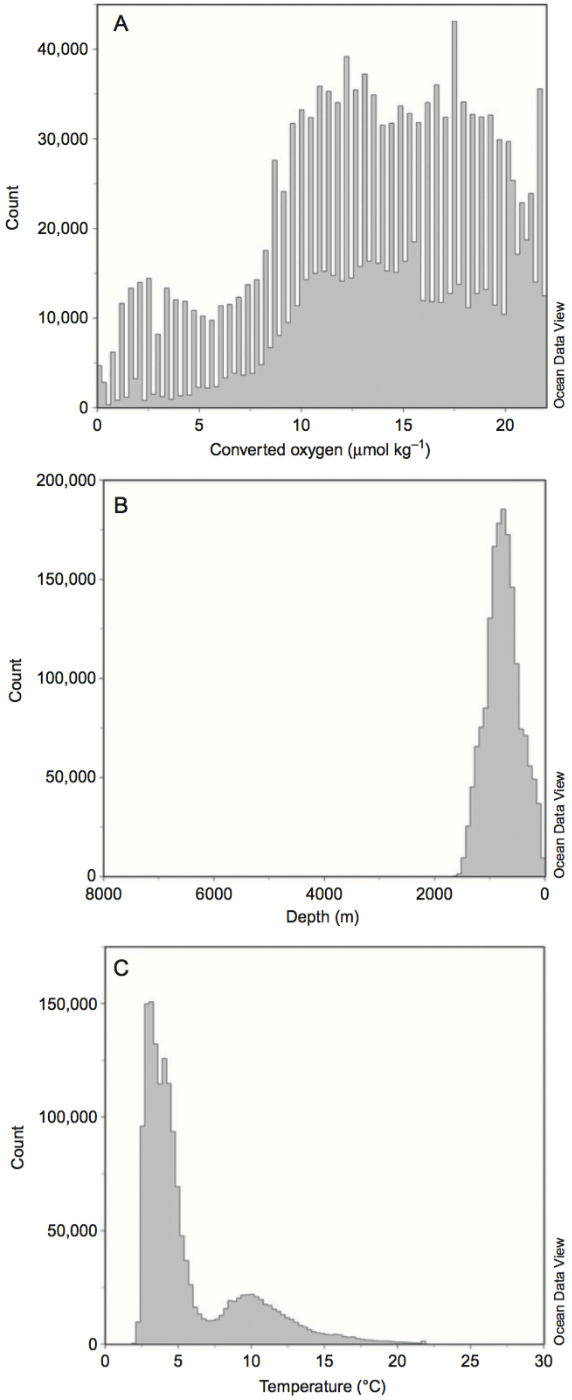

Fig. 1 Characteristics of the world's oxygen minimum zone (OMZ) waters where $O_2 \leq 22$ µmol kg^{-1} with respect to (A) oxygen, (B) water depth, and (C) temperature, based on CTD profile data, downloaded from the World Ocean Database (Boyer et al., 2013) (1973–2009) and plotted using Ocean Data View 4.7.4 (Schlitzer, 2015).

boundary where oxygen concentrations begin to increase (Fig. 2A). Over- and underlying the OMZ is a transitional zone defined by Gilly et al. (2013) as the *oxygen limited zone* (OLZ) where oxygen concentrations are 22–60 μmol kg^{-1} or 0.5–1.5 mL L^{-1}, this is also considered the hypoxic boundary at <20% oxygen saturation (Gray et al., 2002; Hofmann et al., 2011). Previous studies have also used alternative definitions of oxygen thresholds for OMZs (Gilly et al., 2013; Paulmier and Ruiz-Pino, 2009), but this review will consider systems with ≤ 22 μmol kg^{-1} for clarity and consistency (Helly and Levin, 2004; Levin, 2003). This review does not focus on the mechanisms that give rise to and maintain OMZs, but several studies and reviews have looked at these questions in depth (Kamykowski and Zentara, 1990; Keeling et al., 2010; Moffitt et al., 2015b; Paulmier et al., 2006; Peña-Izquierdo et al., 2015; Rogers, 2000; Wyrtki, 1962).

Oxygen Minimum Zone impact the pelagic community (Ekau et al., 2010; Gilly et al., 2013), but also the benthic community in areas where OMZs intersect the continental margins (Gooday et al., 2010; Helly and Levin, 2004; Levin, 2003; Levin et al., 2009). Globally, OMZs cover over

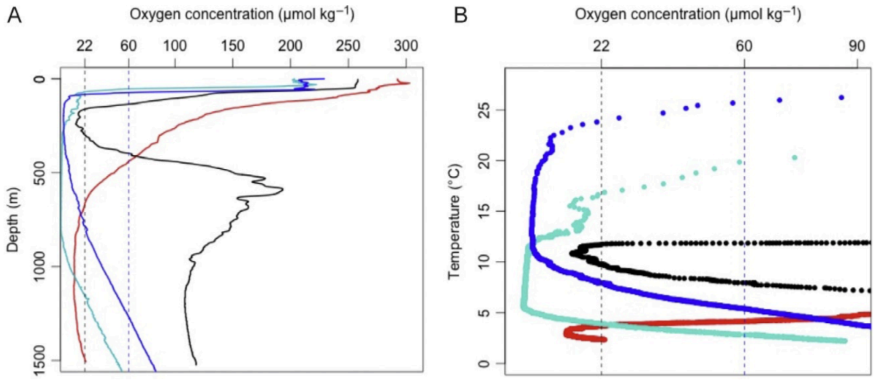

Fig. 2 Oxygen minimum zones (OMZs) in four regions exhibit differing characteristics with relation to (A) thickness, depth of upper and lower boundary, and minimum oxygen concentrations, and (B) local water temperature. *Blue* (*dark grey* in the print version) *dashed line* indicates oxygen limited zone (OLZ) boundary (60 μmol kg^{-1}) and *black dashed line* indicates OMZ boundary (22 μmol kg^{-1}). *Red* (*dark grey* in the print version)—thick, deep, and cold OMZ off Alaska (58° 5.898′N, 147° 47.778′W), *turquoise* (*light grey* in the print version)—very thick, shallow, and temperate OMZ off Costa Rica and Nicaragua (12° 54.828′N, 91° 48.522′W), black—thin, shallow, and temperate OMZ off central Chile (32° 59.880′S, 72° 59.880′W), and *blue* (*dark grey* in the print version)—thick, shallow, and very warm OMZ in the Bay of Bengal (16° 37.800′N, 91° 56.700′E). Conductivity–temperature–depth (CTD) profiles were downloaded from the World Ocean Database (Boyer et al., 2013) and plotted in R (R Core Team, 2012).

1.1 million km^2 of permanently hypoxic continental shelf and bathyal seafloor (Helly and Levin, 2004), and this area is expanding with climate change (Stramma et al., 2010). OMZs are areas of great benthic habitat heterogeneity due to the strong vertical zonation of dissolved oxygen, organic matter content, sediment type, as well as sulphide concentration (Levin et al., 2010) and play an important role in generating deep-sea biodiversity along the continental margins (Gooday et al., 2010; Levin, 2003; Rogers, 2000).

Globally OMZs exhibit notable geographic differences in the following characteristics that are ecologically and physiologically relevant for structuring the demersal fish community: the depth and seasonal variability of the upper and lower boundary, the thickness of the OMZ in the water column, the minimum oxygen levels observed within the OMZ core, the local temperature conditions present within the OMZ, and the geologic age of the ocean basin within which the OMZ occurs. These differences have been described in several papers (Arntz et al., 2006; Hofmann et al., 2011; Paulmier and Ruiz-Pino, 2009) and will be summarized here as they affect demersal fish communities.

2.1 Depth of Upper and Lower OMZ Boundary

Since increasing pressure with depth exerts an influence on continental margin zonation (Carney, 2005), and temperature also declines with increasing depth to 6000 m, the depth of the upper and lower boundary of the OMZ and OLZ is an important characteristic. The shallowest OMZs occur in the tropics, including in the Gulf of California, on the Pacific side of Mexico and Peru; in the northern Indian Ocean; and on the Namibian shelf (Helly and Levin, 2004). In the Humboldt and Benguela Current, the OMZ begins at shelf and upper slope depths (Arntz et al., 2006). These shallow OMZs can have their upper OMZ boundary at 50–100 m depth, meaning that severely hypoxic waters are close to the surface (at times within the euphotic zone) and impact shallower-water fish communities. For example, off the southwest coast of India near the city of Cochin, severely hypoxic OMZ conditions are found at 20 m depth mid-August through October (Banse, 1968). In contrast, the upper boundary of OMZs occurs deeper at higher latitudes. The upper boundary of the California Current OMZ begins at slope depths (400–500 m) (Arntz et al., 2006) and is found at deeper depths off Oregon, Washington, and Canada (600–700 m) than off California (Helly and Levin, 2004). Severely hypoxic waters can be found seasonally at inner shelf depths (20–50 m) in some of these areas such as off Oregon (Grantham et al., 2004;

Keller et al., 2010), or in eutrophic settings such as the Black Sea and Baltic Sea (Daskalov, 2003; Gooday et al., 2010).

The depth of the lower boundary of the OMZ in the California Current, Humboldt Current, and Benguela Current regions vary considerably (Arntz et al., 2006) with the lower boundary occurring at upper slope depths (200–400 m) off Chile and Namibia, and in contrast, extending deeper off Central America, Peru (500 m) and North America (900–1100 m) (Arntz et al., 2006). The lower boundary of the OMZ is also found deeper (>1000 m) in the southern Gulf of California, in the eastern tropical Pacific from 8° to 22°N, and in the northern Arabian Sea and Bay of Bengal (Helly and Levin, 2004). Most OMZ waters occur at depths shallower than 1500 m (Kamykowski and Zentara, 1990) (see Fig. 1).

2.2 OMZ Thickness

The thickness of OMZs (depth between upper and lower boundary) varies from 200 to 1200 m (Helly and Levin, 2004) (see Fig. 2), with the thickness and intensity influencing population dynamics along the continental margin. Thick OMZs likely act as greater barriers to gene flow, than shallow OMZs, and may play a greater role in speciation along continental margins (Rogers, 2000; White, 1988). Areas with thinner OMZs may allow some fish species to move out of low-oxygen conditions when circumstances become too severe or when they are undergoing a more energetically demanding life stage. Some of the thinnest OMZs (<300 m thick) include those off western Africa, off central Chile, off central North America, and in the West Bering Sea (Helly and Levin, 2004; Paulmier and Ruiz-Pino, 2009). The thickest OMZs (>1000 m) include those in the southern Gulf of California, in the eastern tropical North Pacific (>8°N), in parts of the North Pacific (~48–58°N), and in the northern Arabian Sea (Helly and Levin, 2004; Paulmier and Ruiz-Pino, 2009). In the N. Arabian Sea, the OMZ occurs between 100 and 1200 m (Murty et al., 2009) and is most intense off the coasts of Pakistan and west India (Slater and Kroopnick, 1984). Approximately 677,320 km^2 of deep seafloor is intercepted by OMZ waters in the Arabian Sea, making it one of the largest transects of deep seafloor affected by hypoxia in the world (Helly and Levin, 2004).

2.3 Minimum O_2 Levels in the OMZ Core

While OMZs are defined as having O_2 concentrations $\leq 22\ \mu\text{mol kg}^{-1}$, the minimum oxygen levels encountered within the OMZ core vary (see

Fig. 2). The intensity of the OMZ core can give rise to different patterns of faunal zonation within the OMZ and can give rise to additional stressors. Biogeochemical changes, including denitrification, increased bioavailability of trace metals, and H_2S production begin to take place at suboxic conditions where oxygen concentrations fall below 5 μmol kg^{-1} (Paulmier and Ruiz-Pino, 2009), and these may all be additional stressors for the fish community. The OMZs originally thought to have the lowest core oxygen conditions include the northern Arabian Sea, the eastern north tropical Pacific, and the Gulf of California (Helly and Levin, 2004). However, a recent revolution in measurement technology for ultra low oxygen has revealed oxygen concentrations <2 μmol kg^{-1} off Peru, Chile, Namibia, and elsewhere (Kalvelage et al., 2014; Revsbech et al., 2009). The core of the eastern tropical Pacific is functionally anoxic, with oxygen concentrations in the OMZ core found to be <0.1 μmol kg^{-1} between depths of 150 and 800 m (Tiano et al., 2014).

2.4 Local Temperature

The temperature characteristics of the OMZ are influenced by latitude, water masses, and boundary currents, which relate to the depth of the OMZ in the water column. Assembled data from all the world's OMZs reveal a biomodal distribution of temperature: while most OMZs have cold temperatures (<6°C), some have much warmer conditions (10–22°C) (Fig. 1C). Differences in temperature likely have physiological implications for the demersal fish communities that inhabit these regions. While many OMZs occur in tropical latitudes (<25°), important exceptions include the OMZ off Central Chile and throughout the eastern North Pacific, including the seasonal OMZs in the West Bering Sea and Gulf of Alaska (Paulmier and Ruiz-Pino, 2009). Demersal fish living in OMZs with higher temperature conditions may be under greater hypoxia stress because metabolic rates and oxygen demand increase under warmer temperatures (Pörtner et al., 2006). In the Arabian Sea and Bay of Bengal (see Fig. 2B), temperatures are very warm. The lowest temperatures observed off the southwest coast of India near the city of Cochin where OMZ waters occur seasonally at 20 m were 20.9–22°C and offshore at 50 m depth were 19.7–20.3°C (Banse, 1968). Temperatures of 10–12°C found at 800–1000 m off Pakistan and India (Cowie and Levin, 2009; Levin et al., 2013) are nearly twice as warm as other regional OMZs. A study using Argo floats in the Arabian Sea found that water temperatures at OMZ depths were up to 25°C (Prakash et al., 2012). This contrasts greatly with the much colder local temperature conditions of the OMZ off the US West Coast, where OMZ temperatures are 4°C at 770 m off Oregon, 5–6°C at 500–525 m off California, and 3–4°C at 800 m off Alaska (see Fig. 2) (Levin et al., 2010). While oxygen remains above OMZ conditions (~39 μmol kg^{-1}) in the Sulu Sea, these unique oxygen limited conditions in the abyssal zone (3000–5000 m) occur under uniformly warm temperatures (9.9°C) (Gordon et al., 2011).

2.5 Seasonality, Variability, and Biological Responses

Fish can respond to changes in oxygen across a range of timescales from rapid (hour to day) changes in gene expression (Gracey et al., 2001; Tiedke et al., 2014), to longer timescales through changes in the presence and density of specific species leading to altered community structure (Chu and Tunnicliffe, 2015; Keller et al., 2010; Wu, 2002). Natural variability of oxygen levels within OMZs may thus be physiologically and ecologically relevant. Oxygen variability in OMZs occurs on daily, seasonal, and interannual timescales. This appears to depend on latitude, water depth, the presence of monsoon-driven climatological changes, changes in the El Niño Southern Oscillation, and varying strengths of boundary currents and undercurrents (Nam et al., 2015). Greater seasonality in OMZs is noted at higher latitudes (Kamykowski and Zentara, 1990), and two seasonal OMZs have been identified in the West Bering Sea and the Gulf of Alaska where oxygen levels rise above OMZ levels during the summer (Paulmier and Ruiz-Pino, 2009). Off Central America, seasonality in the depth of the upper OMZ boundary has been observed with shoaling characteristic of November/December (Bianchi, 1991; Stromme and Saetersdal, 1988).

Oscillations of the upper boundary of OMZs are thought to be a widespread phenomenon (Murty et al., 2009), however the characteristic variance of the upper boundary is region-specific. At semi-diurnal and diurnal timescales, displacement of the OMZ upper boundary by internal tides has been observed on Volcano 7 in the Pacific Ocean (Wishner et al., 1995). Seasonal changes in upwelling intensity also gives rise to varying characteristics of the OMZ. The upper boundary of the OMZ exhibits more variability than the lower boundary, but both can be influenced by seasonal changes. Off Namibia, the strongest upwelling occurs in late winter (August) and spring (September–November) (Hamukuaya et al., 2001), leading to an expansion of low-oxygen zones. The diversity and distribution of the demersal fish community on the Namibian shelf and upper slope was found to differ before (Winter 1987) and after (Summer 1988) the upwelling season, presumably due to the altered oxygen conditions (Mas-Riera et al., 1990). Off Oregon and Washington, low-oxygen water occurs at shallower depths during the late summer and fall and both catch per unit effort and total species richness have been positively correlated with bottom oxygen concentration (Keller et al., 2015). In the Southern California Bight, the upper boundary of the OMZ shoals during the spring and summer and is found deeper in the winter, due to upwelling and relaxation patterns that drive primary production and respiration (Send and Nam, 2012), as well as to increased advection of Pacific Equatorial Water in the core of the California Undercurrent during the summer (Nam et al., 2015).

Especially for the benthic communities, variability in oxygen conditions driven by undercurrent variability may also be important to consider since all eastern boundary currents have underlying counter-direction undercurrents, and the undercurrent typically overlaps with part of the depth of the OMZ. For example, Thiel (1978) reports that off Portugal and West Africa, the strongest undercurrent flow is observed at depths of 200–300 m (up to 30 cm s^{-1}) (Mittelstaedt, 1976), and the highest tidal activity is found in this range on the upper slope (Horn and Meincke, 1976). Strong seasonal variability of the California Undercurrent in terms of strength, depth, and direction likely contributes to deep-water oxygen variability along the continental margin in the Southern California Bight between 100 and 400 m depth (Bograd et al., 2015; Lynn and Simpson, 1987). These sources of environmental variability can influence the demersal fish community and illustrate that the upper boundary of the OMZ can be a dynamic environment.

In areas that experience strong seasonal monsoons, such as the Indian Ocean, OMZ variability may be even greater. Considerable monsoon-driven variability has been described in the Arabian Sea OMZ (Morrison et al., 1998, 1999; Prakash et al., 2012; Thiel, 1978). The depth of the OMZ off India is changed by the monsoon regime with oxygen-poor water shoaling up the continental shelf during the southwest monsoon (Banse, 1968), leading to decreased catches of fish and prawns by more than 75% from June to September (Sankaranarayanan and Qasim, 1968).

The El Niño Southern Oscillation (ENSO) influences the depth of the thermocline in eastern boundary current regions and thereby influences the characteristics of the OMZ. Off Peru, ENSO events can alter the depth of the upper boundary of the OMZ by nearly 100 m (Levin et al., 2002). In the

Humboldt Current System during an El Niño, the OMZ contracts due to changes at the OMZ upper boundary, which are driven by altered flow of the undercurrent (Arntz et al., 2006). The 1997–1998 El Niño reduced the amount of seafloor affected by the OMZ off Peru by approximately 69% (Helly and Levin, 2004), expanding local fisheries for hake, octopus, and scallop (Arntz et al., 2006). On the southern California shelf, El Niño also enhances oxygenation by reducing primary production (and subsequent respiration) while La Niña conditions do the opposite (Nam et al., 2011)—but few observations are made deeper within the OMZ. While the upper boundary of the OMZ is influenced by ENSO events, there is no indication that the lower boundary or zone below the OMZ is affected by ENSO, although some changes due to altered surface productivity are suggested (Arntz et al., 2006).

3. INFLUENCE OF OXYGEN MINIMUM ZONES ON DEMERSAL FISH COMMUNITY CHARACTERISTICS

Zonation of demersal fish communities has been well studied in areas without OMZs such as the northeast Atlantic and the Australian continental margins (Haedrich and Merrett, 1990; Koslow, 1993; Koslow et al., 1994); however, vertebrates frequently receive less focus than invertebrate community members in OMZ studies, either being left out entirely (Arntz et al., 2006) or being separated from the megafauna *sensu strictu* (Murty et al., 2009). Some OMZ regions such as the Gulf of California, the Pacific margin of Mexico, Central, and South America, and the Bay of Bengal remain grossly understudied; nonetheless, the infrequent descriptions of demersal fish communities in OMZs begin to shed light on some interesting and important patterns. This section will first introduce the oxygen requirements of fish and published hypoxia tolerances of fish within the context of OMZ oxygen conditions, and then identify some characteristic patterns illustrating how OMZs influence demersal fish communities, including changes in abundance and diversity, and the presence of edge effects and single fish species dominance at O_2 levels where most other megafauna are absent.

3.1 Fish Oxygen Requirements Within OMZs

Due to the physicochemical properties of gases in water, oxygen is much more limiting in water than in air. The lower availability of oxygen in water and the greater viscosity of water require that fish must be very efficient at extracting oxygen from the water. Hypoxic thresholds for fish have been reviewed by Davis (1975), Gray et al. (2002), Vaquer-Sunyer and Duarte (2008), and Hofmann et al. (2011), and these studies have found that fish exhibit sublethal and lethal impacts of oxygen at higher thresholds than most invertebrate groups. Oxygen minimum zones represent some of the most hypoxic waters in the world and OMZ oxygen concentrations are lower than most lethal and sublethal oxygen concentrations determined for many fish species in the published literature. However, OMZs are not devoid of fish fauna, making them an opportune system to study how severe hypoxia influences the fish community and how fish adapt to these extreme conditions.

Fish exhibit a range of responses to hypoxia and responses vary with the severity of hypoxia (Davis, 1975). Sublethal responses occur first and include physiological, behavioural, or stress-induced responses. Specific oxygen thresholds can influence fish behaviour, metabolic rate, swimming ability, growth, circulatory dynamics, ventilation, gaseous exchange, blood O_2 saturation, sensitivity to toxins and other environmental stressors, and viability and development of eggs and larvae (Davis, 1975; Farrell and Richards, 2009; Nilsson, 2010; Richards, 2009). Reduced growth rate and food conversion efficiency is a sublethal impact of hypoxia, so growth has been suggested to be a useful criterion for hypoxia influence because it is an expression of the net product of metabolic functions (Davis, 1975). Gray et al. (2002) reported that growth of actively swimming fish is affected at oxygen levels of 183 μmol kg^{-1}.

The oxygen threshold at which oxygen becomes limiting for fish has been defined in many different ways in the literature and is species-specific (Davis, 1975; Hofmann et al., 2011). Of note, there is a research bias towards laboratory studies on Atlantic species (Chu and Tunnicliffe, 2015), which may be less hypoxia tolerant than Pacific species. The oxygen concentration at which a fish switches from being an oxyregulator (O_2 consumption independent of environmental O_2 levels) to an oxyconformer (O_2 consumption dependent on environmental O_2 levels), which is termed the critical oxygen tension (P_{crit}) (Richards, 2009, 2011), is considered to be a physiologically relevant hypoxia threshold. The metabolic index (ratio of O_2 supply to resting metabolic O_2 demand) has also been used to examine critical oxygen levels in marine environments, and this study found that conditions were only viable if they supported metabolic rates at least two to five times resting rates (Deutsch et al., 2015). Much higher hypoxia thresholds such as <50% O_2 saturation have also been used in the coastal literature, since sensitive species begin showing avoidance, reduced growth, and other signs of physiological stress below this level (Breitburg, 2002).

Based on a review of published literature on community responses to low-oxygen conditions, Hofmann et al. (2011) defined "mild hypoxia" to be 107 μmol kg^{-1}, where sensitive species begin to show avoidance (Diaz and Rosenberg, 2008), "hypoxia" to be 61 μmol kg^{-1} where several studies have found that fish are absent (Gewin, 2010; Gray et al., 2002; Kemp et al., 2009; McClatchie et al., 2010), and "severe hypoxia" as 22 μmol kg^{-1} where mass mortality occurs and only highly adapted species are able to survive (Shaffer et al., 2009). One meta-analysis found that the average mean lethal concentration (LC_{50}) for marine benthic fish was 47.12 ± 2.14 μmol kg^{-1}, and the average mean sublethal concentration (SLC_{50}) was 134.92 ± 11.93 μmol kg^{-1} (Vaquer-Sunyer and Duarte, 2008); however, the mean lethal concentrations and sublethal concentrations were calculated using data for only 23 and 15 species of fish respectively. Oxygen conditions in OMZs fall within the "severe hypoxia" category, while oxygen conditions within OLZs fall within the "hypoxia" category.

While oxygen is frequently reported as a concentration, it is important to keep in mind that the partial pressure of oxygen (pO_2) is the more physiologically relevant measurement since it provides the thermodynamic driving force for molecular transfer of oxygen across membranes (Hofmann et al., 2011). Temperature-dependent metabolic rate differences also need to be factored in because aerobic oxygen demand is greater under warmer temperatures (Brown et al., 2004; Deutsch et al., 2015), with the Q_{10} value of oxygen consumption for fish overall found to be 2.3 (Bridges, 1988). Blood–oxygen binding is also temperature sensitive (Mislan et al., 2015). Empirically, several studies have shown that lethal hypoxic conditions for fish are also reached much faster under warmer temperatures (Schurmann and Steffensen, 1992; Secor and Gunderson, 1998). This was not observed by Vaquer-Sunyer and Duarte (2011), but this contradictory result may be influenced by the manner of the meta-analysis and the range of physiological capacities of the fish species that were included in the analysis. The dependence of metabolic rate on environmental temperature suggests that fish living in "warm" OMZs (eg, in the Arabian Sea and Bay of Bengal) may be under additional stress relative to those living in colder or deeper OMZs such as in the California Current System (CCS). Approximating a Q_{10} value of 2 for fish, metabolic demand of demersal fish in the Bay of Bengal OMZ may be four times greater than in the Alaskan OMZ where temperatures at similar oxygen concentrations are 20°C colder (see Fig. 2).

Three additional factors make OMZs particularly inhospitable for fish and may contribute to greater hypoxia stress. While OMZs are very low in oxygen, they also have high concentrations of pCO_2 and have been called carbon-maximum zones (Paulmier et al., 2011). For example, high pCO_2 (>1200 uatm.) and low pH (<7.6) are reported off California (Feely et al., 2008). As a result, OMZ fish are exposed to combined hypoxia–hypercapnia stress. High pCO_2 levels may have additional physiological consequences for respiration under low O_2 conditions because oxygen transport proteins are highly sensitive to pH (Rummer et al., 2013; Seibel and Walsh, 2003). High pCO_2 environmental conditions in other studies have induced a respiratory acidosis in fish, resulting in a decreased oxygen affinity and oxygen carrying capacity of haemoglobin due to the Root effect (Jensen and Weber, 1982, 1985; Jensen et al., 1993; Thomas, 1983). In certain fish species, blood pH can eventually be recovered over time through the exchange of Cl^- for HCO_3^- ions in the gills, leading to a phenomenal accumulation of HCO_3^- in the blood (Jensen and Weber, 1982). It is not known if OMZ fish also have high HCO_3^- levels to compensate for the high pCO_2 environment in which they live.

Because OMZs can have very old water (i.e. isolated from the surface via thermohaline circulation) that has experienced extensive remineralization, they are also high in nitrate and nitrite. Nitrite penetrates red blood cells and oxidizes haemoglobin to methaemoglobin, which cannot transport oxygen, thereby decreasing the blood capacitance and the blood arterial content (Jensen et al., 1987, 1993). Lastly, some OMZs such as off Namibia (Brüchert et al., 2009; Weeks et al., 2004) have high H_2S concentrations, which are usually toxic even in low concentrations because hydrogen sulphide inhibits cytochrome *c* oxidase in the mitochondria, thus blocking the last step of the respiratory chain where oxygen is the terminal electron receptor (Jensen et al., 1993). When exposed to H_2S, haemoglobin loses any oxygen that it is carrying and is transformed into sulphaemoglobin (van Assendelft, 1970). The interacting influence of high pCO_2, high nitrite and H_2S concentrations in OMZs can further make oxygen extraction more difficult for OMZ fish in an already oxygen limited environment. Thus, OMZ-tolerant fish species are truly physiologically remarkable.

3.2 Composition of Demersal Fish Species in OMZs and OLZs

Dissolved oxygen levels play a critical role in influencing megafaunal composition and community structure along the continental margins (Murty et al., 2009; Quiroga et al., 2009) and within submarine canyons (De Leo et al., 2012). Despite the characterization of fish as being relatively intolerant of hypoxic conditions (Vaquer-Sunyer and Duarte, 2008), an assortment of demersal fish species are known from OMZs around the world (Hunter et al., 2011; Stein et al., 2006) (Fig. 3; Table 1). Since responses of demersal fish species to hypoxia are species-specific, a change in community

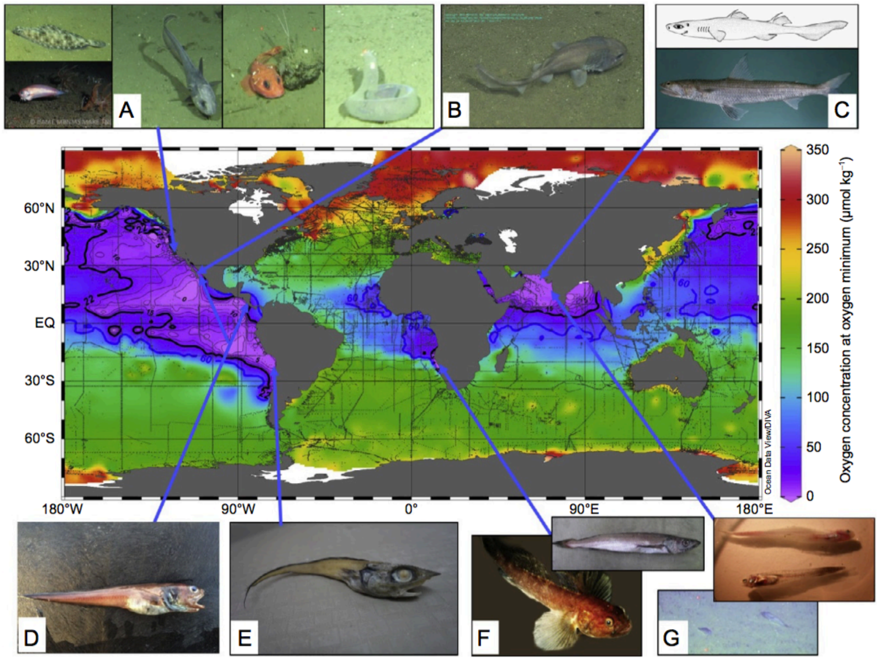

Fig. 3 Map of global spatial distribution of oxygen minimum zones (OMZs) with minimum oxygen concentrations (μmol kg^{-1}) within the water column and dominant resident demersal fish species known from each area. Thick *blue* (*dark grey* in the print version) *contours* show the spatial extent of oxygen limited zones ($\leq$60 μmol kg^{-1}) and thick *black contours* show the spatial extent of oxygen minimum zones ($\leq$22 μmol kg^{-1}). Data downloaded from the World Ocean Database (Boyer et al., 2013) (1973–2009) and plotted using Ocean Data View 4.7.4 and DIVA gridding software (Schlitzer, 2015). OMZ-adapted demersal fish species include: (A) in the Northeast Pacific—*Microstomus pacificus* (upper left), *Careproctus melanurus* (bottom left), *Nezumia liolepis* (middle left), *Sebastolobus alascanus* (middle right), and *Eptatretus deani* (right), (B) in the Gulf of California—*Cephalurus cephalus*, (C) on the Pakistan margin—*Centroscyllium ornatum* and *Saurida tumbil*, (D) in the Gulf of California and Central America—*Cherublemma emmelas*, (E) on the Chilean margin *Trachyrincus villegai*, (F) on the Namibian margin—*Sufflogobius bibarbatus* and *Merluccius capensis*, and (G) on the west Indian margin—*Bregmaceros* sp. and *Liparidae* sp. See Table 1 for citations. *Photographs: SIO Triton ROV and UC Ship Funds (*M. pacificus, N. liolepis, S. alascanus, E. deani, Bregmaceros *sp.), MBARI (*C. cephalus, C. melanurus*), FAO (*C. ornatum*), H. Vestheim (*S. bibarbatus*), N.D. Gallo (*C. emmelas, T. villegai*), F.H. Van der Bank (*M. capensis*), J.E. Randall (*S. tumbil*), W.R. Hunter (*Liparidae *sp.).*

Table 1 Known Demersal Fish Inhabitants of Oxygen Minimum Zones (OMZs)

	Common Name	Location	Depth Range (m)	Temp Range (°C)	Oxygen Range (µmol kg^{-1})	Citations
Myxiniformes						
Myxinidae						
Eptatretus deani	Black hagfish	US Pacific margin (northeastern Pacific)	366–2743	3.6–6.4	13.1–58.2	N.D. Gallo (unpublished data) and Day and Pearcy (1968)
Eptatretus sp.	Hagfish	Canada Pacific margin (northeastern Pacific)	890	3.6–4.0	10.5–15.3	Juniper et al. (2013)
Squaliformes						
Etmopteridae						
Etmopterus sp.	Lantern shark	Indian margin (Arabian Sea)	–	–	–	Hunter et al. (2011)
Centroscyllium ornatum	Ornate dogfish	Pakistan margin (Arabian Sea)	1000–1200	7.4–8.7	6.7–17.0	Murty et al. (2009)
Centrophoridae						
Centrophorus granulosus	Gulper shark	Yemen margin (Arabian Sea)	50–1440	5.2–12.9	13.3–212.7	Kukharev (2015)
Carcharhiniformes						
Scyliorhinidae						
Apristurus brunneus	Brown catshark	California margin (northeastern Pacific)	79–1448	2.9–5.4	13.1–70.9	N.D. Gallo (unpublished data)

Continued

Table 1 Known Demersal Fish Inhabitants of Oxygen Minimum Zones (OMZs)—cont'd

	Common Name	Location	Depth Range (m)	Temp Range (°C)	Oxygen Range (µmol kg^{-1})	Citations
Parmaturus xaniurus	Filetail catshark	California margin to Gulf of California (northeastern Pacific)	88–1250	3.3–9.4	13.1–143.5	N.D. Gallo (unpublished data)
Cephalurus cephalus	Lollipop shark	Gulf of California	275–927	9.4	6.1	Aguirre-Villaseñor and Salas-Singh (2012)
Halaelurus spp.	Tiger catshark	Yemen margin (Arabian Sea)	–	–	13.3	Kukharev (2015)
Cephalurus sp. cf.	Catshark	Chilean margin (southeastern Pacific)	313–327	10.9–11.5	3.0–3.84	J. Sellanes Universidad Catolica del Norte (UCN) (unpublished data)
Proscylliidae						
Eridacnis radcliffei	Pygmy ribbontail catshark	Yemen margin (Arabian Sea)	71–766	–	13.3–174.9	Kukharev (2015)
Rajiformes						
Arhynchobatidae						
Bathyraja interrupta	Sandpaper skate	Oregon margin (northeastern Pacific)	64–1500	3.1–8.3	13.1–273.4	Day and Pearcy (1968)
Bathyraja trachura	Roughtail skate	Oregon margin (northeastern Pacific)	213–2550	1.6–7.0	18.4–156.2	Day and Pearcy (1968)
Bathyraja sp.	Skate	Indian margin (Arabian Sea)	–	–	–	Hunter et al. (2011)

Pleuronectiformes						
Pleuronectidae						
Microstomus pacificus	Dover sole	US Pacific margin (northeastern Pacific)	10–1370	2.9–11.5	13.1–318.9	Friedman et al. (2012) and Day and Pearcy (1968)
Embassichthys bathybius	Deep-sea sole	US and Canada Pacific margin (northeastern Pacific)	125–1800	2.4–6.4	13.1–54.3	N.D. Gallo (unpublished data), Day and Pearcy (1968), and Juniper et al. (2013)
Lyopsetta exilis	Slender sole	US and Saanich Inlet (northeastern Pacific)	25–800	4.2–8.7	14.0–244.6	Matabos et al. (2012) and Chu and Tunnicliffe (2015)
Paralichthyidae						
Hippoglossina macrops	Bigeye flounder	Chilean margin (southeastern Pacific)	34–580	10.6–16.5	22–83.5	J. Sellanes (UCN) (unpublished data)
Bothidae						
Monolene maculipinna	Pacific deep-water flounder	Costa Rica to Peru (eastern tropical Pacific)	205–384	13.0–27.5	16.2–175.4	Bianchi (1991)
Soleidae						
Austroglossus microlepis	West coast sole	Namibia to South Africa (southeastern Atlantic)	100–400	7.8–14.5	16.0–218.9	Hamukuaya et al. (2001)

Continued

Table 1 Known Demersal Fish Inhabitants of Oxygen Minimum Zones (OMZs)—cont'd

	Common Name	Location	Depth Range (m)	Temp Range (°C)	Oxygen Range (µmol kg^{-1})	Citations
Anguilliformes						
Nettastomatidae						
Facciolella equatorialis	Dogface witch-eel	California margin (northeastern Pacific)	500–1000	6.2–8.2	9.2–47.7	N.D. Gallo (unpublished data)
Nettastoma sp.	Duckbill eel	Yemen margin (Arabian Sea)	–	–	13.3	Kukharev (2015)
Congridae						
Congridae sp.	Conger eel	Indian margin (Arabian Sea)	–	–	–	Hunter et al. (2011)
Congridae sp.	Conger eel	Pakistan margin (Arabian Sea)	1200	7.4	13.4–17.0	Murty et al. (2009)
Synaphobranchidae						
Synaphobranchus sp.	Cutthroat eel	Indian margin (Arabian Sea)	–	–	–	Hunter et al. (2011)
Serrivomeridae						
Serrivomer sp.	Sawtooth eel	Pakistan margin (Arabian Sea)	1100	8	9.4–11.2	Murty et al. (2009)

Notacanthiformes						
Halosauridae						
Halosaurus sp.	Halosaur	Pakistan margin (Arabian Sea)	1200	7.4	13.4–17.0	Murty et al. (2009)
Notocanthidae						
Notocanthus sp.	Deep-sea spiny eel	Pakistan margin (Arabian Sea)	1100	8	9.4–11.2	Murty et al. (2009)
Aulopiformes						
Synodontidae						
Saurida tumbil	Greater lizardfish	Pakistan margin (Arabian Sea)	4–700	11.0–26.6	4.9–206.5	Murty et al. (2009)
Saurida undosquamis	Brushtooth lizardfish	Yemen margin (Arabian Sea)	1–350	11.3–28.3	13.3–210.9	Kukharev (2015)
Harpadon squamosus	Lizardfish	Yemen margin (Arabian Sea)	–	–	13.3	Kukharev (2015)
Beryciformes						
Trachichthyidae						
Hoplostethus spp.	Roughy	Yemen margin (Arabian Sea)	–	–	13.3	Kukharev (2015)

Continued

Table 1 Known Demersal Fish Inhabitants of Oxygen Minimum Zones (OMZs)—cont'd

	Common Name	Location	Depth Range (m)	Temp Range (°C)	Oxygen Range (μmol kg^{-1})	Citations
Perciformes						
Stichaeidae						
Plectobranchus evides	Bluebarred prickleback	Saanich Inlet (northeastern Pacific)	84–368	7.6–8.6	7.9–205.6	Chu and Tunnicliffe (2015) and Matabos et al. (2012)
Agonidae						
Xeneretmus latifrons	Blacktip poacher	US Pacific margin, Saanich Inlet (northeastern Pacific)	18–486	4.6–8.7	7.4–244.6	Chu and Tunnicliffe (2015) and Matabos et al. (2012)
Bathyagonus nigripinnis	Blackfin starsnout poacher	Canada Pacific margin (northeastern Pacific)	18–1290	3.0–8.3	10.5–201.7	Juniper et al. (2013)
Zoarcidae						
Zoarcid sp.	Eelpout	Canada Pacific margin (northeastern Pacific)	890	3.6–4	10.5–15.3	Juniper et al. (2013)
Serranidae						
Diplectrum macropoma	Mexican sand perch	Mexico to Peru (eastern tropical Pacific)	1–220	16.6–16.8	17.5–120.3	Bianchi (1991)
Trichiuridae						
Trichiurus nitens	Pacific cutlassfish	Mexico to Peru (eastern tropical Pacific)	160–250	13	17.5	Bianchi (1991)
Lepturacanthus spp.	Hairtail	Yemen margin (Arabian Sea)	–	–	13.3	Kukharev (2015)

Gobiidae						
Sufflogobius bibarbatus	Bearded goby	Namibia and South Africa (southeastern Atlantic)	10–340	7.8–14.5	10.0–218.8	Hamukuaya et al. (2001), Mas-Riera et al. (1990), Utne-Palm et al. (2010), and Salvanes et al. (2011)
Carangidae						
Trachurus trachurus capensis	Horse mackerel	Gulf of Guinea to South Africa (southeastern Atlantic)	0–500	5.4–22.0	16–252.0	Hamukuaya et al. (2001)
Carangidae sp.	Carangid	Pakistan margin (Indian Ocean)	300	14.8	4.9–5.4	Murty et al. (2009)
Epigonidae						
Epigonus sp.	Deep-water cardinalfish	Pakistan margin (Arabian Sea)	140	18.2	4.9	Murty et al. (2009)
Acropomatidae						
Synagrops adeni	Aden splitfin	Yemen margin (Arabian Sea)	60–600	–	13.3	Kukharev (2015)
Percophidae						
Bembrops caudimacula	Opal fish	Yemen margin (Arabian Sea)	160–505	14.4–17.4	13.3–192.3	Kukharev (2015)
Centrolophidae						
Psenopsis cyanea	Indian ruff	Yemen margin (Arabian Sea)	179–400	–	15.5–55.5	Kukharev (2015)

Continued

Table 1 Known Demersal Fish Inhabitants of Oxygen Minimum Zones (OMZs)—cont'd

	Common Name	Location	Depth Range (m)	Temp Range (°C)	Oxygen Range (μmol kg^{-1})	Citations
Scombridae						
Scomber australasicus	Japanese mackerel	Yemen margin (Arabian Sea)	9–494	7.7–24.0	13.3–279.7	Kukharev (2015)
Ophidiiformes						
Bythitidae						
Cataetyx rubrirostris	Rubynose brotula	US Pacific margin (northeastern Pacific)	288–1000	4.9	9.0–20.6	N.D. Gallo (unpublished data)
Ophidiidae						
Cherublemma emmelas	Black brotula	Baja California to Northern Chile (eastern tropical Pacific)	15–902	6.1–20.4	3.9–219.6	Aguirre-Villaseñor and Castillo-Velázquez (2011), Bianchi (1991), and Stromme and Saetersdal (1988)
Holcomycteronus sp.	Cusk-eel	Indian margin (Arabian Sea)	–	–	–	Hunter et al. (2011)
Brotulotaenia sp.	Cusk-eel	Pakistan margin (Arabian Sea)	1000–1200	7.4–8.7	6.7–17.0	Murty et al. (2009)
Genypterus maculatus	Black cusk-eel	Chilean margin (southeastern Pacific)	82–328	9.2–11.8	17.9–50.9	Chilean Fisheries Development Program, FIP2004-09
Genypterus blacodes	Rock ling	Chilean margin (southeastern Pacific)	58–450	7.2–11.3	21.7–110.4	Chilean Fisheries Development Program, FIP2004-09

Gadiformes						
Macrouridae						
Nezumia liolepis	Smooth grenadier	Volcano 7 (eastern equatorial Pacific), US Pacific margin (northeastern Pacific)	450–1660	4.5–6.5	3.5–43.8	Friedman et al. (2012), Wishner et al. (1990, 1995), and Levin et al. (1991)
Coryphaenoides acrolepis	Strong-scaled rattail	Oregon margin (northeastern Pacific)	300–3700	1.7–6.9	18.8–158.8	Day and Pearcy (1968)
Coryphaenoides pectoralis	Pectoral rattail	Oregon margin (northeastern Pacific)	140–3500	1.8–4.6	17.1–256.4	Day and Pearcy (1968)
Coryphaenoides sp.	Grenadier	Indian margin (Arabian Sea)	–	–	–	Hunter et al. (2011)
Trachyrincus villegai	Grey grenadier	Northern Peru to Central Chile (southeastern Pacific)	250–980	–	2.6	Quiroga et al. (2009)
Merlucciidae						
Merluccius productus	North Pacific hake	US Pacific margin (northeastern Pacific), Saanich Inlet	3–1000	1.6–23.0	13.1–241.1	Chu and Tunnicliffe (2015)
Merluccius angustimanus	Panama hake	Mexico-Columbia (eastern tropical Pacific)	2–523	15.4–21.1	17.5–222.7	Bianchi (1991) and Stromme and Saetersdal (1988)

Continued

Table 1 Known Demersal Fish Inhabitants of Oxygen Minimum Zones (OMZs)—cont'd

	Common Name	Location	Depth Range (m)	Temp Range (°C)	Oxygen Range (μmol kg^{-1})	Citations
Merluccius capensis	Cape hake	Angola to South Africa (southeastern Atlantic)	20–512	6.1–19.8	10.9–236.7	Hamukuaya et al. (2001), Mas-Riera et al. (1990), and Woodhead et al. (1998)
Merluccius gayi gayi	Whiting	Chilean margin (southeastern Pacific)	58–450	6.4–12.3	16.8–253.0	Chilean Fisheries Development Program, FIP2004-09
Bregmacerotidae						
Bregmaceros bathymaster	East Pacific codlet	Gulf of California (eastern tropical Pacific)	32–500	7.6–15.4	9.2–31.5	Davies et al. (2015)
Bregmaceros cantori	Striped codlet	Cariaco Trench, Venezuela to Brazil (western Atlantic)	450–846	14.2–26.9	4.0–222.7	Baird et al. (1973), Milliken and Houde (1984), and Love et al. (2004)
Bregmaceros sp.	Codlet	Indian margin (Arabian Sea)	540	12.1	0.34	Hunter et al. (2011)
Bregmaceros sp.	Codlet	Pakistan margin (Indian Ocean)	300	14.8	4.9–5.4	Murty et al. (2009)
Moridae						
Physiculus roseus	Rosy cod	Yemen margin (Arabian Sea)	277–510	–	13.3	Kukharev (2015)

Osmeriformes						
Argentinidae						
Argentina aliceae	Alice argentina	Nicaragua to Peru (eastern tropical Pacific)	73–300	13.8–17.1	16.2–46.4	Bianchi (1991)
Cottiformes						
Liparidae						
Careproctus melanurus	Blacktail snailfish	US Pacific margin (northeastern Pacific)	89–2286	1.8–7.2	13.1–133.0	Friedman et al. (2012), Day and Pearcy (1968), and Stein et al. (2006)
Liparidae sp.	Snailfish	Indian margin (Arabian Sea)	540	12.1	0.34	Hunter et al. (2011)
Scorpaeniformes						
Scorpaenidae						
Pontinus sierra	Speckled scorpionfish	Gulf of California to Panama (eastern tropical Pacific)	15–307	13.0–13.6	14.4–20.1	Bianchi (1991)
Sebastidae						
Sebastolobus alascanus	Shortspine thornyhead	US Pacific margin (northeastern Pacific)	54–1600	3.5–7.8	13.1–171.9	Friedman et al. (2012) and Day and Pearcy (1968)
Sebastolobus altivelis	Longspine thornyhead	US Pacific margin (northeastern Pacific)	201–1757	2.7–8.6	13.1–112.4	Friedman et al. (2012) and Day and Pearcy (1968)

Continued

Table 1 Known Demersal Fish Inhabitants of Oxygen Minimum Zones (OMZs)—cont'd

	Common Name	Location	Depth Range (m)	Temp Range (°C)	Oxygen Range (μmol kg^{-1})	Citations
Sebastolobus sp.	Thornyhead	Canada Pacific margin (northeastern Pacific)	890	3.6–4	10.5–15.3	Juniper et al. (2013)
Anoplopomatidae						
Anoplopoma fimbria	Sablefish	US and Canada Pacific margin (northeastern Pacific)	175–2740	1.8–14.6	13.1–318.9	Friedman et al. (2012), Day and Pearcy (1968), and Juniper et al. (2013)
Triglidae						
Chelidonichthys capensis	Gurnard	Southeastern Atlantic and western Indian Ocean	10–390	6.1–20.5	16–222.3	Hamukuaya et al. (2001) and Mas-Riera et al. (1990)
Peristediidae						
Satyrichthys adeni	Yellowfinned searobin	Yemen margin (Arabian Sea)	71–378	7.9–17.3	13.3–213.1	Kukharev (2015)
Batrachoidiformes						
Batrachoididae						
Aphos porosus	Banded toadfish	Chilean margin (southeastern Pacific)	11–120	14.8–16.5	22–84.4	J. Sellanes (UCN) (unpublished data)

Order, family, species, common name, location, depth range (m), temperature range (°C), and oxygen range (μmol kg^{-1}), based on the Cited Literature, FishBase, and Encyclopedia of Life.

composition is observed along oxygen gradients as hypoxia-intolerant species are lost and tolerant species become abundant and dominate the community. Some studies of community shifts have been conducted across oxygen gradients (both with regard to latitude and depth) and insight has been gained from community changes during El Niño and La Niña conditions which greatly alter oxygenation. Based on previous research, we will focus at the regional level to categorize intolerant (those that show avoidance or mortality to severely hypoxic conditions) and tolerant (those inhabiting waters where $O_2 \leq 22\ \mu mol\ kg^{-1}$) species. The names of known OMZ-dwelling fish species from around the world are compiled in Table 1.

3.3 Regional Patterns in Space and Time

3.3.1 California Current Ecosystem

The US West Coast fish communities are among the best-studied on continental margins in part due to the extensive sampling by the National Oceanic and Atmospheric Administration (NOAA) Northwest Fisheries Science Center Groundfish Trawl Survey (Keller et al., 2010, 2012, 2015), research by the Monterey Bay Aquarium Research Institute (MBARI) (Stein et al., 2006) and the Scripps Institution of Oceanography on local OMZ communities, as well as the long-running oceanographic time-series from the California Cooperative Fisheries Investigation (CalCOFI) (Netburn and Koslow, 2015). Because the OMZ in the NE Pacific rarely reaches suboxic ($<5\ \mu mol\ kg^{-1}\ O_2$) conditions, numerous demersal fish species are frequent habitants. In Monterey Canyon, California, six demersal and benthic fish species are present at ~450–1000 m water depths where the OMZ intercepts the continental margin (Friedman et al., 2012). These include the liparid, *Careproctus melanurus*, the sebastids, *Sebastolobus alascanus* and *Sebastolobus altivelis*, the anoplopomatid, *Anoplopoma fimbria*, the macrourid, *Nezumia liolepis*, and the pleuronectid *Microstomus pacificus*. These six species also occur in the OMZ off San Diego, California, at depths of ~450–800 m, in addition to the brotulid, *Cataetyx rubrirostris*, the nettastomatid, *Facciolella equatorialis*, the scyliorhinids, *Apristurus brunneus* and *Parmaturus xaniurus*, the pleuronectid, *Embassichthys bathybius*, and the myxinid, *Eptatretus deani* (N.D. Gallo et al., unpublished data). In the deeper OMZ off Oregon at 600–1100 m, the macrourids, *Coryphaenoides acrolepis* and *Coryphaenoides pectoralis*, the pleuronectids, *M. pacificus* and *E. bathybius*, the sebastids, *S. alascanus* and *S. altivelis*, the liparid, *C. melanurus*, the anoplopomatid, *A. fimbria*, the myxinid, *Eptatretus* sp., and the arhynchobatids, *Bathyraja interrupta* and *Bathyraja trachura*, were found to be common community members (Day and Pearcy, 1968). *Microstomus pacificus*, occupies the greatest depth range (57–1217 m) of any fish species on the US West Coast (Keller et al., 2015), showing tolerance to a broad range of temperature, pH, oxygen, and pressure conditions.

In an analysis of the probability of occurrence of four mainly non-OMZ-dwelling Eastern Pacific demersal fish species, the chimaera, *Hydrolagus colliei*, and the pleuronectid, *Eopsetta jordani*, were found to be sensitive to near-bottom oxygen concentration, while the sebastid, *Sebastes elongatus*, and pleuronectid, *M. pacificus* showed no changes in probability of occurrence in relation to bottom oxygen concentrations (Keller et al., 2015). The lack of response from *S. elongatus* is surprising given that rockfish are thought to be sensitive to hypoxia, however this species is not found within the OMZ and may be sensitive to severely hypoxic conditions but not oxygen concentrations in its native depth range. High rockfish (*Sebastes* sp.) mortalities were observed off Oregon during an incursion of hypoxic water onto the inner shelf (<70 m) (Grantham et al., 2004). The pleuronectid, *Hippoglossus stenolepis*, also appears to be intolerant of OMZ conditions and exhibits an apparent minimum dissolved oxygen threshold of $\sim$39 μmol kg^{-1} (Sadorus et al., 2014).

Several studies from Canada have also shown responses of the demersal fish community to changes in oxygen as well as considerable tolerance to hypoxia. Due to the presence of a shallow-water sill and high productivity in the Saanich Inlet, the inlet becomes seasonally hypoxic, and changes are observed in the epibenthic community at 100 m (Chu and Tunnicliffe, 2015; Matabos et al., 2012). More than half of the variance in the entire epibenthic species assemblage was explained by components of the oxygen regime (Chu and Tunnicliffe, 2015). The pleuronectid, *Lyopsetta exilis*, was abundant during severely hypoxic ($O_2 < 22$ μmol kg^{-1}) conditions when bacterial mats were present (Chu and Tunnicliffe, 2015; Matabos et al., 2012). Interestingly, *L. exilis* is a common species along the entire US Pacific margin but, does not occur within the OMZ off California or Oregon, even though it commonly inhabits severely hypoxic waters in Saanich Inlet. This is likely because its distribution along the US Pacific margin is being set by other environmental factors (depth, temperature, prey availability) or their interaction with hypoxia tolerance (Vaquer-Sunyer and Duarte, 2011). The bathymasterid, *Ronquilus jordani*, the cottid, *Scorpaenichthys marmoratus*, the pleuronectid, *Lepidopsetta bilineata*, the stichaeidid, *Lumpenus sagittal*, the paralichthyid, *Citharichthys* sp., and the gadid *Theragra chalcogramma* all appeared only after oxygen content increased to >22 μmol kg^{-1} (Chu and Tunnicliffe, 2015; Matabos et al., 2012). Differing results were found by Chu and Tunnicliffe (2015) and Matabos et al. (2012), for the presence of the stichaeid, *Plectobranchus evides*, the agonid, *Xeneretmus latifrons*, and the merlucciid, *Merluccius productus* under severely hypoxic conditions ($O_2 < 22$ μmol kg^{-1}) in the Saanich Inlet, with their presence being noted by Chu and Tunnicliffe (2015), and absence noted by Matabos et al. (2012). Rockfish (*Sebastes* sp.) were only present during the highest oxygen periods (∼88–131 μmol kg^{-1}) and were absent when conditions were severely hypoxic (Matabos et al., 2012). Interestingly, oxygen appears to also control species interactions. For example, Doya et al. (2016) noted that squat lobster–pleuronectid interactions may be mediated by oxygenation in Saanich Inlet.

At a deeper site (890 m) off Canada in Barkley Canyon, the NEPTUNE observatory recorded the presence of the following fish species living under severely hypoxic conditions (O_2 ∼10.5–15.3 μmol kg^{-1}) within the OMZ core: the anoplopomatid, *A. fimbria*, the myxinid, *Eptatretus* sp., an unidentified zoarcid, the agonid, *Bathyagonus nigripinnis*, the sebastid, *Sebastolobus* sp., and the pleuronectid, *E. bathybius* (Juniper et al., 2013). Of these, *A. fimbria* was the only fish species present consistently during the year-long study, while other species were more sporadic (Juniper et al., 2013).

3.3.2 Eastern Tropical Pacific—Gulf of California

The Gulf of California, which hosts an extension of the NE Pacific OMZ, is an interesting area for studying the influence of severe hypoxic conditions on the demersal fish community due to the presence of a very thick OMZ with a shallow upper boundary in the southern Gulf of California. The few published studies that are available document several fish species living at very low-oxygen levels, such as the ophidiid, *Cherublemma emmelas*, at ∼5.7–8.8 μmol kg^{-1} (Aguirre-Villaseñor and Castillo-Velázquez, 2011), and the scyliorhinid, *Cephalurus cephalus*, living at ∼6.1 μmol kg^{-1} (Aguirre-Villaseñor and Salas-Singh, 2012) (Fig. 3). Additional demersal fish distributions in the Gulf of California are provided by Fischer et al. (1995), but oxygen values are not given for the observations; however, based on the depth distributions provided (Fischer et al., 1995) and the known hydrography of the Gulf of California (Aguirre-Villaseñor and Salas-Singh, 2012), there are likely many other fish species living under OMZ conditions. Larval midwater fish habitats in the Gulf of California are known to be affected by the steep oxygen gradients, with shallow hypoxic conditions partitioning groups of fish species but not affecting total larval fish abundance (Davies et al., 2015), and interestingly, the highest larval fish species richness was observed within the subsurface hypoxic habitat (~8.8–43.8 μmol kg^{-1}), which was dominated by the codlet, *Bregmaceros bathymaster* (Davies et al., 2015).

3.3.3 Eastern Tropical Pacific—Volcano 7

Volcano 7 is an inactive seamount at 13°23′ N and 102°27′ W, which rises from a depth of 3400 m to 730 m and penetrates the OMZ (72–1302 m) in the eastern tropical Pacific with the lowest oxygen levels present at the summit (~3.5–3.9 μmol kg^{-1}) (Wishner et al., 1990, 1995). The lowest megafaunal abundances (including fish) on the seamount were observed at the uppermost region when oxygen was ~3.5–3.9 μmol kg^{-1}, while the highest megafaunal abundances (including fish) were observed at only slightly higher oxygen levels of ~4.8–7 μmol kg^{-1}. This illustrates the nonlinearity of community responses to small changes in environmental oxygen conditions. The only megafauna observed on the upper summit of Volcano 7 were the macrourid, *N. liolepis*, (49.2% of the megafauna community), and solitary sessile coelenterates (Levin et al., 1991). Just below the upper summit, where oxygen levels were slightly higher (~5.7 μmol kg^{-1}) and where the range in oxygen levels was greater due to internal tide oscillations (Wishner et al., 1990, 1995), diversity of the megafauna community increased and *N. liolepis*, anemones, galatheid crabs, serpulid polychaetes, sponges, and ophiuroids dominated the community (Levin et al., 1991). *Nezumia liolepis* was the only megafauna species consistently observed on both the upper and lower summit, but abundances were much higher on the lower summit, with 1.8 individuals m^{-2} being the maximum density observed (Wishner et al., 1990).

3.3.4 Eastern Tropical Pacific—Mexico and Central America

The Pacific Coast of Mexico is a very data-poor region, even though the thick and intense OMZ likely exerts a strong influence on the demersal fish communities along the margin. Off Central America, the OMZ can be 1200 m thick with an upper boundary that can be as shallow as 50 m (Bianchi, 1991; Wyrtki, 1966) and temperatures at the upper boundary are relatively warm (~15°C) (Bianchi, 1991; Levin et al., 2015) (see Fig. 2B). OMZ conditions were typically found at the edge of the continental shelf and upper slope throughout the year (Stromme and Saetersdal, 1988). Oxygen concentrations at the OMZ core are much lower than in the core of the US West Coast or Alaskan OMZ (see Fig. 2A).

Bianchi (1991) examined how environmental conditions structure demersal assemblages using data from 348 trawls spanning 10–500 m depths, along 685 nautical miles of coastline including the shelf and slope edge of southern Mexico, Guatemala, El Salvador, Honduras, Nicaragua, and northern Costa Rica. This study found that the assemblage characterized as living at the lowest oxygen concentrations encountered in the study (O_2 ~17.5 ± 4.4 μmol kg^{-1}, $T = 13 \pm 1$°C) was characterized by the highest abundances of individuals and the highest biomass, with much of the biomass due to galatheid crustaceans. Several demersal fish species were also common community components in this OMZ assemblage and included the argentinid, *Argentina aliceae*, the serranid, *Diplectrum macropoma*, the merlucciid, *Merluccius angustimanus*, the trichiurid, *Trichiurus nitens*, the scorpaenid, *Pontinus sierra*, and the bothid, *Monolene maculipinna* (Bianchi, 1991). *Diplectrum macropoma* was the only demersal fish species that was unique to the OMZ community and not part of the other seven identified assemblages (Bianchi, 1991). Demersal fish species that are present in the assemblage that is characterized by oxygen limited conditions (O_2 ~30.6 ± 4.4 μmol kg^{-1}), but are absent from the OMZ assemblage and may be intolerant of OMZ conditions include the stromateid, *Peprilus snyderi*, the batrachoidid, *Porichthys nautopaedium* (now *P. margaritatus*), the triglid, *Prionotus quiescens* (now *P. stephanophrys*), the synodontid, *Synodus evermanni*, the ogcocephalid, *Zalieutes elater*, and the paralichthyid, *Citharchthys platophrys* (Bianchi, 1991). Additional sampling carried out outside of Nicaragua in deeper water (300–350 m) found that demersal species assemblages associated with OMZ conditions exhibited low faunal diversity, but the ophidiid, *C. emmelas*, and the merlucciid, *M. angustimanus*, were some of the only species present under these conditions (Stromme and Saetersdal, 1988), suggesting high hypoxia tolerance. Most demersal fish species that form important fisheries off Central America, including butterfish (*Peprilus* spp.), sea bass (*Hemanthias* sp. and *Diplectrum euryplectrum*), snapper (*Lutjanus* sp.), and grunts (*Pomadasys* sp. and *Orthopristis* sp.), are not components of the OMZ assemblage (Stromme and Saetersdal, 1988), suggesting that fisheries resources here may be particularly vulnerable to habitat compression within the relatively narrow zone above the OMZ, as severely hypoxic waters expand with climate change.

3.3.5 Humboldt Current Ecosystem—Peru and Chile

There has been more historical focus on the influence of ENSO events and changes in oxygenation on the pelagic community in the Humboldt Current System than the demersal community because the pelagic fish community is very important economically. At present, the western coast of South America produces more fish per unit area than any other region in the world ocean (Montecino and Lange, 2009). Industrial demersal fisheries are comparatively small in the Humboldt Current System, making up <1% of total fish landings in Peru (Montecino and Lange, 2009). However, there are some demersal fish species including the macrourid, *Macruronus magellanicus*, the merlucciids, *Merluccius gayi gayi* and *Merluccius gayi peruanus*, the arhynchobatid, *Raja chilensis* (now *Sympterygia lima*), the ophidiids, *Genypterus* spp., and the paralichthyids, *Paralichthys* spp. and *Hippoglossina* sp., that are commonly landed off Peru and Chile (Montecino and Lange, 2009). The hake fishery in Peru (*Merluccius gayi peruanus*) has recently shown a significant decline, attributed both to overfishing and population vulnerability to environmental stress (Ballón et al., 2008; Guevara-Carrasco and Lleonart, 2008; Montecino and Lange, 2009). Fish scales and osseous skeletal materials in laminated sediment cores have been used as a proxy for studying changes in fish abundances in the Peruvian and Chilean OMZ over historical time (Díaz-Ochoa et al., 2009; Milessi et al., 2005). While these cores shed light on historical changes for pelagic species, relatively few data are available about the demersal communities because scales and skeletal materials from small pelagics dominate the cores (Díaz-Ochoa et al., 2009; Milessi et al., 2005).

The OMZ in the eastern South Pacific is thickest (>600 m) and shallowest (<150 m) off Peru, and the upper boundary shoals near the coast extending into the euphotic zone in some places (Fuenzalida et al., 2009). As a result, the demersal fish community off Peru is likely intimately shaped by the steep oxygen gradients and severely hypoxic conditions, but there are few published studies of this community. A study of benthic biomass changes across oxygen and depth gradients for filamentous bacteria, macrobenthos, and demersal fish catch was carried out at 65 stations spanning 35–359 m and oxygen conditions from ~9.2 to 68.7 μmol kg^{-1} (Rosenberg et al., 1983). Macrobenthic biomass peaked at ~26.3 μmol kg^{-1} and then declined with decreasing oxygen levels. Demersal fish catches appeared to peak between ~35 and 17.5 μmol kg^{-1}, and fish catches were positively correlated to high macrobenthic biomass ($p < 0.001$), but negatively correlated to the occurrence of filamentous bacteria ($p < 0.01$) that occur in severely hypoxic environments (Rosenberg et al., 1983). Additional analysis of data in Rosenberg et al. (1983) indicate no significant difference between demersal fish catch for areas where $O_2 > 22$ μmol kg^{-1} (519.76 ± 197.90 kg/20 min) and where $O_2 < 22$ μmol kg^{-1} (315.52 ± 258.98 kg/20 min), but that variance in catches increases in the severely hypoxic areas. Below 15.3 μmol kg^{-1}, demersal fish catches were much lower (<100 kg/20 min) for all samples (Fig. 4B) (Rosenberg et al., 1983). Unfortunately, no data were given in Rosenberg et al. (1983) about the composition of these catches and it is likely that the composition of the fish community differs at the severely hypoxic sites. Based on the published latitudinal and bathymetric distribution of a number of fish species off Peru and Chile (Fischer et al., 1995; Sielfeld and Vargas, 1999) in areas and depths where severely hypoxic conditions are known (Fuenzalida et al., 2009; Helly and Levin, 2004), there are likely

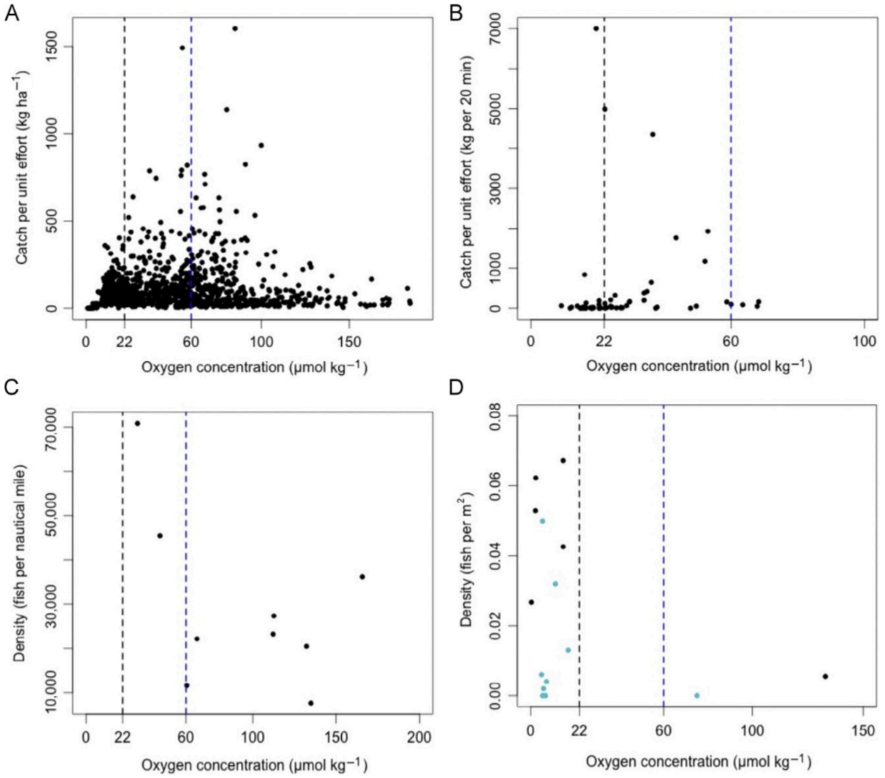

Fig. 4 Changes in fish catch per unit effort (CPUE) or density with oxygen concentrations (μmol kg^{-1}) in four different oxygen minimum zone (OMZ) regions: (A) US West Coast from Keller et al. (2015), (B) Peruvian margin from Rosenberg et al. (1983), (C) Namibian margin from Mas-Riera et al. (1990), (D) Arabian Sea including data from Murty et al. (2009) (*turquoise*; *light grey in the print version*) from the Pakistan margin and Hunter et al. (2011) (*black*) from the west Indian margin. *Blue* (*dark grey* in the print version) *dashed line* indicates the oxygen limited zone (OLZ) boundary (60 μmol kg^{-1}) and *black dashed line* indicates the OMZ boundary (22 μmol kg^{-1}).

many demersal fish species in the Humboldt Current System that are highly adapted to living under severe hypoxia.

A study using Agassiz trawls at depths ranging from 120 to 2201 m at three locations off Chile, found that depth and dissolved oxygen levels were the main factors responsible for influencing megafaunal changes along the shelf and slope (Quiroga et al., 2009). Where oxygen levels fell below ~6.66 μmol kg^{-1}, megafaunal species were nearly absent, however one species of macrourid, *Trachyrincus villegai*, was captured in the OMZ at 317 m (O_2 ~2.6 μmol kg^{-1}) (Quiroga et al., 2009) (Table 1; Fig. 3). Interestingly, this species was only observed at this one OMZ core station and was not captured during any additional trawls in higher oxygen conditions suggesting that it may be an OMZ specialist. Compared to the distribution of demersal fish species along oxygen gradients on the US margin, it appears the Chilean fish community is relatively depauperate based on the findings of Quiroga et al. (2009); even sites outside of the OMZ exhibited lower species richness and abundance. However, this may also be an artefact of the different trawl types used for sampling off Chile and off the United States.

New unpublished trawl data (J. Sellanes, Universidad Catolica del Norte, personal communication, 22 January 2016) off Coquimbo, Chile (~30°S), reveal that three additional demersal fish species inhabit the Chilean OMZ (depth ~50–300 m, O_2 ~2.2–22.0 μmol kg^{-1}): the paralichthyid, *Hippoglossina macrops*; the batrachoidid, *Aphos porosus*; and the scyliorhinid, *Cephalurus* sp. cf. Unpublished trawl data from 2004 from the Chilean Fisheries Development Program (IFOP, 2005), spanning 29–42°S and depths 58–450 m, reveal three demersal fisheries species also inhabiting the Chilean OMZ (O_2 ~16.9–22.0 μmol kg^{-1}): the merlucciid, *Merluccius gayi gayi*; and the ophidiids, *Genypterus maculatus* and *Genypterus blacodes*. Therefore, further research may show that demersal fish are also well represented in the Chilean OMZ benthic community.

Changes in the benthic community due to increased oxygenation during El Niño events also offer insight into the sensitivity of certain species to hypoxia. During El Niño, the merlucciid, *Merluccius gayi peruanus*, which usually lives north of Chimbote, Peru, due to the low-oxygen conditions in the south, extends its distribution southward and beyond the slope margin, and switches to a demersal life style because of the improved oxygen and food conditions at the seafloor (Arntz et al., 2006; Espino, 1999; Espino et al., 1985; Wosnitza-Mendo and Espino, 1986). The sciaenid, *Sciaena deliciosa*, also migrate offshore and feed on anchovies that have a deeper depth distribution during El Niño conditions (Arntz and Tarazona, 1989). ENSO-driven changes in the meiofauna and macrofauna communities (Gutierrez et al., 2008; Levin et al., 2002; Sellanes et al., 2007) may also give rise to different prey availability for demersal fish during El Niño conditions.

3.3.6 Benguela Current Ecosystem—Namibia

In the Benguela Current, only a small part of the Namibian coastline is exposed to OMZ conditions, unlike the widespread OMZs in the California Current, Humboldt Current, and Indian Ocean (Fig. 3). The lowest averaged seafloor values of dissolved oxygen are $<13.1\ \mu\text{mol kg}^{-1}$ and occur on the inner shelf immediately north of Walvis Bay (Dingle and Nelson, 1993). Both north and south of Walvis Bay, oxygen concentrations increase above $43.8\ \mu\text{mol kg}^{-1}$. Several studies off Namibia have shown that oxygen levels play a major role in determining the composition and distribution of the demersal fish community and that certain fish assemblages are specifically present at low-oxygen levels (Hamukuaya et al., 2001; Mas-Riera et al., 1990). On the shelf and upper slope, five distinct assemblages were observed based on multiple bottom trawl samples collected during the years 1992–1996, and spanning 17–29°S along the Namibian coastline at depths between 50 and 600 m (Hamukuaya et al., 2001). Teleosts were the dominant demersal taxa (92–96%), followed by chondrichthyans (2–6%), and invertebrates (1–3%) (Hamukuaya et al., 2001). Analysis of trawl data indicated four clear assemblages along the shelf and upper slope and revealed a clear spatial correlation between the distribution of low-oxygen levels and the distribution of the northern shelf assemblage. The northern shelf assemblage was composed of the merlucciid, *Merluccius capensis*, the gobiid, *Nematogobius bibarbatus* (now *Sufflogobius bibarbatus*), and the triglid, *Chelidonichthys capensis*; these species made up 76–80%, 12–17%, and 2–3% of the community respectively (Hamukuaya et al., 2001). Following the upwelling season when oxygen levels $<43.8\ \mu\text{mol kg}^{-1}$ expanded to cover the region, this northern shelf assemblage expanded its distribution into deeper water from 50–280 m to 50–346 m (Mas-Riera et al., 1990). This community also exhibited responses to seasonal (Macpherson and Gordoa, 1992) and interannual (Hamukuaya et al., 2001) variability, with the northern and central shelf assemblages expanding into deeper water during the Benguela Niño (1993 and 1995) (Hamukuaya et al., 2001).

Other dominant species that were present off Namibia where O_2 levels were $<22\ \mu\text{mol kg}^{-1}$, included the carangid, *Trachurus trachurus capensis*, and the soleid, *Austroglossus microlepis* (Hamukuaya et al., 2001). *Sufflogobius* *bibarbatus* and *A. microlepis* are also known to occur off South Africa at similar depths but under higher oxygen conditions (Roel, 1987). Species that were excluded from these severely hypoxic regions off Namibia, but were dominant within the OLZ included the sparid, *Dentex macrophthalmus*, the albulid, *Pterothrissus belloci*, the acropomatid, *Synagrops microlepis*, the chlorophthalmid, *Chlorophthalmus atlanticus*, the lophiid, *Lophius vomerinus*, and the sebastid, *Helicolenus dactylopterus* (Mas-Riera et al., 1990). The incredible hypoxia tolerance of *S. bibarbatus*, and the keystone role this species may have in the hypoxic Namibian shelf ecosystem, have been noted in several studies (Salvanes et al., 2011; Utne-Palm et al., 2010).

Hypoxia-intolerant fish species have also been noted in the Benguela Current. The merluciid, *Merluccius paradoxus*, the zeid, *Zeus capensis*, and the scyliorhinid, *Holohalaelurus regani*, contract their range to the more southern area during the upwelling season when oxygen levels on the northern shelf are low and expand northward prior to the upwelling season when oxygen levels are higher (Mas-Riera et al., 1990), suggesting that they are sensitive to low-oxygen concentrations ($<$43.8–65.6 μmol kg^{-1}). Mortality was observed for the soleid, *Solea bleekeri*, the sebastid, *H. dactylopterus*, the sciaenid, *Argyrosomus* sp., the scyliorhinid, *Haploblepharus pictus*, the sparid, *Pachymetopon blochii*, and the clinid, *Clinus* sp., during hypoxic events occurring during March–May of 1997 (Arntz et al., 2006). However, it is difficult to attribute these directly to hypoxia intolerance given that sulphide (H_2S) eruptions frequently accompany hypoxic events on the inner shelf off Namibia. Hake have also been observed to show avoidance behaviour during these hypoxic events and typically migrate offshore (Arntz et al., 2006; Bailey et al., 1985). The two dominant species of hake in the Benguela Current (*M. capensis* and *M. paradoxus*) exhibit different tolerances to low--oxygen conditions. *Merluccius capensis* is dominant in areas with extremely low-oxygen concentrations, and can tolerate oxygen concentrations as low as ~10.9 μmol kg^{-1} (Woodhead et al., 1998), while *M. paradoxus* is dominant at similar depths but in areas where oxygen levels are $>$65.6–87.5 μmol kg^{-1} (Mas-Riera et al., 1990). Future research could use these two congeneric species to identify adaptations that confer hypoxia tolerance in *Merluccius*.

In contrast to oxygen conditions off Namibia, the shelf and upper slope of Angola does not experience $O_2 < 43.8$ μmol kg^{-1} and the deep continental slope assemblage (~350–550 m) identified living under OLZ conditions was composed of the merlucciid, *Merluccius polli*, the albulid, *P. belloci*, the ogcocephalid, *Dibranchus atlanticus*, the macrourid, *Malacocephalus occidentalis*, the acropomatid, *S. microlepis*, the chlorophthalmid, *C. atlanticus*, the solenocerid, *Solenocera africana*, the morid, *Laemonema* sp., the trichiurid, *Benthodesmus tenuis*, and the centrophorid, *Centrophorus granulosus* (Bianchi, 1992). In South Africa, oxygen conditions are also higher than off Namibia and shelf and upper slope communities do not experience OMZ conditions (Smale et al., 1993) (see Fig. 3).

3.3.7 Northern Indian Ocean—Arabian Sea

The Arabian Sea can be divided oceanographically into areas north and south of 15°N, each with considerable difference in fish composition (Madhupratap et al., 2001). In the north, the OMZ occurs at a shallower depth than in the south, which may give rise to some of these differences. Nearly all landings of Bombay duck (the synodontid, *Harpadon nehereus*) which makes up 7% of total landings in the Arabian Sea, and the majority of croakers, eels, elasmobranchs, catfish, and threadfins, are caught north of 15°N (Madhupratap et al., 2001). In contrast, the majority of perches and flatfish are caught south of 15°N (Madhupratap et al., 2001).

The influence of monsoon-driven, low-oxygen conditions on nearshore, demersal fisheries species on the west coast of India received significant attention in the 1950–1970s (Banse, 1959, 1968; Carruthers et al., 1959). Off Cochin in the Arabian Sea, the deoxygenation of near-bottom water during the SW monsoon resulted in the regular disappearance of demersal fishes on the shelf and the area covering the middle and outer shelf between Cochin and Karachi became unprofitable for trawling (Banse, 1968). Paired hydrographic and trawl data from the shelf off Cochin showed that demersal fish disappeared within several days from the shallower part of the shelf (<20 m) with the onset of the SW monsoon (~June), suggesting that the fish were rapidly escaping upwelling-driven low-oxygen conditions (Banse, 1959). The acropomatid, *Synagrops japonicus*, a typically abundant species (>1000 lbs per haul) and an important fisheries species, was noted to have changed its distribution, thus avoiding upwelled hypoxic waters off Cochin (Banse, 1959). Oxygen concentrations below $\sim 22\ \mu\text{mol kg}^{-1}$ appeared to be critical to this change in distribution (Banse, 1959, 1968), suggesting that the species is not tolerant to OMZ conditions but sometimes inhabits areas within the OLZ. Other fish that appear to be sensitive to upwelled, severely hypoxic conditions include the cynoglossid, *Cynoglossus macrostomus*, which disappears from shore along the Malabar Coast during the onset of the SW monsoon and returns to shore by midwater after the monsoon has passed (George, 1958). *Cynoglossus macrostomus* appears to wait out the severely hypoxic conditions by moving into deeper areas during the monsoon months (Khan and Nandakumaran, 1993). The habitat of the gobiid, *Trypauchen vagina*, has also been documented to become compressed to inshore, shallower waters at the onset of monsoon conditions (Seshappa, 1953). Upon relaxation of upwelling, and return to oxygen-rich conditions, favourable trawling conditions were observed to become rapidly re-established within days (Banse, 1959) indicating that these fish respond quickly to oxygen changes and return to their preferred habitat when preferable oxygen conditions are re-established. Of note, mortality was observed off Cochin during the flood tide in the peak of the upwelling season, when dead fish were reported to float into the harbour of Cochin, and it was thought that the fish were being trapped in the deoxygenated, upwelled water (Banse, 1968).

While fish do not appear to be tolerant of OMZ conditions in the shallower ecosystems of the Arabian Sea, in deeper water fish are important components of the margin community. A study conducted on the Pakistan margin using photographic transects through the OMZ at nine depths (140, 300, 400, 700, 900, 1000, 1100, 1200, and 1850 m) revealed that while benthic invertebrates (megafauna *sensu stricto*) were entirely absent in the OMZ core and lower transition zone (300–900 m, $O_2 \sim 5.3$–6.6 μmol kg^{-1}), fish and natant decapods were fairly common at 300 m, and fish were the only metazoan megafauna seen in photographs from 700 m ($O_2 \sim 5.3$ μmol kg^{-1}) (Murty et al., 2009). Eleven fish species were observed on the Pakistan margin OMZ: the bregmacerotid, *Bregmaceros* sp.; the ophidiid, *Brotulotaenia* sp.; an unidentified carangid, *Carangidae* sp.; the halosaur, *Halosaurus* sp.; the notocanthid, *Notocanthus* sp.; the synodontid, *Saurida tumbil*; the serrivomerid, *Serrivomer* sp.; the epigonid, *Epigonus* sp.; Actinopterygii sp.; the congrid, *Congridae* sp.; the etmopterid, *Centroscyllium ornatum* (Murty et al., 2009) (Table 1). A study conducted using video footage from the west Indian margin at depths between 530 and 2000 m, identified the following fish taxa living within or just below the OMZ: the liparid, *Liparidae* sp.; the ophidiid, *Holcomycteronus* sp.; the macrourid, *Coryphaenoides* sp.; the congrid, *Congridae* sp.; the synaphobranchid, *Synaphobranchus* sp.; the etmopterid, *Etmopterus* sp.; the arhynchobatid, *Bathyraja* sp. (Hunter et al., 2011). The study also listed *Gobiidae* sp., however this was a misidentification and was really a bregmacerotid, *Bregmaceros* sp., (L.A. Levin, personal observation, 20 July 2015). *Liparidae* sp. and *Bregmaceros* sp. were the resident fish fauna within the OMZ core (Hunter et al., 2011). Contrary to common expectation, such observations suggest that these fish species may be some of the most hypoxia-tolerant megafauna on the margins of the Arabian Sea.

In the northwestern Arabian Sea, off Yemen, several permanent demersal fish OMZ inhabitants were described by Kukharev (2015) including the synodontids, *Saurida undosquamis* and *Harpadon squamosus*, the trichiurid, *Lepturacanthus* spp., the peristediid, *Satyrichthys adeni*, the acropomatid, *Synagrops adeni*, the percophid, *Bembrops caudimacula*, the morid, *Physiculus roseus*, the nettastomatid, *Nettastoma* sp., the trachichthyid, *Hoplostethus* spp., the centrophorid, *C. granulosus*, the scyliorhinid, *Halaelurus* spp., and the proscylliid, *Eridacnis radcliffei*. Kukharev (2015) notes that two species also diurnally migrate into the OMZ from shallower depths, including the centrolophid, *Psenopsis cyanea*, and the scombrid, *Scomber australasicus*.

In the Sea of Oman, severely hypoxic water is found at shallower depths during the summer and fall (22 μmol kg^{-1} boundary at ~130 m) and deeper during the winter and spring (22 μmol kg^{-1} boundary at ~180 m). Nearshore, the OMZ upper boundary can occur even shallower (~90 m) and over 70% of the Omani shelf can be covered by OMZ conditions (Piontkovski and Al-Oufi, 2014). Oxygen depletion in Omani coastal waters has resulted in periodic fish kills, with the frequency of fish kill incidences increasing in the fall in the western Arabian Sea (Piontkovski et al., 2012). Seasonal oxycline shoaling during the summer and fall also results in habitat compression for myctophids and artisanal fisheries species (Piontkovski and Al-Oufi, 2014). Habitat compression of fisheries species results in increased fisheries landings and there was a significant relationship found between the depth of the ~87.5 μmol kg^{-1} oxygen boundary and the total landings of sailfish, with landings increasing in a nonlinear fashion due to habitat compression for the species as the oxycline shoaled (Piontkovski and Al-Oufi, 2014). Demersal fish species also appeared to exhibit habitat compression and were found to be concentrated closer to the coast during the low-oxygen conditions of the fall. Demersal species were widely distributed on the shelf during the higher oxygen conditions characteristic of the winter monsoon (Piontkovski and Al-Oufi, 2014). Shoaling of severely hypoxic waters during the fall was hypothesized to have led to the displacement of the shelf fish community and to changes in demersal fish species diversity. Diversity was almost twice as high in March (38 unique species observed) when oxygen was higher, in comparison to November (22 unique species observed) when oxygen was lower (McIlwain et al., 2011). Most species were either present in lower abundances or absent in the lower oxygen conditions in November, with the carangid, *Decapterus russelli*, which was previously a dominant species, showing dramatic declines in abundance (McIlwain et al., 2011). In contrast, several species including the agonid, *Holapogon maximus*; the carangid, *Carangoides* sp. (identified as *Carangoides* sp. 2); the muraenid, *Gymnothorax* spp.; the nemipterid, *Nemipterus japonicas*; the serranid, *Epinephelus epistictus*; and the triakid, *Iago omanensis*, increased in abundance during the low-oxygen conditions (McIlwain et al., 2011), which may indicate that they are more tolerant of these severely hypoxic conditions. McIlwain et al. (2011) noted that oxygen was not measured during the course of their study but that comparisons were made using hydrographic data from other studies in the area in which seasonal oxygen measurements were made.

3.3.8 Northern Indian Ocean—Bay of Bengal

To our knowledge, no scientific studies have focused on the role of oxygen gradients in structuring the demersal fish community in the Bay of Bengal, which has a thick OMZ (Fig. 2). This represents a large data gap in our knowledge. The OMZ on the East Indian margin extends from 100 to 900 m, and O_2 is $<15.3\ \mu\text{mol kg}^{-1}$ in the OMZ core (Raman et al., 2015). Reports describing demersal resources have been produced by the Food and Agriculture Administration of the United Nations (Nishida and Sivasubramaniam, 1986) but paired data on environmental variables and demersal community composition are not available. Based on the identified depth distribution (300–600 m) and the known hydrography of the region, it is probable that the chloropthalmid, *Chlorophthalmus* sp., the peristediid, *Peristedion* sp., the acropomatids, *Acropoma* sp. and *Synagrops* sp., the synodontid, *Saurida* sp., the nomeids, *Cubiceps* sp. and *Psenes* sp., the centrolophid, *Palinurichthys* sp., the scyliorhinid, *Haploblepharus* sp., the carcharhinid, *Scoliodon* sp., the sphyrnid, *Sphyrna* sp., the squatinid, *Squatina* sp., the nettastomatid, *Nettastoma* sp., and unidentified triacanthodids and priacanthids reside within the OMZ in severely hypoxic conditions in the Bay of Bengal (Nishida and Sivasubramaniam, 1986).

3.4 Effects of Oxygen on Fish CPUE, Biomass, and Density

In reviewing the available studies on demersal fish communities in OMZs, the relationship between oxygen levels and demersal fish density, biomass, or catch per unit effort (CPUE) is variable (Fig. 4). In many regions, studies find a decrease in demersal fish density, biomass, or CPUE with decreasing oxygen levels, although this effect is typically nonlinear with greater reductions happening below certain oxygen thresholds. This oxygen threshold is region-specific and likely influenced by the geologic history of the area, the local depth, and temperature of the OMZ, and the demersal fauna present in that area.

Along the entire US Pacific Coast, the CPUE of demersal fish species exhibited significant positive relationships with near-bottom oxygen concentrations (Keller et al., 2015). Near-bottom oxygen concentrations exert a stronger influence on demersal fish CPUE at lower oxygen concentrations (DO $<\sim$60 μmol kg^{-1}) (Keller et al., 2015), implying a nonlinear response of community biomass to oxygen concentration. Bottom oxygen concentration explained up to 84% of the variation in biomass for individual species and 31–69% of the depth-specific variation in biomass along a hypoxic gradient off Oregon (Keller et al., 2010). Off Peru, CPUE of demersal fish catches decreases strongly when oxygen levels falls below 15.3 μmol kg^{-1} (Rosenberg et al., 1983). Between Bombay and Karachi in the Indian Ocean, CPUE of commercially exploited fishes also appears to be positively related to the oxygen content of the near-bottom water and during the southwest monsoon and postmonsoon seasons when oxygen declines, the entire shelf <50 m off the west coast of India and Pakistan may be devoid of exploitable concentrations of the demersal fish species (Banse, 1968). Similarly, in the Baltic, bottom trawling becomes unprofitable when low-oxygen conditions result in cod either moving away or moving into the midwater (Berner and Schemainda, 1957).

Other studies have indicated that there is variability in the influence of oxygenation on fish density. The highest densities of fish observed by Murty et al. (2009) on the Pakistan margin in the Arabian Sea were observed at 300 m within the OMZ core, where oxygen levels were 5.36 μmol kg^{-1} and the temperature was 14.8°C. At this depth, the community was composed of, in order of dominance, the synodontid, *Saurida tumbil*, the bregmacerotid, *Bregmaceros* sp., and the carangid, *Carangidae* sp., and the total density was 0.05 individuals m^{-2} (Murty et al., 2009). In the northwest Arabian Sea on the Yemen margin, high biomass populations of demersal fish were also found in the OMZ (Kukharev, 2015). In contrast, on the Indian margin of the Arabian Sea, the OMZ core community at 530 m depth (O_2 $\sim$0.34 μmol kg^{-1}) was characterized by low densities of fish (0.02–0.03 individuals m^{-2}), with liparids being one of the community members present in the OMZ core (Hunter et al., 2011). The Indian margin is a much higher-energy area with more mineral input from rivers and may not provide the same level of food as on the Pakistan margin. Within the lower boundary of the OMZ (800–1100 m), fish densities increased and were approximately two times higher than within the OMZ core (Hunter et al., 2011). Off Hawaii, where oxygen concentrations do not reach OMZ conditions, the general pattern was also a reduction in demersal fish abundances at intermediate depths where oxygen conditions were lowest (~30.6 μmol kg^{-1}) (De Leo et al., 2012).

Interesting anomalies of very high demersal fish catches for areas with low-oxygen concentrations have also been reported. The largest catch included in the analysis of Banse (1968) (539 lb of commercially important fish caught in 45 min) was obtained at an oxygen concentration of ~21 μmol kg^{-1}. Increased landings off Bombay have been reported at the start of the northeast monsoon when OMZ conditions are found inshore at 35 m depth (Carruthers et al., 1959). Off Namibia, the highest demersal fish densities were obtained in the regions with the lowest oxygen concentrations, with ~70,000 fish/nautical mile captured by trawl in an area where the mean oxygen concentration was ~31.1 μmol kg^{-1} and ranged from ~0 to 74.4 μmol kg^{-1} (Mas-Riera et al., 1990). In the Sea of Oman, fisheries landings also increase as oxyclines shoal and low-oxygen conditions are found at shallower depths (Piontkovski and Al-Oufi, 2014). High densities of demersal fish have also been described near Volcano 7 at very low oxygen conditions (4.8–7 μmol kg^{-1}) (Levin et al., 1991; Wishner et al., 1995) and in the Gulf of California (N.D. Gallo, unpublished data). These high-density regions tend to be dominated by single species. Food tends to be plentiful in these environments, in the form of phytodetritus and meiofauna, which generally tolerate extremely low oxygen levels (Levin, 2003). Other OMZ studies conducted off northern Chile (Quiroga et al., 2009) do not provide evidence for these zones of greater density in the demersal fish community (Quiroga et al., 2009), known as *edge effects* (Mullins et al., 1985), but it is possible that the depth where edge effects of certain species would be observed were missed by the sampling. Continuous sampling across oxygen gradients using an ROV, submersible, or photosled, is more likely to detect edge effects than spatially separated trawl sampling, as edge effects can occur in response to very small, but physiologically relevant, changes in pO_2.

High-density areas surrounding low-oxygen regions are also observed in coastal and estuarine "dead zones". Organisms avoided lethal oxygen thresholds by aggregating at short distances from the edge of the hypoxic zone in the Gulf of Mexico (Craig, 2012). This aggregation was particularly apparent for finfish, which are considered relatively intolerant of oxygen stress, and the result was an increase in fish biomass in areas surrounding the hypoxic zone (Craig, 2012). Breitburg (2002) found that while demersal fish harvest decreased in areas of persistent, year-round hypoxia or anoxia in the water column, areas that only had seasonal hypoxia in the semi-enclosed European Seas were characterized by high fish harvest. It is important to keep in mind that increased organic matter is a confounding factor in severely hypoxic zones, and that total benthic standing stock is positively related to increased organic matter (Thiel, 1978), so some of these high-density patterns may be due to organic enrichment of the benthic community and others due to habitat compression from hypoxic conditions. In coastal and estuarine systems, the relationship between fish abundance and hypoxia is not straightforward because hypoxia is often eutrophication-driven, which can give rise to elevated fish abundances in the overlying, better-oxygenated surface waters (Breitburg, 2002). This mosaic of low-oxygen waters in close proximity to highly oxygenated, productive waters in coastal systems has prevented the decrease in abundance of fish expected if just considering the low-oxygen concentration of the bottom waters (Breitburg, 2002; Breitburg et al., 2009). Given that the studies on demersal fish communities in OMZs are relatively limited, additional studies may help resolve the relationship between oxygen and abundance patterns.

3.5 Effects of Oxygen on Fish Diversity

In general, demersal fish species diversity decreases with decreasing oxygen conditions across regions, but specific oxygen thresholds that induce this change are region-specific. Species richness exhibited significant positive relationships with near-bottom oxygen concentrations within the hypoxic region off Oregon (Keller et al., 2010) and along the entire US Pacific coast (Keller et al., 2015). Near-bottom oxygen concentrations exert a stronger influence on species richness at lower oxygen concentrations (DO $< \sim 60$ μmol kg^{-1}) (Keller et al., 2015), implying a nonlinear response of community biomass to oxygen concentration. In the seasonally hypoxic Saanich Inlet, higher fish species richness was observed during periods of higher oxygen concentration, while single-species dominance by *L. exilis* was typically characteristic of severely hypoxic conditions (Matabos et al., 2014). Increased homogenization and decreased species richness in the Saanich Inlet under severely hypoxic conditions was also observed by Chu and Tunnicliffe (2015).

In the Benguela Current off Namibia, the low oxygen, central shelf demersal fish assemblage was characterized by the lowest diversity and high dominance by a few species, compared to the other four identified assemblages (Hamukuaya et al., 2001). This study found a positive relationship between oxygen saturation and demersal fish species diversity, where diversity increases but appears to reach a threshold between oxygen concentrations of 43.8–65.6 μmol kg^{-1} (Hamukuaya et al., 2001). Beyond this, oxygen levels did not seem to affect demersal fish community diversity. Mas-Riera et al. (1990) also found that oxygen conditions exerted a strong influence over demersal fish community diversity off Namibia. The lowest values for Shannon–Weiner diversity index (H′) obtained during the study (based on 146 trawl samples taken along the shelf and upper slope of Namibia) were obtained for the northern shelf association which was characterized by the lowest oxygen conditions, whereas the highest values for diversity were observed for the transitional subcommunity; diversity was 2.5 times higher even though it was immediately adjacent to the low-oxygen northern shelf association. Similarly, in the southern shelf region, an increase in oxygen led to a noticeable increase in diversity (Mas-Riera et al., 1990). Mas-Riera et al. (1990) also notes that off northwest Africa the diversity of the shelf and upper slope demersal fish fauna (Roel et al., 1985) is higher than that found off Namibia, which could be due to the strong upwelling intensity and OMZ conditions found off Namibia.

In the Chilean OMZ, fish species richness was low, with one species observed by Quiroga et al. (2009) in northern Chile and no species observed in central Chile. Quiroga et al. (2009) found that species richness increased below the OMZ with three species observed at 365 m off Concepcion (central Chile) and nine species observed at 864–895 m off Antofagasta northern Chile. Unpublished trawl data from report FIP2004-09 from the Chilean Fisheries Development Program (IFOP, 2005), spanning 29–42°S, depths 58–450 m, and O_2 ~16.9–253.1 μmol kg^{-1}, also show lower fish species richness within the Chilean OMZ (see Fig. 5C), but higher species richness (2–5 species in the OMZ) than observed by Quiroga et al. (2009). Within the Pakistan margin OMZ, the greatest fish species richness with a total of four species was observed at depths below the OMZ core (1100 and 1200 m) where oxygen levels began to increase to 11.17 and 16.97 μmol kg^{-1} (Murty et al., 2009). However, high species richness with a total of three unique species was also observed at 300 m where oxygen levels were much lower (5.36 μmol kg^{-1}) (Murty et al., 2009).

The demersal fish species richness in different OMZs appears to vary, from few species observed off Chile (Quiroga et al., 2009; Table 1) to more than 15 demersal fish species known from the US West Coast OMZ (Day and Pearcy, 1968; Friedman et al., 2012; Keller et al., 2015; N.D. Gallo, unpublished data) (Table 1). However, these differences may be due to some regions being understudied and additional research may reveal more hypoxia-tolerant species living in these areas. At a regional scale, OMZs may lead to

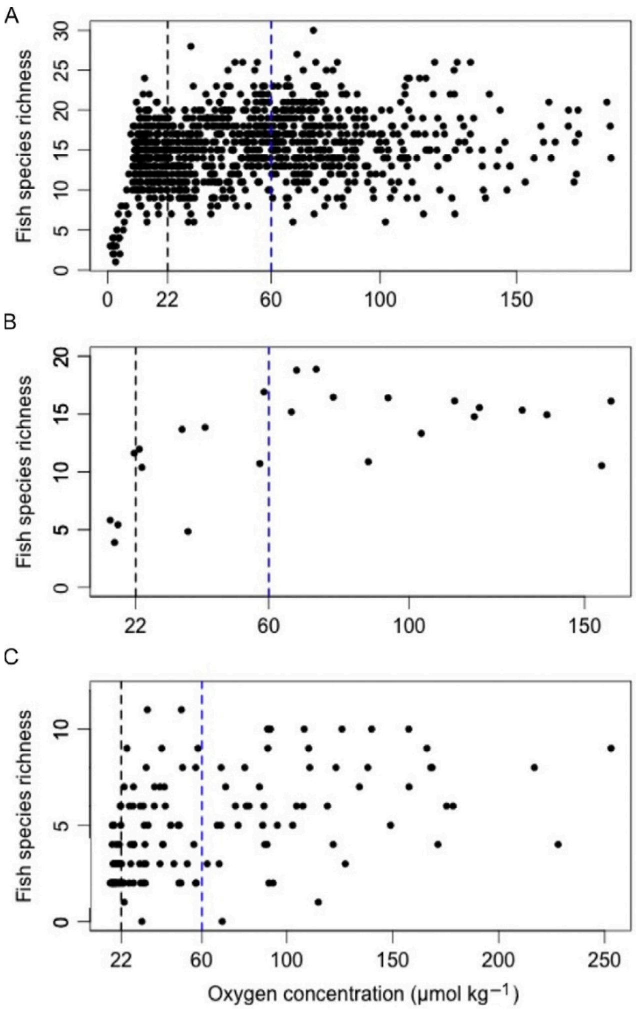

Fig. 5 Changes in fish species richness with oxygen concentrations (µmol kg^{-1}) (A) off the US West Coast from Keller et al. (2015), (B) off the Namibian coast from Hamukuaya et al. (2001), data extracted using Web Plot Digitizer, and (C) off the Chilean coast (29–42°S and depths 58–450 m) from unpublished data by the Chilean Fisheries Development Program (IFOP, 2005). *Blue* (*dark grey* in the print version) *dashed line* indicates the oxygen limited zone (OLZ) boundary (60 µmol kg^{-1}) and *black dashed line* indicates the oxygen minimum zone (OMZ) boundary (22 µmol kg^{-1}).

enhanced biodiversity by acting as barriers to gene flow and creating strong gradients which exert selective pressure on specific physiological traits (Rogers, 2000; White, 1988). Studies on how the expansion and contraction of OMZs over geologic time may have influenced the evolution of closely related slope and shelf demersal fish species such as the sebastids, *S. alascanus* and

S. altivelis, off the US West Coast, the pleuronectids, *M. pacificus* and *E. bathybius*, off the US West Coast, and the merlucciids, *M. capensis* and *M. paradoxus*, off Namibia, as well as others, would be informative.

3.6 Comparison of Trends Between Invertebrate and Demersal Fish Communities in OMZs

Invertebrates often provide food for demersal fish, so it is informative to ask whether fish patterns in OMZs mirror those of sediment-dwelling invertebrates. Metazoan meiofauna in general have been found to be more tolerant of hypoxic conditions than macrofauna (Josefson and Widbom, 1988; Levin et al., 1991; Rogers, 2000) with nematodes dominating the meiofauna under low-oxygen conditions (Diaz and Rosenberg, 1995; Gooday et al., 2010; Levin et al., 1991). For the most part, it appears that trends in the demersal fish community resemble trends for meio, macro, and invertebrate megafauna across oxygen gradients, although the oxygen thresholds governing changes in diversity and abundance of the fish community are different (Gooday et al., 2010). One of the interesting findings is that extremely hypoxia-tolerant demersal fish species appear to be able to live under oxygen conditions where most nonvertebrate megafauna are absent or extremely rare due to the severely hypoxic conditions (Murty et al., 2009). This suggests that fish in these areas may be preying on macrofauna or meiofauna. Changes in distribution can lead to shifts in the relative importance of a specific species and give rise to altered carbon flow pathways in the food web (Breitburg, 2002). Similar to the high-density edge effects observed for the demersal fish community in some areas under severely hypoxic conditions, abundant macrobenthic communities have also been reported at low-oxygen concentrations from off Peru, California, Volcano 7, and Oman (Levin et al., 1991, 2000; Mullins et al., 1985; Rosenberg et al., 1983).

4. BEHAVIOURAL AND PHYSIOLOGICAL ADAPTATIONS CONFERRING TOLERANCE TO LOW O_2 ENVIRONMENTS

There are many definitions of hypoxia (Hofmann et al., 2011) and the body of literature on adaptations suggests that there are multiple ways to become hypoxia tolerant. This is consistent with the fact that hypoxia tolerance has evolved independently many times in fishes (Friedman et al., 2012; Mandic et al., 2009). Multiple pieces have been written about the mechanisms underlying molecular responses of an organism to oxygen limitation (Davis, 1975; Farrell and Richards, 2009; Kramer, 1987; Nilsson, 2010; Pollock et al., 2007; Rankin and Jensen, 1993; Richards, 2009; Wells, 2009; Wu, 2002, 2009), which can arise both from insufficient oxygen in the environment, as well as insufficient oxygen supply due to high active metabolic rate. Fish are exposed to hypoxic conditions in several environments, including tide pools, river mouths, ice-covered lakes, eutrophic estuaries, or enclosed bodies of water, and OMZs. Most previous studies and reviews have focused on Amazonian, estuarine, lake, and tidepool fishes to understand hypoxia sensitivity and tolerance, and few have looked at the adaptations of fish living under naturally occurring, chronic, severely hypoxic conditions such as OMZs. While some fish die when exposed to low-oxygen waters, such as the high mortality of rockfish reported off Oregon during the upwelling of OMZ waters onto the shelf (Grantham et al., 2004), others live in OMZ environments and have evolved the capacity to survive under severely hypoxic conditions (Friedman et al., 2012). Behavioural, morphological, and molecular adaptations to hypoxia will be briefly reviewed here in order to better understand some of the patterns of changes in abundance and diversity of the fish community under OMZ conditions that have been previously explored in this chapter. Understanding which adaptations confer tolerance to hypoxia is important to understanding which fish species will be resilient to living in a more oxygen-deficient future ocean.

4.1 Responses of OMZ Fish Species to Severely Hypoxic Conditions

Two theoretical, not mutually exclusive mechanisms have been proposed in the literature as methods of coping with reduced oxygen availability: increased oxygen extraction from the environment (through increased gill surface area, ventilation behaviour, increased oxygen affinity in respiratory pigments, or other molecular changes), or reduced oxygen demand (through metabolic suppression or anaerobic metabolism) (Childress and Seibel, 1998; Friedman et al., 2012; Seibel, 2011). Known behavioural, morphological, and physiological adaptations of OMZ demersal fish species are listed in Table 2.

Response of hypoxia-tolerant cellular systems to lack of oxygen occurs in two phases: defense and rescue (Hochachka et al., 1996). The first step includes suppressing ATP-demand and ATP-supply pathways by downregulating protein synthesis through translational arrest, and downregulating

Table 2 Physiological, Behavioural, and Morphological Adaptations of Demersal Fish Species to Life Under Severely Hypoxic Conditions Found in Oxygen Minimum Zones

	Description	**Citation**
Behavioural adaptations		
Sluggish movement		
Sebastolobus alascanus	Sluggish movement	Yang et al. (1992) and Friedman et al. (2012)
Increased ventilation rate		
Sufflogobius bibarbatus	Increased ventilation rate	Salvanes et al. (2011)
Interactions with sediment		
Bregmaceros sp.	Bury themselves into sediment	Hunter et al. (2011)
Cherublemma emmelas	Bury head into sediment	N.D. Gallo (unpublished data)
Anoplopoma fimbria	Crash body into sediment	L.A. Levin (unpublished data)
Sufflogobius bibarbatus	Bury themselves into sediment	Salvanes et al. (2011)
Reproductive adaptations		
Microstomus pacificus	Ontogenetic migration	Hunter et al. (1990)
Sebastolobus alascanus	Ontogenetic migration	Day and Pearcy (1968)
Anoplopoma fimbria	Ontogenetic migration	Day and Pearcy (1968)
Careproctus melanurus	Embryos and larvae develop in crab gill cavity	Peden and Corbett (1973) and Somerton and Donaldson (1998)
Morphological adaptations		
Increased gill surface area		
Careproctus melanurus	High gill surface area	Friedman et al. (2012)
Anoplopoma fimbria	High gill surface area	Friedman et al. (2012)
Microstomus pacificus	High gill surface area	Friedman et al. (2012)
Nezumia liolepis	High gill surface area	Friedman et al. (2012)
Cephalurus cephalus	High gill surface area	Compagno (1984)
Change in muscle composition		
Microstomus pacificus	Gelatinous white muscle	Hunter et al. (1990)

Table 2 Physiological, Behavioural, and Morphological Adaptations of Demersal Fish Species to Life Under Severely Hypoxic Conditions Found in Oxygen Minimum Zones—cont'd

	Description	Citation
Change in swimbladder		
Bregmaceros cantori	Daily increase in mass and volume of swimbladder	Love et al. (2004)
Physiological adaptations		
Enzymatic changes		
Sebastolobus alascanus	Blood and heart LDH enzymatic adaptations, low aerobic enzymatic activity	Yang et al. (1992) and Friedman et al. (2012)
Sebastolobus altivelis	Low aerobic enzymatic activity	Friedman et al. (2012)
Careproctus melanurus	High aerobic enzymatic activity	Friedman et al. (2012)
Anoplopoma fimbria	High aerobic enzymatic activity, loss of bNHE, modified Root effect	Friedman et al. (2012) and Rummer et al. (2010)
Microstomus pacificus	Decrease in anaerobic capacity	Vetter et al. (1994)
Increase in haemoglobin		
Saurida tumbil	Bright red gills with presumed high haemoglobin concentration	Murty et al. (2009)
Cherublemma emmelas	Bright red gills with presumed high haemoglobin concentration	N.D. Gallo (unpublished data)

ion-channel ATP use by channel arrest (Hochachka et al., 1996). It is thought that cells that are not hypoxia-tolerant are not able to recover from this translational arrest of protein synthesis, while hypoxia-tolerant cells respond to extended periods of hypoxia by activating "rescue" mechanisms that begin to upregulate the expression of several key proteins, thus allowing low-level metabolic activity but with dramatically reduced ATP turnover rates (Hochachka et al., 1996). Haeme-based proteins that are known to sense changes in oxygen tension in numerous organisms are thought to be the oxygen sensors responsible for detecting hypoxic conditions and subsequently activating hypoxia-dependent transcription factors (Bunn and Poyton, 1996). In fish, as well as in mammals, a heterodimeric transcription factor called hypoxia-inducible factor 1 (HIF-1), regulates target genes that are activated in hypoxic conditions (Semenza, 1998). While research has not been conducted to identify this response in OMZ fish species, it is the fundamental cellular response to hypoxia, and is likely to occur in these fish.

In one of the few studies on hypoxia adaptations of demersal fish to OMZ conditions, Friedman et al. (2012) examined the demersal fish present in the US West Coast OMZ, and compared the gill surface area and white muscle enzyme activities to conspecifics not found in the OMZ. Of the four orders of fish studied (Scorpaeniformes, Pleuronectiformes, Cottiformes, and Gadiformes) types of adaptations differed, suggesting flexibility in evolving hypoxia tolerance. The pleuronectid, *M. pacificus*, had a gill surface area 1.8–3 times larger than conspecifics that occupied higher oxygen areas on the continental shelf, increasing oxygen extraction ability (Friedman et al., 2012). Several studies have also noted that as *M. pacificus* migrates into the OMZ, it undergoes an increase in water content and the muscle tissue becomes more gelatinous, resulting in a ~20% decrease in caloric density per gram wet weight (Hunter et al., 1990; Vetter et al., 1994). These morphological adaptations may be key to the very broad depth distribution (57–1217 m) of *M. pacificus* that extends through the whole OMZ (Keller et al., 2015).

Increasing gill surface area under hypoxic conditions appears to be a common adaptation across different orders of fish and also is a relatively plastic trait (Chapman et al., 2000; Nilsson, 2007; Sollid et al., 2003), with changes to the lamellar surface area of the gills able to occur as rapidly as 12–24 h (Matey et al., 2008). *Nezumia liolepis*, a macrourid known to live under OMZ conditions both in the US West Coast OMZ and near Volcano 7 (Wishner et al., 1990, 1995), also had increased gill surface area (Friedman et al., 2012). Larger gill surface area appears to also be an adaptation in cartilaginous fish, and the large head and expanded gills of the scyliorhinid, *C. cephalus*, are thought to be an adaptation to the severely hypoxic conditions in the Gulf of California (Compagno, 1984).

In contrast, other OMZ species in the order Scorpaeniformes exhibit enzymatic adaptations to OMZ conditions. The sebastid, *S. alascanus*, has specific blood and heart enzyme adaptations that allowed for greater reliance on anaerobic metabolism (Yang et al., 1992). However, enzymatic substrates for aerobic metabolism have been found to be reduced in both the sebastids, *S. alascanus* and *S. altivelis*, suggesting low aerobic activities under OMZ conditions (Friedman et al., 2012). The two congeneric *Sebastolobus* species were not found to have increased gill surface area (Friedman et al., 2012), suggesting they adapt to hypoxic conditions primarily through behavioural modifications and reduced enzymatic activity, and not through morphological adaptations. While increased reliance on anaerobic metabolism has been proposed as a mechanism for maintaining cellular energy demand under hypoxia, this requires large glycogen stores (Vornanen et al., 2009), an opportunity to repay the oxygen debt, and a strategy for eliminating lactic acid. Some freshwater fish species including the cyprinids, *Carassius auratus*, *C. caraccius*, and *Rhodeus amarus*, have evolved efficient ways to eliminate toxic end products through ethanol excretion (Vornanen et al., 2009). Migrating myctophids in the Arabian Sea have also been described as utilizing alcohol dehydrogenase to excrete ethanol (Torres et al., 2012). However, increased reliance on anaerobic metabolism is likely more beneficial for fish living in environments where they are exposed to periodic hypoxia and not chronic hypoxia, therefore is likely not an important adaptation of demersal fish living in OMZs. No evidence of increased lactate dehydrogenase activity or increase in anaerobic poise was observed in the sebastids, *S. alascanus* or *S. altivelis*, in response to OMZ conditions (Vetter and Lynn, 1997). Anaerobic capacity was found to decrease in response to OMZ conditions in the pleuronectid, *M. pacificus* (Vetter et al., 1994).

The two most active and mobile OMZ-dwelling species examined by Friedman et al. (2012) were the liparid, *C. melanurus* and the anoplopomatid, *A fimbria*. These species exhibited large gill surface area and high aerobic enzymatic activity, documented through a high concentration of malate dehydrogenase (MDH) and citrate synthase (CS) enzymes, which are within the citric acid cycle and are utilized during aerobic metabolism (Friedman et al., 2012). Unfortunately, a liparid from outside of the OMZ was not available for comparison with *C. melanurus*, and *A. fimbria* was present both outside of, and within the OMZ, so interpretation of these results as OMZ adaptations is more difficult. A separate study by Rummer et al. (2010) did find that *A. fimbria* had specialized adaptations to tolerate hypoxic conditions, based on the magnitude of its Root effect. The Root effect is a pH-dependent reduction in haemoglobin-oxygen carrying capacity and is hypothesized to have evolved to enhance tissue oxygen delivery in fish (Rummer et al. 2013). Rummer et al. (2010) found that *A. fimbria* exhibits a Root effect that most closely resembles that of a hypoxia-tolerant cyprinid, *Cyprinus carpio*, as opposed to a Root effect characteristic of other studied Scorpaeniformes. This suggests that *A. fimbria* has evolved both morphological and physiological adaptations to hypoxic conditions.

4.2 Critical Oxygen Level

The critical oxygen level (P_{crit}) is the partial pressure of oxygen ($p\mathrm{O}_2$) at which a fish transitions from being an oxyregulator (oxygen consumption rate is independent of environmental oxygen conditions) to being an oxyconformer (where oxygen consumption rate becomes dependent on environmental oxygen conditions) (Richards, 2011), and is an important concept in considering the oxygen niches of demersal fish. At P_{crit}, aerobic scope (the difference between maximum metabolic rate and standard metabolic rate) is zero, meaning that energy can no longer be used for locomotion, reproduction, or growth (Farrell and Richards, 2009; Pörtner and Peck, 2010; Pörtner et al., 2010). Hypoxia-tolerant fish have been found to have lower critical oxygen levels than hypoxia-intolerant fish. Mandic et al. (2009) found that hypoxia tolerance was phylogenetically independently associated with enhanced oxygen extraction capacity in sculpins. Routine oxygen consumption rate, mass-specific gill surface area, and whole-blood haemoglobin oxygen-binding affinity (P_{50}) accounted for 75% of the variation in P_{crit} (Mandic et al., 2009). Species with a low P_{crit} had low routine metabolic rates, a large gill surface area, and high whole-blood haemoglobin oxygen binding affinity (Mandic et al., 2009). However, P_{crit} alone does not appear to be a perfect predictor of hypoxia tolerance of fish (Speers-Roesch et al., 2013). The critical oxygen level identified for *S. bibarbatus*, the bearded goby that lives in severely hypoxic conditions off Namibia, was $5.45 \pm 0.22\%$ of air saturation ($\sim 10\ \mu\mathrm{mol\ kg}^{-1}$), but the gobies tolerated levels of $<0.3\ \mu\mathrm{mol\ kg}^{-1}$ dissolved oxygen for 4.5 h without any equilibrium loss or decrease in escape responsiveness (Salvanes et al., 2011).

4.3 Blood Adaptations to Hypoxic Conditions

Differences in fish haemoglobins have also been proposed as physiological strategies allowing fish to survive in changing environments. Fish living in low-oxygen environments were found to have higher haemoglobin oxygen affinities than fish living in higher oxygen environments (Powers, 1980; Wells, 2009). The intrinsic haemoglobin oxygen affinity is genetically determined, meaning that changes must take place over generations, but physiological plasticity can be provided by regulating intracellular concentrations of allosteric modifier molecules (Powers, 1980), thus giving rise to faster modifications to decreased environmental oxygen. The presence of multiple haemoglobins in fishes (Powers, 1980) may allow fish to quickly respond to altered environmental conditions. Decreasing red blood cell organic phosphate levels also leads to an increase in haemoglobin oxygen affinity due to the influence of ATP on the Bohr effect (Powers, 1980). Differences in the lactate dehydrogenase (LDH) phenotype have also been shown to increase haemoglobin oxygen affinity through differing regulation of intraerythrocyte ATP concentration (Powers, 1980; Powers et al., 1979).

Increasing haematocrit or haemoglobin levels is also a physiological adaptation to hypoxic conditions in certain species. The freshwater cyprinid, *Pimephales promelas*, was found to increase haematocrit levels in response to hypoxic conditions (MacLeod and Smith, 1966), and the bright red gills of *Saurida tumbil* living in the Arabian Sea OMZ on the Pakistan margin were hypothesized to be due to high haemoglobin concentrations (Murty et al., 2009). *Cherublemma emmelas* collected from the Gulf of California OMZ also had very bright red gills and likely have high haemoglobin concentrations (N.D. Gallo, unpublished data). Higher oxygen extraction capacity due to increased haemoglobin concentration, increased haemoglobin-oxygen affinity, and decreased red cell ATP concentration, are also hypoxia adaptations of the eel *Anguilla anguilla* (Wood and Johansen, 1972). The haemoglobin oxygen dissociation curve shifts to the left in hypoxia-tolerant species (Wells, 2009; Wood and Johansen, 1972) and high oxygen affinity of haemoglobin, may be a consistent adaptation to low-oxygen conditions. Interestingly, midwater deep scattering layer fishes that live in Eastern Tropical Pacific OMZ conditions were found to have surprisingly low haemoglobin affinities for oxygen (Douglas et al., 1976). For fish living under OMZ conditions, based on the Bohr effect, it would be beneficial to tightly regulate levels of CO_2 at the gill and tissue. Having low CO_2/high pH at the gills would shift the blood oxygen dissociation curve to the left, thus increasing haemoglobin oxygen affinity and oxygen uptake. Having high CO_2/low pH at the tissue would shift the blood oxygen dissociation curve to the right, thus allowing for more oxygen offloading to the tissues. Studies with OMZ fish species are needed to test this.

4.4 Molecular Responses of Fish to Hypoxia

Molecular responses are also recognized as determining the hypoxia tolerance of different fish species, but these results are usually based on short-term hypoxia exposure, are biased towards fresh or shallow-water species, and may not be as informative for the chronic hypoxia experienced by OMZ demersal fish species. Gracey et al. (2001) found that the gobiid, *Gillichthys* *mirabilis*, which lives in low-oxygen burrows in estuarine environments, survives hypoxia by altering gene expression in a tissue-specific manner, downregulating genes for protein synthesis and locomotion, while upregulating genes for anaerobic ATP production and gluconeogenesis. Exposure of two fish that naturally live in the Elbe estuary, the percid, *Gymnocephalus cernuus*, and the pleuronectid, *Platichthys flesus*, to hypoxic conditions resulted in large tissue-specific gene expression changes in myoglobin, neuroglobin, and caspase 3, along with an increase in respiratory pigment levels in the gills (Tiedke et al., 2014). Changes in globin expression under hypoxic conditions have also been observed in freshwater zebrafish (Roesner et al., 2006) and goldfish (Roesner et al., 2008). These molecular changes in gene-expression channel energy to essential metabolic processes while increasing oxygen extraction capability. In a comparison of two closely related sculpins, the hypoxia-tolerant intertidal *Oligocottus maculosus* and the hypoxia-intolerant subtidal *Blepsias cirrhosis*, Mandic et al. (2014) found that while a number of genes showed a similar hypoxia-induced transcription pattern in both species, the difference in hypoxia tolerance between the species may partly be explained by a large set of genes involved in fatty acid oxidation and oxidative phosphorylation that showed divergent transcriptional patterns in response to hypoxic conditions. The genes in the conserved hypoxia response in the two species were involved in glycolysis and apoptosis (Mandic et al., 2014). Hypoxia inducible factor (HIF) is the transcription factor that results in hypoxia-mediated changes in gene expression (Semenza, 1998). Extremely hypoxia-tolerant fish such as the grass carp, *Ctenopharyngodon idellus*, may also have novel isoforms of key proteins, such as HIF-1 alpha, that may confer greater hypoxia tolerance through differential hypoxia-specific transcriptional and translational regulation (Law et al., 2006). To the knowledge of the authors, no studies have looked at molecular gene responses of OMZ fish species to oxygen stress.

4.5 Metabolic Depression Under Hypoxic Conditions

Metabolic depression is an important component of the hypoxia response, and hypoxia-tolerant animals are though to extend their period of survival under severely hypoxic conditions through a depression of basal metabolic rate (Richards, 2010). For this reason, evolutionary lineages of fish that naturally have lower basal metabolic rates or live in deep-sea, food-poor, or cold-water conditions, may be pre-adapted for survival under severely hypoxic conditions. A consistent trend of decreasing metabolic enzyme activity with depth has been found across 61 species of demersal fish (Drazen et al., 2015). Recently, a physiological trade-off was found between hypoxia tolerance and aerobic exercise capacity in four species of fresh and shallow-water centrarchids (Crans et al., 2015), but similar studies have not been conducted for OMZ fish.

4.6 Behavioural Adaptations

Avoidance, altered breathing, decreased feeding, and altered phototaxis are all reported behaviours of fish in response to low oxygen (Davis, 1975). Altering breathing behaviour either by hyperventilation, increasing breathing frequency or stroke volume, or by switching from periodic or episodic breathing to continuous breathing are all possible fish responses to hypoxia (Perry, 2011). Hyperventilation during hypoxia also produces a respiratory alkalosis, leading to an elevation of red blood cell pH and increasing the affinity of haemoglobin for oxygen by the Bohr effect, and increasing O_2 uptake (Brauner and Randall, 1998; Perry, 2011). Salvanes et al. (2011) found that the gobiid living in the Namibian OMZ, *S. bibarbatus*, is able to tolerate hypoxic conditions for long periods by increasing ventilation rate.

Oxygen minimum zone-tolerant fish may also have habitat-specific behavioural adaptations including selection of microhabitats and semi-diurnal, diurnal, and seasonal migrations. For example, OMZ species such as the sebastids, *S. alascanus* and *S. altivelis*, may preferentially utilize microhabitats that are exposed to greater water flow (eg, presence of rocks or mounds that modify and increase turbulence and flow). Orientation into the current or selection of microhabitats with greater water flow over respiratory surfaces would increase the gas exchange rate (Brewer and Hofmann, 2014). While it is unclear what the physiological significance of the behaviour is, several OMZ fish species have been observed interacting with the sediment in unexpected ways. *Bregmaceros* sp. were observed burying themselves into the sediment in the Arabian Sea OMZ core (Hunter et al., 2011). In the Gulf of California OMZ core, ophidiids of the species *C. emmelas* were observed with their heads buried in the sediment (N.D. Gallo, unpublished data). In the Namibian OMZ, *S. bibarbatus* also associates closely with the sediment, burying into it when in danger, despite the high concentrations of methane and hydrogen sulphide in the sediments (Salvanes et al., 2011). The anoplopomatid, *A. fimbria*, has also been observed ramming its head into the sediment in the OMZ on the California and Oregon margin (L.A. Levin, unpublished data).

There are also reports of fish exhibiting sluggish behaviour, decreased feeding, and higher disease susceptibility and a lowered immune response in fish exposed to oxygen conditions slightly above lethal conditions (Shepard, 1955). To the knowledge of the authors, no studies have looked at how OMZ conditions influence the immune responses of demersal fish species living in OMZs, and it is possible that fish living under OMZ conditions may be more disease and parasite prone due to a lowered immune response. Grenadiers living in the Gulf of California OMZ appear to have higher external parasite loads than grenadiers observed in other areas (L.A. Kuhnz, MBARI, personal communication, 8 September 2015).

4.7 Life-History Trends

Different stages in the life history of a species can have different tolerances to hypoxia. In the shallow-water marine sparid, *Pagrus major*, metabolic rates were highest and hypoxia tolerance was lowest during metamorphosis (Ishibashi et al., 2005). Within a species, smaller individuals can have a higher tolerance to low-oxygen levels compared with their larger counterparts (Burleson et al., 2001; Cerezo and Garcia, 2004; Pörtner and Knust, 2007; Robb and Abrahams, 2003). During the monsoon-driven shoaling of severely hypoxic waters on the Omani shelf, greater abundances of small individuals of the nemipterid, *Parascolopsis aspinosa*, and the triakid, *I. omanensis*, were observed. In the same area, an observed trend of decreasing length with depth for several fish species including the serranid, *E. epistictus*, and the lutjanid. *Pristipomoides filamentosus*, was also attributed to the greater sensitivity of larger individuals to hypoxia (McIlwain et al., 2011). Merrett and Marshall (1980) note that the slope fish community off northwest Africa differed from the fish fauna characteristic of the non-upwelling western North Atlantic fish community in that the dominant species in the African slope community were found to be of smaller mean size and there was no evidence of the "bigger-deeper" phenomenon (Mettett and Haedrich, 1997). Interestingly, an opposite pattern is seen off the US West Coast, where most OMZ-dwelling demersal fish species, including the sebastid, *S. alascanus*, the pleuronectid, *M. pacificus*, and the anoplopomatid, *A. fimbria*, undergo an ontogenetic migration with larvae in surface waters, juveniles settling at shallower depths, and the largest and oldest individuals present within the OMZ (Day and Pearcy, 1968; Hunter et al., 1990). The relationship between hypoxia tolerance and body size is not simple, however, and a recent review found that body size had little or no impact on the ability of fish to take up oxygen during hypoxic conditions, but that larger individuals may be at an advantage when anaerobic metabolism is employed because small individuals reach lethal levels of anaerobic end products faster (Nilsson and Ostlund-Nilsson, 2008).

Reproductive and early life-history strategies may also function as adaptations to hypoxic conditions. For example, the peak spawning period of Malabar sole off India occurs after the low-oxygen monsoon period (Khan and Nandakumaran, 1993). While liparids are known to deposit eggs on a variety of biogenic substrates, including bivalve shells (DeMartini, 1978), polychaete tubes (Marliave and Peden, 1989), and sponges (Chernova, 2014), certain liparids have a unique reproductive strategy involving sexual parasitism of lithodid crabs (Somerton and Donaldson, 1998). *C. melanurus*, an OMZ-dwelling liparid off the US West Coast, lays its eggs in the gill cavity of the Brown Box Crab (*Lopholithodes foraminatus*; Peden and Corbett, 1973), which may increase oxygenation of the eggs during early development. Development is an energetically costly process requiring high oxygen levels; reduced larval growth, retarded development and deformities of embryos are all common features of early development in hypoxic conditions (Alderdice et al., 1958; Kajimura et al., 2005). While 98% of the spawning biomass of the OMZ-dwelling pleuronectid, *M. pacificus*, in central California is found within the OMZ, larvae and juveniles inhabit the upper water column and settle on the upper slope (Hunter et al., 1990). In contrast, young *S. altivelis* are found within the OMZ core off San Diego (N.D. Gallo, unpublished data).

4.8 Feeding Strategies of Species Living in OMZs

Low oxygen conditions have been linked with lower proportions of carnivory in the polychaete community due to high mobility and metabolic demand (Sperling et al., 2013), raising the possibility that carnivory in demersal fish living in OMZs may also be selected against. Fish living under severely hypoxic conditions may select food from the surrounding environment that is less metabolically costly to either obtain or digest, and may be more reliant on detrital production, as opposed to predation at higher trophic levels. *S. bibarbatus* off Namibia have been found to consume jellyfish and sulphidic diatomaceous mud, thus transferring otherwise “dead-end” resources back into the food chain (Utne-Palm et al., 2010). Based on isotopic signatures, jellyfish, which may represent an easy food to digest, contributed 17–60% of the diet of *S. bibarbatus* (Utne-Palm et al., 2010), while gut content analysis showed that polychaetes, euphausiids, and amphipods were also important diet components (Cedras et al., 2011). Fish experiencing oxygen stress may also feed less (Farrell and Richards, 2009), as has been observed using gut content analysis for *S. alascanus* in the OMZ core in the Southern California Bight (N.D. Gallo, unpublished data). In estuarine systems, seasonal hypoxia is known to influence the trophic structure of the benthic community by diverting energy from consumers to microbes (Baird et al., 2004; Diaz and Rosenberg, 2008).

5. IMPLICATIONS FOR A WARMING OCEAN AND EXPANDING OXYGEN MINIMUM ZONES

5.1 Influences of Ocean Oxygen on Marine Communities Through Time

The geologic record is rich with evidence of widespread changes in marine oxygen conditions through time (Jacobs and Lindberg, 1998; Jenkyns, 2010; Moffitt et al., 2014, 2015a,b; Norris et al., 2013; White, 1988). Historical changes in marine oxygen conditions, and the expansion and contraction of OMZs though time, likely played an important role in the evolution and modern-day distribution of deep-sea species, as well as the diversity patterns observed in bathyal and abyssal deep-sea fauna today (Armstrong, 1996; Jeppsson, 1990; Rogers, 2000; White, 1988). Major extinctions or radiations of marine fauna are associated with periods of widespread marine anoxia or the return to fully oxygenated conditions (Moffitt et al., 2015a; Rogers, 2000). Increases in atmospheric oxygen around 400 million years ago were correlated with the radiation of large predatory fish, which required higher oxygen conditions (Dahl et al., 2010). The expansion of oxygen minima during the mid and late Cretaceous, Eocene, and Miocene periods are thought to have promoted widespread episodes of allopatric speciation at intermediate depths (500–2500 m) (White, 1988). The Cretaceous/Paleogene Event, during which OMZs significantly expanded and an oceanic anoxic event occurred (White, 1988), produced a major shift in the functional diversity of the coastal bony fish community. Aerobically active predatory fishes, similar to modern tuna, billfish, and jacks, exhibited particularly large losses (Friedman, 2009), while fishes in the true open ocean, far from coastal OMZs, were more resilient to the extinction event (Sibert et al., 2014).

Rogers (2000) describes the transition between a warm, oxygen-poor (S-phase) and cool, oxygen-rich (P-phase) ocean. Modern-day ocean conditions are characteristic of a P-phase ocean, with deep, cold circulation originating from the poles, a well-oxygenated deep ocean, and disjunct mid-water OMZs. In the past, transitions to a warm (S-phase) ocean were accompanied by major extinction events of deep-sea fauna and an upslope migration by the bathyal fauna into better-oxygenated conditions on the shelf. In contrast, invasion and colonization of the abyssal zone is hypothesized to have taken place during the transition to "cool" (P-phase) conditions. There is a parabolic distribution of fish and invertebrate species diversity with depth, which peaks in the bathyal zone (Rex and Etter, 2010; White, 1988). Extinctions of abyssal fauna and repeated speciation events of the bathyal fauna during these transitions from P to S-phase oceans are hypothesized to explain the observed high bathyal species diversity and the comparatively low diversity and young age of the abyssal fish fauna in today's oceans (Rogers, 2000; White, 1988).

In some cases, margins with OMZs may actually have higher species diversity across the entire margin due to repeated speciation events, as OMZs expanded and contracted through geologic time (Rogers, 2000). For example, Merrett and Marshall (1980) estimate that the fish diversity along the continental margin off northwest Africa is likely to be about two times greater that that of a similar depth range in the temperate western North Atlantic, based on comparison to data from Cohen and Pawson (1977) from the western North Atlantic. Interestingly, the fossil record shows that several of the demersal fish families known from OMZs (Ophidiidae, Bythididae, Macrouridae, Scorpaenidae, Notacanthidae) appeared within a relatively short time (83–50 Ma) (Patterson, 1993). Other families that appeared during this time were Moridae and Trachichthyidae, which are typically deep-sea species that likely also have lower basal metabolic rates. Future studies should examine how past conditions in ocean oxygenation influenced the evolution of the demersal fish fauna known from today's OMZs.

5.2 Ocean Deoxygenation

As oceans warm due to anthropogenic climate change, the oceans lose oxygen in a process known as ocean deoxygenation (Keeling et al., 2010). Long-term ocean monitoring shows that oxygen concentrations in the ocean have declined during the 20th century (Stramma et al., 2010; Whitney et al., 2007), and the Intergovernmental Panel for Climate Change 5th Assessment Report predicts that it is likely that large decreases in oceanic dissolved oxygen will occur during the 21st century (Ciais et al., 2013). The possible implications of expansion of low-oxygen waters have long been recognized (Kamykowski and Zentara, 1990) and Redfield et al. (1963) stated that the margin of safety against anoxia development in the deep ocean is not large, and that significant areas exist in the Pacific Ocean where oxygen is nearly exhausted.

Areas that are already low in oxygen, such as naturally occurring OMZs, are particularly vulnerable to changes in the global ocean oxygen inventory. For example, a 1°C warming throughout the upper ocean is predicted to increase the volume of hypoxic areas by 10% and triple the volume of suboxic waters (Deutsch et al., 2011). The volume and spatial extent of OMZs is predicted to increase with anthropogenic ocean warming and related changes to oceanic circulation (Keeling et al., 2010). Model and observational data show that coastal upwelling-favourable winds in poleward portions of eastern boundary upwelling systems have increased, leading to lower oxygen and lower pH conditions for those margins (Garcia-Reyes et al., 2016). Over the last half-century, vertical expansions of OMZ boundaries and declining core oxygen values have already been documented in the eastern tropical Atlantic and the equatorial Pacific with consequences for marine organisms (Stramma et al., 2008, 2010). The emergence of anoxic conditions (Chan et al., 2008) and OMZ expansion have been documented in the California Current System, with hypoxic waters shoaling vertically by up to 90 m from 1984–2006 (Bograd et al., 2008).

Decreases in ocean oxygen are accompanied by increasing ocean temperatures and decreasing ocean pH. As oceanic temperatures warm with climate change, oxygen consumption rates at depth increase (Stramma et al., 2008). The combined effects of warming and oxygen loss this century are projected to reduce the upper ocean's metabolic index (ratio of O_2 supply to resting metabolic O_2 demand) by ~20% globally and by ~50% in northern high-latitude regions, forcing poleward and vertical contraction of metabolically viable habitats and species ranges (Deutsch et al., 2015). Climate models predict substantial warming and deoxygenation throughout most of the upper ocean (Bopp et al., 2013; Keeling et al., 2010) and the Pacific is prone to some of the largest reductions in metabolic index, driven by its larger projected fractional decrease in oxygen (Deutsch et al., 2015).

Habitat compression, sublethal, and lethal impacts are all potential responses of fishes to low-oxygen conditions (Ekau et al., 2010). Fish species that live in today's OMZs may experience range expansions as severely hypoxic waters expand while hypoxia-intolerant species will likely exhibit range contractions (Gilly et al., 2013). Habitat compression due to OMZ expansion has already been documented for pelagic billfish in the tropical northeast Atlantic (Prince et al., 2010; Stramma et al., 2011) and in the Pacific Oceans (Prince and Goodyear, 2006), as well as for midwater fish in the southern California Current ecosystem (Koslow et al., 2011), but has not yet been documented for demersal fish species in the published literature. However, the shoaling of hypoxic waters above the OMZ in the Southern California Bight has reduced the habitat of rockfish in the Cowcod Conservation Area (McClatchie et al., 2010). Range contractions and expansions of fish species may result in changes to the continental margin food web, and may also affect fisheries yield. The expansion of hypoxic zones is also predicted to lead to a decrease in biodiversity in the affected habitats (Levin et al., 2009).

5.3 Implications for Fisheries Management

Upwelling ecosystems are some of the world's most productive ecosystems and the intermediate zone between the intertidal and the upper boundary of the OMZ is of utmost importance for both artisanal and demersal fisheries (Arntz et al., 2006). Although some OMZ-adapted fish species, including the sebastids *S. alascanus* and *S. altivelis* (Vetter, 1996), the pleuronectid, *M. pacificus* (Vetter et al., 1994), the anoplopomatid, *A. fimbria* (Norse et al., 2012) (Fig. 6), and the merlucciid, *M. capensis* (Mas-Riera et al., 1990) are commercially important species, in most areas, many commercially important fish species are excluded from these severely hypoxic zones (Arntz et al., 2006). Muscular tissue is more calorically expensive to maintain (Hunter et al., 1990), and therefore most muscular, aerobically active fish species that are preferred fisheries items will be excluded from OMZs. Although the pleuronectid, *M. pacificus*, is a fisheries species and is adapted to OMZ conditions, individuals living within the OMZ become more gelatinous (Hunter et al., 1990) and these individuals are no longer profitable to land because they are more difficult to fillet (C. Meng, Captain of F/V Noah's Ark, personal communication, 21 July 2014). In the Arabian Sea on the West Coast of India, reductions in fish catch due to the upwelling of low-oxygen water during the southwest monsoon have been reported by multiple studies (Banse, 1959, 1968). Fish species living in OMZs also tend to be longer-lived species, such as the sebastid, *S. alascanus*, which is reported to live over 100 years (Butler et al., 1995), so different considerations for sustainable fisheries management apply (Mettett and Haedrich, 1997; Norse et al., 2012). Considerations of bycatch are also important.

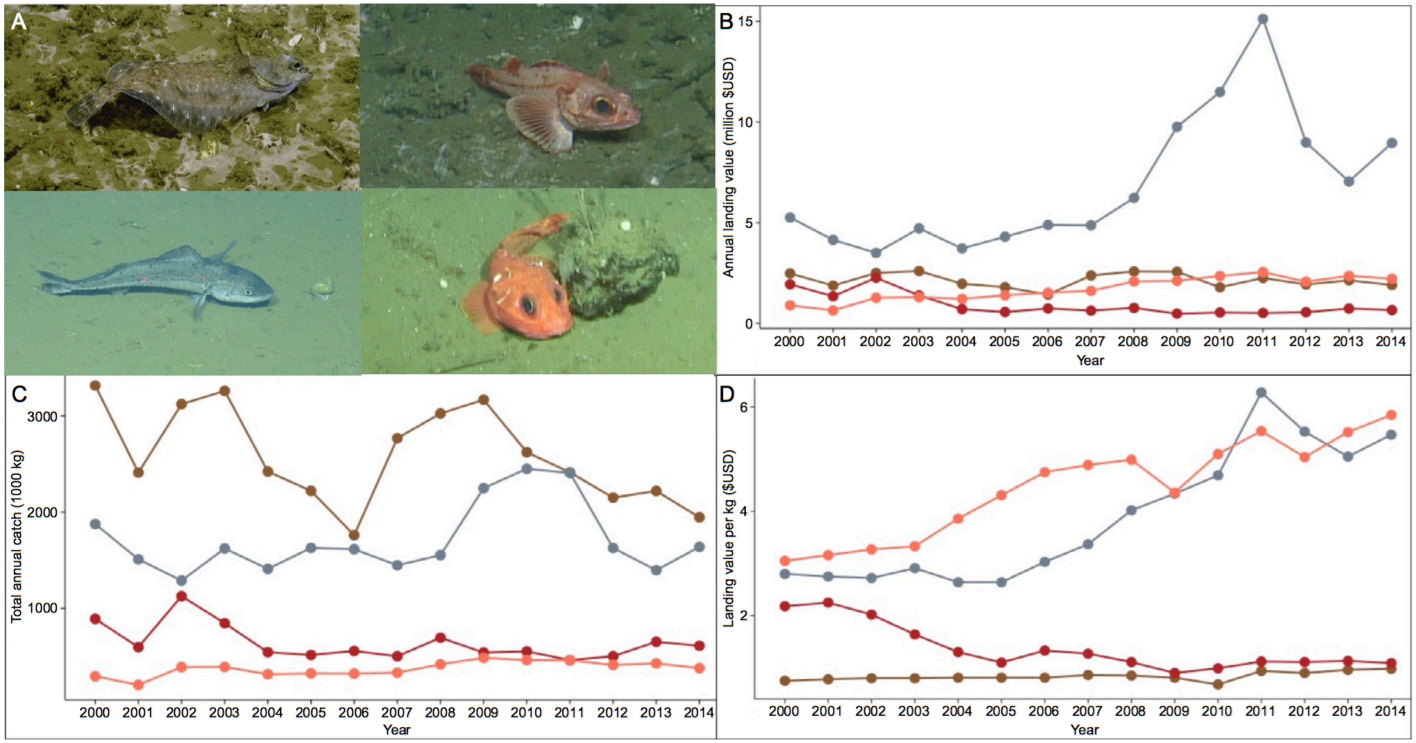

Fig. 6 Several oxygen minimum zone (OMZ) adapted fish species are economically important in the United States, including (A) *Microstomus pacificus* (upper left), *Sebastolobus altivelis* (upper right), *Anoplopoma fimbria* (lower left), and *Sebastolobus alascanus* (lower right). California fisheries landing data from 2000–2014 for *M. pacificus* (*brown*; *dark grey* in the print version), *A. fimbria* (*grey*), *S. alascanus* (*orange*; *light grey in the print version*), and *S. altivelis* (*maroon*; *dark grey* in the print version) showing (B) annual landing value in millions of $USD, (C) total annual catch in thousands of kg, and (D) landing value per kg ($USD). Data were assembled from the California Department of Fish and Wildlife annual California commercial landings reports. During this period, *M. pacificus* and *A. fimbria* make up the greatest mass of landings, *S. alascanus* and *A. fimbria* are the most profitable per kg, and *A. fimbria* is the most economically important OMZ-dwelling demersal fisheries species with an annual landing value in California of up to $15 million USD. *Photographs: E/V Nautilus (*M. pacificus, S. altivelis*, and* A. fimbria*), SIO Triton ROV UC Ship Funds (*S. alascanus*).*

While the reproductive biomass of *M. pacificus* occurs within the OMZ at depths of 500–900 m where these fish are very gelatinous and not profitable for landing, reproductive individuals are still captured as bycatch by trawlers fishing for *S. alascanus* and *S. altivelis* at these depths (C. Meng, Captain of F/V Noah's Ark, personal communication, 21 July 2014).

Many important fisheries species including *Sebastes* sp. off the US West Coast (Grantham et al., 2004; McClatchie et al., 2010) and butterfish (*Peprilus* spp.), sea bass (*Hemanthias* sp. and *D. euryplectrum*), snapper (*Lutjanus* sp.), and grunts (*Pomadasys* sp. and *Orthopristis* sp.) off Central America (Stromme and Saetersdal, 1988) are hypoxia intolerant and not components of the OMZ assemblage. The general pattern that emerges is that demersal fisheries are likely to be negatively impacted overall by the expansion of OMZs in a warming world. While the immediate impacts may be regional increases in catches due to habitat compression for intolerant species, overall, the decreased habitat may negatively impact the population dynamics of the fisheries species. In the Southern California Bight Cowcod Conservation Area, an 18% habitat loss for rockfish due to hypoxia exposure is predicted over 20 years (McClatchie et al., 2010), showing that these changes can occur relatively quickly.

Expanding OMZs can also reduce prey availability for fisheries species. The CalCOFI icthyoplankton time-series (1951–2008) indicates that decreasing oxygen levels in the CCS is correlated with a marked decline (~63%) in the region's mesopelagic fishes which serve as a major food web link to higher trophic levels (Koslow et al., 2011). Bioacoustic and trawl sampling on CalCOFI cruises have also shown that dissolved oxygen concentrations off southern California are key in determining the depth of the lower boundary of the deep scattering layer which includes fish and invertebrate prey (Netburn and Koslow, 2015). At a global scale, seawater oxygen concentration is the best single predictor of the migration depth of the diel vertical migrating community and migration depth is shallower in regions with OMZs (Bianchi et al., 2013). These findings have important implications for altered bentho-pelagic coupling in an ocean with thicker and more intense OMZs. OMZ expansion will also reduce infaunal invertebrate biodiversity at depths of 200–1500 m on upwelling margins, potentially altering trophic support of demersal and benthic fishery species (Sperling et al., 2016).

Fisheries management should take into consideration how climate-change driven ocean impacts such as warming, ocean acidification, ocean oxygen loss, and altered productivity patterns influence the environmental carrying capacity and available ranges of the fisheries species of interest. Ecosystem-based fisheries management needs to incorporate oxygen availability into vulnerability assessments, spatial management, and marine protected area designation. In developing countries, there is a real need for additional oceanographic monitoring to address these changes in real time. Biological time-series, which are currently greatly lacking (Koslow and Couture, 2013), will be key to understanding how altered oceanographic conditions influence demersal and pelagic fish populations and communities in a warming ocean.

6. CONCLUSIONS

Globally, OMZs and OLZs are important oceanographic features in the Pacific, Atlantic, and Indian Ocean, and are characterized by severely hypoxic conditions, which are physiologically challenging for supporting demersal fish communities. Oxygen minimum zone thickness, depth of the OMZ upper boundary, minimum oxygen levels within the OMZ core, local temperatures, and diurnal, seasonal, and interannual oxycline variability differ regionally, with the thickest and shallowest OMZs occurring in the tropics. Although most fish are not hypoxia-tolerant, some fish species are and have evolved physiological, behavioural, and morphological adaptations that allow them to live under the severely hypoxic, hypercapnic, and at times sulphidic, conditions found in OMZs. At least 77 representative demersal fish species in 44 families and 16 orders, including Scorpaeniformes, Gadiiformes, Pleuronectiformes, Cottiformes, Ophidiiformes, Anguilliformes, Perciformes, Notacanthiformes, Aulopiformes, Osmeriformes, Carcharhiniformes, Squaliformes, Rajiformes, Myxiniformes, Batrachoidiformes, and Beryciformes, have been reported living in OMZs. No single fish family or genus has been able to exploit all OMZs. However, each region has its own set of OMZ-adapted demersal fish species, illustrating that evolutionary adaptation to OMZ conditions has occurred multiple times in multiple groups. The severely hypoxic conditions in OMZs lead to decreased demersal fish diversity, but fish density and biomass trends are variable and dependent on region-specific thresholds. A trend of decreasing density under severely hypoxic conditions, with nonlinear declines in density observed under lower oxygen conditions, appears when more data are available for a region. In data-poor areas, this trend may be masked by the presence of edge effects (high-density bands of a single-species living close to a physiological threshold). Demersal fish tend to follow similar patterns as meiofauna, macrofauna, and invertebrate megafauna in OMZs (Gooday et al., 2010), however, in OMZs with extremely low-oxygen conditions (Arabian Sea, Gulf of California), demersal fish may be present even when most invertebrate megafauna are excluded (Murty et al., 2009). Therefore, some OMZ-adapted fish species may be more hypoxia-tolerant than OMZ-adapted invertebrates, contrary to expectation. It is likely that region-specific oxygen thresholds are critical in determining shifts in demersal fish density and diversity, though a more in-depth analysis with additional data is needed to specify these thresholds, and different regions will likely be characterized by different thresholds.

Oxygen minimum zones represent a fascinating place to study the physiological and ecological consequences of oxygen-limiting environments; moreover there is a timely, practical importance to understanding how they influence demersal fish communities. Expansions and contractions of OMZs in the past have affected fish evolution and diversity (Friedman, 2009; Rogers, 2000; Sibert et al., 2014; White, 1988). Current patterns of ocean warming, along with alterations in circulation and productivity patterns, are leading to oxygen loss in many marine ecosystems (Deutsch et al., 2011; Garcia-Reyes et al., 2016; Keeling et al., 2010). Areas with OMZs have experienced oxygen declines, leading to the expansion and shoaling of OMZs (Bograd et al., 2008; Stramma et al., 2008, 2010). These changes are expected to lead to decreases in demersal fish community diversity, changes in species composition, and altered trophic pathways on affected margins. Habitat compression is expected for hypoxia-intolerant species (McClatchie et al., 2010), causing increased susceptibility to overfishing for fisheries species. The general pattern suggests that demersal fisheries are likely to be negatively impacted overall by the expansion of OMZs in a warming world. Ecosystem-based fisheries management needs to incorporate oxygen availability into vulnerability assessments, spatial management, and marine protected area designation.

7. ADVANCING UNDERSTANDING/FUTURE ISSUES

Our review of the scientific literature shows that some areas such as the continental shelf and margin of Central and South America and the Bay of Bengal remain poorly studied and limited information is available on how oxygen gradients influence demersal fish community structure and function. Demersal fish are important components of the benthic community and more work is warranted on how oxygen gradients shape demersal fish assemblages and influence carbon transfer in these understudied, severely hypoxic regions. Additional research should determine at which pO_2 thresholds the greatest amount of species turnover occurs, and how these thresholds are influenced by local temperatures and CO_2, since these will be ecologically relevant considerations for predicting changes in the demersal fish community under climate change scenarios. In order to sustainably manage demersal fisheries in areas with expanding OMZs, there will be a need to integrate information on changes in environmental oxygen levels with data on species-specific hypoxia tolerances (P_{crit}, aerobic scope, metabolic index, P_{50}–pO_2 at which 50% of the blood is oxygenated), which give rise to the oxygen niche of a species (Deutsch et al., 2015; Mislan et al., 2015; Pörtner and Knust, 2007; Pörtner and Peck, 2010; Pörtner et al., 2010). Recent technological advances in using satellite archival tags to measure in situ dissolved oxygen concentrations in the natural environment occupied by the individual (Coffey and Holland, 2015) may be highly informative in determining the environmental niche of the species. These environmental and physiological data must then be considered from an ecological framework, to understand how species interactions and food web dynamics, including predator and prey abundances, may be affected. Additional research is needed on the adaptations of OMZ-specialized fish to the extreme environments in which they live, which include chronic severely hypoxic and hypercapnic, and at times sulphidic, conditions. Most studies on molecular responses and adaptations of fish to hypoxia have focused on freshwater, estuarine, or intertidal fish species, with none known to the authors focusing on OMZ-adapted fish. Knowledge regarding how OMZ-adapted species cope under these conditions may improve our understanding of which species may be tolerant or vulnerable to future climate change impacts.

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REFERENCES

Aguirre-Villaseñor, H., Castillo-Velázquez, R., 2011. New depth record of *Cherublemma emmelas*, black brotula (Ophidiiformes: Ophidiidae) from the Gulf of California. Mexico. Rev. Mex. Biodivers. 82 (2), 713–715 (in spanish).

Aguirre-Villaseñor, H., Salas-Singh, C., 2012. New records of the lollipop catshark *Cephalurus cephalus* (Scyliorhinidae) from the Gulf of California. Mexico. Rev. Mex. Biodivers. 83 (1), 298–300 (in spanish).

Alderdice, D.F., Wickett, W.P., Brett, J.R., 1958. Some effects of temporary exposure to low dissolved oxygen levels on Pacific salmon eggs. J. Fish. Res. Board Can. 15, 229–249.

Armstrong, H.A., 1996. Biotic recovery after mass extinction: the role of climate and ocean-state in the post-glacial (Late Ordovician—Early Silurian) recovery of the conodonts. In: Hart, M.B. (Ed.), Biotic Recovery from Mass Extinction Events, vol. 102. Geological Society Special Publication, pp. 105–117.

Arntz, W.E., Tarazona, J., 1989. Effects of El Niño 1982–83 on benthos, fish and fisheries off the South American Pacific coast. In: Glynn, P.W. (Ed.), Global Ecological Consequences of the 1982–83 El Niño-Southern Oscillation. Oceanographic Series, 52. Elsevier, Amsterdam, pp. 323–360.

Arntz, W.E., Gallardo, V.A., Gutierrez, D., Isla, E., Levin, L.A., Mendo, J., Neira, C., Rowe, G.T., Tarazona, J., Wolff, M., 2006. El Niño and similar perturbation effects on the benthos of Humboldt, California, and Benguella Current upwelling ecosystems. Adv. Geosci. 6, 243–265.

Bailey, G.W., de Beyers, C.J., Lipschitz, K., 1985. Seasonal variation of oxygen deficiency in waters off southern South West Africa in 1975 and 1976 and its relation to the catchability and distribution of the cape rock lobster *Jasus lalandii*. S. Afr. J. Mar. Sci. 3, 197–214.

Baird, R.C., Wilson, D.F., Milliken, D.M., 1973. Observations on *Bregmaceros nectabanus* Whitley in the anoxic, sulfurous water of the Cariaco Trench. Deep-Sea Res. I 20, 503–504.

Baird, D., Christian, R.R., Peterson, C.H., Johnson, G.A., 2004. Consequences of hypoxia on estuarine ecosystem function: energy diversion from consumers to microbes. Ecol. Appl. 14, 805–822.

Ballón, M., Wosnitza-Mendo, C., Guevara-Carrasco, R., Bertrand, A., 2008. The impact of overfishing and El Niño on the condition factor and reproductive success of Peruvian hake, *Merluccius gayi peruanus*. Prog. Oceanogr. 79, 300–307.

Banse, K., 1959. On upwelling and bottom-trawling off the southwest coast of India. J. Mar. Biol. Ass. India 1, 33–49.

Banse, K., 1968. Hydrography of the Arabian Sea shelf of India and Pakistan and effects on demersal fishes. Deep Sea Res. Oceanogr. Abstr. 15, 45–48.

Berner, M., Schemainda, R., 1957. Uber den Einfluss der hydrographischen Situation—insbesondere des Durchluftungszustandes—auf die vertikale Verteilung und den Fang der Laichdorschschwarme im Bornholmbecken. Z. Fisch. N.F. 6, 331–342.

Bianchi, G., 1991. Demersal assemblages of the continental shelf and slope edge between the Gulf of Tehuantepec (Mexico) and the Gulf of Papagayo (Costa Rica). Mar. Ecol. Prog. Ser. 73, 121–140.

Bianchi, G., 1992. Demersal assemblages of the continental shelf and upper slope of Angola. Mar. Ecol. Prog. Ser. 81, 101–120.

Bianchi, D., Galbraith, E.D., Carozza, D.A., Mislan, K.A.S., Stock, C.A., 2013. Intensification of open-ocean oxygen depletion by vertically migrating animals. Nat. Geosci. 6, 545–548.

Bograd, S.J., Castro, C.G., Lorenzo, E.D., Palacios, D.M., Bailey, H., Gilly, W., Chavez, F.P., 2008. Oxygen declines and the shoaling of the hypoxic boundary in the California Current. Geophys. Res. Lett. 35, L12607.

Bograd, S.J., Pozo Buil, M., Di Lorenzo, E., Castro, C.G., Schroeder, I.D., Goericke, R., Anderson, C.R., Benitez-Nelson, C., Whitney, F.A., 2015. Changes in source waters to the Southern California Bight. Deep-Sea Res. II 112, 42–52.

Bopp, L., Resplandy, L., Orr, J.C., Doney, S.C., Dunne, J.P., Gehlen, M., Halloran, P., Heinze, C., Ilyina, T., Séférian, R., Tjiputra, J., Vichi, M., 2013. Multiple stressors of ocean ecosystems in the 21st century: projects with CMIP5 models. Biogeosciences 10, 6225–6245.

Boyer, T.P., Antonov, J.I., Baranova, O.K., Coleman, C., Garcia, H.E., Grodsky, A., Johnson, D.R., Locarnini, R.A., Mishonov, A.V., O'Brien, T.D., Paver, C.R., Reagan, J.R., Seidov, D., Smolyar, I.V., Zweng, M.M., 2013. World Ocean Database 2013, NOAA Atlas NESDIS 72, Levitus, S. (Ed.), Mishonov, A. (Technical Ed.), Silver Spring, MD, 209 pp.

Brauner, C.J., Randall, D.J., 1998. The linkage between oxygen and carbon dioxide transport. In: Perry, S.F., Tufts, B. (Eds.), Fish Physiology. Fish Respiration, 17. Academic Press, New York, pp. 283–319.

Breitburg, D., 2002. Effects of hypoxia, and the balance between hypoxia and enrichment, on coastal fishes and fisheries. Estuaries 25 (4B), 767–781.

Breitburg, D.L., Hondorp, D.W., Davias, L.A., Diaz, R.J., 2009. Hypoxia, nitrogen, and fisheries: integrating effects across local and global landscapes. Annu. Rev. Mar. Sci. 1, 329–349.

Brewer, P.G., Hofmann, A.F., 2014. A plea for temperature in descriptions of the oceanic oxygen status. Oceanography 27, 160–167.

Bridges, C.R., 1988. Respiratory adaptations in intertidal fish. Am. Zool. 28, 79–96.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Towards a metabolic theory of ecology. Ecology 85, 1771–1789.

Brüchert, V., Currie, B., Peard, K.R., 2009. Hydrogen sulphide and methane emissions on the central Namibian shelf. Progr. Oceanogr. 83, 169–179.

Bunn, H.F., Poyton, R.O., 1996. Oxygen sensing and molecular adaptation to hypoxia. Physiol. Rev. 76, 839–885.

Burleson, M.L., Wilhelm, D.R., Smatresk, N.J., 2001. The influence of fish size on the avoidance of hypoxia and oxygen selection by largemouth bass. J. Fish Biol. 59 (5), 1336–1349.

Butler, J.L., Kastelle, C., Rubin, K., Heijnis, D.K.-H., Jacobson, L., Andrews, A., Wakefield, W.W., 1995. Age determination of shortspine thornyhead, *Sebastes alascanus*, using otolith sections and 210Pb:226Ra ratios: Administrative Report. National Marine Fisheries Service Southwest Fisheries Science Center, La Jolla.

Carney, R.S., 2005. Zonation of deep biota on continental margins. Oceanogr. Mar. Biol. 43, 211–278.

Carruthers, J.N., Gogate, S.S., Naidu, J.R., Laevastu, T., 1959. Shorewards upslope of the layer of minimum oxygen off Bombay: its influence on marine biology, especially fisheries. Nature 183, 1084–1087.

Cedras, R.B., Salvanes, A.-G.V., Gibbons, M.J., 2011. Investigations into the diet and feeding ecology of the bearded goby *Sufflogobius bibarbatus* off Namibia. Afr. J. Mar. Sci. 33, 313–320.

Cerezo, J., Garcia, B., 2004. The effects of oxygen levels on oxygen consumption, survival and ventilatory frequency of sharpsnout sea bream (*Diplodus puntazzo* Gmelin, 1789) at different conditions of temperature and fish weight. J. Appl. Ichthyol. 20, 488–492.

Chan, F., Barth, J.A., Lubchenco, J., Kirincich, A., Weeks, H., Peterson, W.T., Menge, B.A., 2008. Emergence of anoxia in the California Current large marine ecosystem. Science 319, 920.

Chapman, L., Galis, F., Shinn, J., 2000. Phenotypic plasticity and the possible role of genetic assimilation: hypoxia-induced trade-offs in the morphological traits of an African cichlid. Ecol. Lett. 3, 387–393.

Chernova, N.V., 2014. New species of the genus *Careproctus* (Liparidae) from the Kara Sea with notes on spongiophilia, reproductive commensalism between fishes and sponges (Rossellidae). J. Ichthyol. 54 (8), 501–512.

Childress, J.J., Seibel, B.A., 1998. Life at stable low oxygen: adaptations of animals to oceanic oxygen minimum layers. J. Exp. Biol. 201, 1223–1232.

Chu, J.W.F., Tunnicliffe, V., 2015. Oxygen limitations on marine animal distributions and the collapse of epibenthic community structure during shoaling hypoxia. Glob. Change Biol. 21 (8), 2989–3004.

Ciais, P., Sabine, C., Bala, G., Bopp, L., Brovkin, V., Canadell, J., Chhabra, A., DeFries, R., Galloway, J., Heimann, M., Jones, C., Le Quéré, C., Myneni, R.B., Piao, S., Thornton, P., 2013. Carbon and other biogeochemical cycles. In: Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (Eds.), Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK/NY, USA.

Coffey, D.M., Holland, K.N., 2015. First autonomous recording of in situ dissolved oxygen from free-ranging fish. Anim. Biotelem. 3, 47.

Cohen, D.M., Pawson, D.L., 1977. Observations from the DSRV Alvin on populations of benthic fishes and selected larger invertebrates in and near DWD-106: Baseline report of environmental conditions in deepwater dumpsite 106. U.S. Department of Commerce, NOAA, Dumpsite Evaluation Report 77-1, 2, Biological characteristics.

Compagno, L.J.V., 1984. Species catalogue. Sharks of the world. An annotated and illustrated catalogue of sharks species known to date. Part. 2. Carcharhiniformes. FAO Fish. Synop. 4, 251–655.

Cowie, G.L., Levin, L.A., 2009. Benthic biological and biogeochemical patterns and processes across an oxygen minimum zone (Pakistan margin, NE Arabian Sea). Deep Sea Res. II 56, 261–270.

Craig, J.K., 2012. Aggregation on the edge: effects of hypoxia avoidance on the spatial distribution of brown shrimp and demersal fishes in the Northern Gulf of Mexico. Mar. Ecol. Prog. Ser. 445, 75–95.

Crans, K.D., Pranckevicius, N.A., Scott, G.R., 2015. Physiological tradeoffs may underlie the evolution of hypoxia tolerance and exercise performance in sunfish (Centrarchidae). J. Exp. Biol. 218, 3264–3275.

Dahl, T.W., Hammarlund, E.U., Anbar, A.D., Bond, D.P.G., Gill, B.C., Gordon, G.W., Knoll, A.H., Nielsen, A.T., Schovsbo, N.H., Canfield, D.E., 2010. Devonian rise in atmospheric oxygen correlated to the radiations of terrestrial plants and large predatory fish. PNAS 107, 17911–17915.

Daskalov, G., 2003. Long-term changes in fish abundance and environmental indices in the Black Sea. Mar. Ecol. Prog. Ser. 255, 259–270.

Davies, S.M., Sanchez-Velasco, L., Beier, E., Godinez, V.M., Barton, E.D., Tamayo, A., 2015. Three-dimensional distribution of larval fish habitats in the shallow oxygen minimum zone in the Eastern Tropical Pacific Ocean off Mexico. Deep-Sea Res. I 101, 118–129.

Davis, J.C., 1975. Minimal dissolved oxygen requirements of aquatic life with emphasis on Canadian species: a review. J. Fish. Res. Bd. Can. 32 (12), 2295–2332.

Day, D., Pearcy, W., 1968. Species associations of benthic fishes on the continental shelf and slope off Oregon. J. Fish. Res. Bd. Can. 25 (12), 2665–2675.

De Leo, F.C., Drazen, J.C., Vetter, E.W., Rowden, A.A., Smith, C.R., 2012. The effects of submarine canyons and the oxygen minimum zone on deep-sea fish assemblages off Hawaii. Deep-Sea Res. I 64, 54–70.

DeMartini, E.E., 1978. Apparent paternal care in *Liparis fucensis* (Pisces: Cyclopteridae). Copeia 1978 (3), 537–539.

Deutsch, C., Brix, H., Ito, T., Frenzel, H., Thompson, L., 2011. Climate-forced variability of ocean hypoxia. Science 333, 336–339.

Deutsch, C., Ferrel, A., Seibel, B., Pörtner, H.-O., Huey, R.B., 2015. Climate change tightens a metabolic contraint on marine habitats. Science 348, 1132–1136.

Diaz, R., Rosenberg, R., 1995. Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. Oceanogr. Mar. Biol. 33, 245–303.

Diaz, R.J., Rosenberg, R., 2008. Spreading dead zones and consequences for marine ecosystems. Science 321, 926–929.

Díaz-Ochoa, J.A., Lange, C.B., Pantoja, S., De Lange, G.J., Guttierez, D., Munoz, P., Salamanca, M., 2009. Fish scales in sediments from off Callao, central Peru. Deep-Sea Res. II 56, 1124–1135.

Dingle, R.V., Nelson, G., 1993. Sea-bottom temperature, salinity and dissolved oxygen on the continental margin off south-western Africa. S. Afr. J. Mar. Sci. 13, 33–49.

Douglas, E.L., Friedl, W.A., Pickwell, G.V., 1976. Fishes in oxygen-minimum zones: blood oxygenation characteristics. Science 191, 957–959.

Doya, C., Aguzzi, J., Chatzievangelou, D., Costa, C., Company, J.P., Tunnicliffe, V., 2016. The seasonal use of small-scale space by benthic species in a transiently hypoxic area. J. Mar. Syst. 154 (B), 280–290.

Drazen, J.C., Friedman, J.R., Condon, N.E., Aus, E.J., Gerringer, M.E., Keller, A.E., Clarke, M.E., 2015. Enzyme activities of demersal fishes from the shelf to the abyssal plain. Deep-Sea Res. I 100, 117–126.

Ekau, W., Auel, H., Pörtner, H.-O., Gilbert, D., 2010. Impacts of hypoxia on the structure and processes in pelagic communities (zooplankton, macro-invertebrates and fish). Biogeosciences 7, 1669–1699.

Espino, M., 1999. "El Niño 1997–98": su efecto sobre el ambiente y los recursos pesqueros del Peru. In: Tarazona, J., Castillo, E. (Eds.), El Niño 1997–98 y su impacto sobre los ecosistemas marino y terrestre. Rev. Per. Biol., vol. Extraordinario, pp. 97–109 (in spanish).

Espino, M., Benites, C., Maldonado, M., 1985. Situacion de la poblacion de merluza durante "El Niño". In: Arntz, W.E., Landa, A., Tarazona, J. (Eds.), El Niño. Su impacto en la fauna marina. Bol. Inst. Mar Peru-Callao spec. vol., pp. 159–162 (in spanish).

Farrell, A., Richards, J., 2009. Defining hypoxia: an integrative synthesis of the responses of fish to hypoxia. Fish Physiol. 27, 487–503.

Feely, R.A., Sabine, C.L., Hernandez-Ayon, J.M., Ianson, D., Hales, B., 2008. Evidence for upwelling of corrosive "acidified" water onto the continental shelf. Science 320, 1490–1492.

Fischer, W., Krupp, F., Schneider, W., Sommer, C., Carpenter, K.E., Niem, V.H., 1995. GuiaFAO para la identificacion de especies para los fines de la pesca. In: Pacifico centro-oriental. Vertebrados–Parte 1 vol. I–III. FAO, Rome, pp. 1–1813.

Friedman, M., 2009. Ecomorphological selectivity among marine teleost fishes during the end- Cretaceous extinction. PNAS 106 (13), 5218–5223.

Friedman, J.R., Condon, N.E., Drazen, J.C., 2012. Gill surface area and metabolic enzyme activities of demersal fishes associated with the oxygen minimum zone off California. Limnol. Oceanogr. 57 (6), 1701–1710.

Fuenzalida, R., Schneider, W., Garcés-Vargas, J., Bravo, L., Lange, C., 2009. Vertical and horizontal extension of the oxygen minimum zone in the eastern South Pacific Ocean. Deep-Sea Res. II 56, 992–1003.

Garcia-Reyes, M., Sydeman, W.J., Schoeman, D.S., Rykaczewski, R.R., Black, B.A., Smit, A.J., Bograd, S.J., 2016. Under pressure: climate change, upwelling, and eastern boundary upwelling ecosystems. Front. Mar. Sci. 2 (109). http://dx.doi.org/10.3389/fmars.2015.00109.

George, P.C., 1958. Sole Fisheries. Fisheries of the West Coast of India. Central Marine Fisheries Research Station, Mandapam Camp, pp. 51–54.

Gewin, V., 2010. Dead in the water. Nature 466, 812–814.

Gilly, W.F., Beman, J.M., Litvin, S.Y., Robison, B.H., 2013. Oceanographic and biological effects of shoaling of the oxygen minimum zone. Annu. Rev. Mar. Sci. 5, 393–420.

Gooday, A.J., Bett, B.J., Escobar, E., Ingole, B., Levin, L.A., Neira, C., Raman, A.V., Sellanes, J., 2010. Habitat heterogeneity and its influence on benthic biodiversity in oxygen minimum zones. Mar. Ecol. 31, 125–147.

Gordon, A.L., Tessler, Z.D., Villanoy, C., 2011. Dual overflows into the deep Sulu Sea. Geophys. Res. Lett. 38, L18606.

Gracey, A.Y., Troll, J.V., Somero, G.N., 2001. Hypoxia-induced gene expression profiling in the euryoxic fish *Gillichthys mirabilis*. PNAS 98 (4), 1993–1998.

Grantham, B.A., Chan, F., Nielsen, K.J., Fox, D.S., Barth, J.A., Huyer, A., Lubchenko, J., Menge, B.A., 2004. Upwelling-driven nearshore hypoxia signals ecosystem and oceanographic changes in the northeast Pacific. Nature 429, 749–754.

Gray, J.S., Wu, R.S.S., Or, Y.Y., 2002. Effects of hypoxia and organic enrichment on the coastal marine environment. Mar. Ecol. Prog. Ser. 238, 249–279.

Guevara-Carrasco, R., Lleonart, J., 2008. Dynamics and fishery of the Peruvian hake: between nature and man. J. Mar. Syst. 71, 249–259.

Gutierrez, D., Enriquez, E., Purca, S., Quipuzcoa, L., Marquina, R., Flores, G., Graco, M., 2008. Oxygenation episodes on the continental shelf of central Peru: remote forcing and benthic ecosystem response. Prog. Oceanogr. 79, 177–189.

Haedrich, R.L., Merrett, N.R., 1990. Little evidence for faunal zonation or communities in deep sea demersal fish faunas. Prog. Oceanogr. 24, 239–250.

Hamukuaya, H., Bianchi, G., Baird, D., 2001. The structure of demersal assemblages off Namibia in relation to abiotic factors. S. Afr. J. Mar. Sci. 23, 397–417.

Helly, J.J., Levin, L.A., 2004. Global distribution of naturally occurring marine hypoxia on continental margins. Deep-Sea Res. I 51, 1159–1168.

Hochachka, P.W., Buck, L.T., Doll, C.J., Land, S.C., 1996. Unifying theory of hypoxia tolerance: molecular/metabolic defense and rescue mechanisms for surviving oxygen lack. PNAS 93, 9493–9498.

Hofmann, A.F., Peltzer, E.T., Walz, P.M., Brewer, P.G., 2011. Hypoxia by degrees: establishing definitions for a changing ocean. Deep-Sea Res. I 58, 1212–1226.

Horn, W., Meincke, J., 1976. Note on the tidal current field in the continental slope area off Northwest Africa. Mem. Soc. Roy. Sci. Liege 6 (10), 31–42.

Hunter, J., Butler, J., Kimbrell, C., Lynn, E., 1990. Bathymetric patterns in size, age, sexual maturity, water content, and caloric density of Dover sole, *Microstomus pacificus*. CalCOFI Rep. 31, 132–144.

Hunter, W.R., Oguri, K., Kitazato, H., Ansari, Z.A., Witte, U., 2011. Epi-benthic megafaunal zonation across an oxygen minimum zone at the Indian continental margin. Deep-Sea Res. I 58, 699–710.

IFOP, 2005. Proyecto FIP No 2004-09: Evaluación hidroacústica de merluza común, año 2004. Chilean Fisheries Development Program. Unpublished Report FIP 2004-09. http://www.fip.cl/Archivos/Hitos/Informes/inffinal%202004-09.pdf. (in spanish).

Ishibashi, Y., Inoue, K., Nakatsukasa, H., Ishitani, Y., Miyashita, S., Murata, O., 2005. Ontogeny of tolerance to hypoxia and oxygen consumption of larval and juvenile red sea bream, *Pagrus major*. Aquaculture 244, 331–340.

Jacobs, D.K., Lindberg, D.R., 1998. Oxygen and evolutionary patterns in the sea: onshore/offshore trends and recent recruitment of deep-sea faunas. PNAS 95, 9396–9401.

Jenkyns, H.C., 2010. Geochemistry of oceanic anoxic events. Geochem. Geophys. Geosyst. 11, Q03004.

Jensen, F.B., Weber, R.E., 1982. Respiratory properties of tench blood and hemoglobin. Adaptation to hypoxic-hypercapnic water. Molec. Physiol. 2, 235–250.

Jensen, F.B., Weber, R.E., 1985. Kinetics of the acclimational responses of tench to combined hypoxia and hypercapnia I and II. J. Comp. Physiol. 156B, 197–211.

Jensen, F.B., Andersen, N.A., Heisler, N., 1987. Effects of nitrite exposure on blood respiratory properties, acid-base and electrolyte regulation in the carp (*Cyprinus carpio*). J. Comp. Physiol. 157B, 533–541.

Jensen, F.B., Nikkinmaa, M., Weber, R.E., 1993. Environmental perturbations of oxygen transport in fishes: causes, consequences and compensations. In: Rankin, J.C., Jensen, F.B. (Eds.), Fish Ecophysiology. Chapman & Hall, London, pp. 161–179.

Jeppsson, L., 1990. An oceanic model for lithological and faunal changes tested on the Silurian record. J. Geol. Soc. Lond. 147, 663–674.

Josefson, A.B., Widbom, B., 1988. Differential response of benthic macrofauna and meiofauna to hypoxia in the Gullmar Fjord basin. Mar. Biol. 100, 31–40.

Juniper, S.K., Matabos, M., Mihaly, S., Ajayamohan, R.S., Gervais, F., Bui, A.O.V., 2013. A year in Barkley Canyon: a time-series observatory study of mid-slope benthos and habitat dynamics using the NEPTUNE Canada network. Deep-Sea Res. II 92, 114–123.

Kajimura, S., Aida, K., Duan, C., 2005. Insulin-like growth factor-binding protein-1 (IGFBP-1) mediates hypoxia-induced embryonic growth and developmental retardation. PNAS 102, 1240–1245.

Kalvelage, T., Lavik, G., Jensen, M.M., Revsbech, N.P., Schunck, H., Loescher, C., Desai, D.K., LaRoche, J., Schmitz-Streit, R., Kuzpers, M.M.M., 2014. Aerobic microbial respiration in oceanic oxygen minimum zones. Geophys. Res. Abstr. 16, EGU2014–EGU8109.

Kamykowski, D., Zentara, S., 1990. Hypoxia in the world ocean as recorded in the historical data set. Deep-Sea Res. I 37, 1861–1874.

Keeling, R.F., Kortzinger, A., Gruber, N., 2010. Ocean deoxygenation in a warming world. Annu. Rev. Mar. Sci. 2, 199–229.

Keller, A.A., Simon, V., Chan, F., Wakefield, W.W., Clarke, M.E., Barth, J.A., Kamikawa, D., Fruh, E.L., 2010. Demersal and invertebrate biomass in relation to an offshore hypoxic zone along the US West Coast. Fish. Oceanogr. 19 (1), 76–87.

Keller, A., Wallace, J., Horness, B., 2012. Variations in eastern North Pacific demersal fish biomass based on the US west coast groundfish bottom trawl survey (2003–2010). Fish. Bull. 110, 205–222.

Keller, A.A., Ciannelli, L., Wakefield, W.W., Simon, V., Barth, J.A., Pierce, S.D., 2015. Occurrence of demersal fishes in relation to near-bottom oxygen levels within the California Current large marine ecosystem. Fish. Oceanogr. 24 (2), 162–176.

Kemp, W.M., Testa, J.M., Conley, D.J., Gilbert, D., Hagy, J.D., 2009. Temporal responses of coastal hypoxia to nutrient loading and physical controls. Biogeosciences 6 (12), 2985–3008.

Khan, M.F., Nandakumaran, K., 1993. Population dynamics of Malabar sole *Cynoglossus macrostomus* Norman along Calicut coast. Indian J. Fish. 40 (4), 225–230.

Koslow, J., 1993. Community structure in North Atlantic deep-sea fishes. Prog. Oceanogr. 31, 321–338.

Koslow, J.A., Couture, J., 2013. Comment: follow the fish. Nature 502, 163–164.

Koslow, J., Bulman, C., Lyle, J., 1994. The mid-slope demersal fish community off south-eastern Australia. Deep-Sea Res. I 41, 113–141.

Koslow, J.A., Goericke, R., Lara-Lopez, A., Watson, W., 2011. Impact of declining intermediate-water oxygen on deepwater fishes in the California Current. Mar. Ecol. Prog. Ser. 436, 207–218.

Kramer, D., 1987. Dissolved oxygen and fish behavior. Environ. Biol. Fishes 18 (2), 81–92.

Kukharev, N.N., 2015. On fish aggregations in the oxygen minimum zones in the North-Western Arabian Sea. Труды ЮгНИРО, T. 53, 149–172 (in Russian).

Law, S.H.W., Wu, R.S.S., Ng, P.K.S., Yu, R.M.K., Kong, R.Y.C., 2006. Cloning and expression analysis of two distinct HIF-alpha isoforms—gcHIF-1alpha and gcHIF- 4alpha—from the hypoxia-tolerant grass carp, *Ctenopharyngodon idellus*. BMC Mol. Biol. 7, 15.

Levin, L.A., 2003. Oxygen minimum zone benthos: adaptation and community response to hypoxia. Oceanogr. Mar. Biol. 41, 1–45.

Levin, L.A., Huggett, C.L., Wishner, K.F., 1991. Control of deep-sea benthic community structure by oxygen and organic-matter gradients in the eastern Pacific Ocean. J. Mar. Res. 49, 763–800.

Levin, L.A., Gage, J.D., Martin, C., Lamont, P.A., 2000. Macrobenthic community structure within and beneath the oxygen minimum zone, NW Arabian Sea. Deep-Sea Res. II 47, 189–226.

Levin, L.A., Gutierrez, D., Rathburn, A., Neira, C., Sellanes, J., Munoz, P., Gallardo, V., Salamanca, M., 2002. Benthic processes on the Peru margin: a transect across the oxygen minimum zone during the 1997–98 El Niño. Prog. Oceanogr. 53, 1–27.

Levin, L., Ekau, W., Gooday, A., 2009. Effects of natural and human-induced hypoxia on coastal benthos. Biogeosciences 6, 2063–2098.

Levin, L.A., Mendoza, G.F., Gonzalez, J.P., Thurber, A.R., Cordes, E.E., 2010. Diversity of bathyal macrofauna on the northeastern Pacific margin: the influence of methane seeps and oxygen minimum zones. Mar. Ecol. 31, 94–110.

Levin, L.A., McGregor, A.L., Mendoza, G.F., Woulds, C., Cross, P., Witte, U., Gooday, A.J., Cowie, G., Kitazato, H., 2013. Macrofaunal colonization across the Indian margin oxygen minimum zone. Biogeosciences 10, 7161–7177.

Levin, L.A., Mendoza, G.F., Grupe, B.M., Gonzalez, J.P., Jellison, B., Rouse, G., Thurber, A.R., Warren, A., 2015. Biodiversity on the rocks: macrofauna inhabiting authigenic carbonate at Costa Rica methane seeps. PLoS One 10, e0131080.

Love, R.H., Fisher, R.A., Wilson, M.A., Nero, R.W., 2004. Unusual swimbladder behavior of fish in the Cariaco Trench. Deep-Sea Res. I 51, 1–16.

Lynn, R.J., Simpson, J.J., 1987. The California current system: the seasonal variability of its physical characteristics. J. Geophys. Res. 92 (C12), 12947–12966.

MacLeod, J.C., Smith Jr., L.L., 1966. Effect of pulpwood fiber on oxygen consumption and swimming endurance of the fathead minnow, *Pimephales promelas*. Trans. Am. Fish. Soc. 95, 71–84.

Macpherson, E., Gordoa, A., 1992. Trends in the demersal fish community off Namibia from 1983 to 1990. S. Afr. J. Mar. Sci. 12, 635–649.

Madhupratap, M., Nair, K.N.V., Gopalakrishnan, T.C., Haridas, P., Nair, K.K.C., Venugopal, P., Gauns, M., 2001. Arabian Sea oceanography and fisheries of the west coast of India. Curr. Sci. 81 (4), 355–361.

Mandic, M., Todgham, A.E., Richards, J.G., 2009. Mechanisms and evolution of hypoxia tolerance in fish. Proc. R. Soc. B 276 (1657), 735–744.

Mandic, M., Ramon, M.L., Gracey, A.Y., Richards, J.G., 2014. Divergent transcriptional patterns are related to differences in hypoxia tolerance between the intertidal and the subtidal sculpins. Mol. Ecol. 23, 6091–6103.

Marliave, J.B., Peden, A.E., 1989. Larvae of *Liparis fucensis* and *Liparis callyodon*: is the "cottoid bubblemorp [sic]" phylogenetically significant? Fish. Bull. 87, 735–743.

Mas-Riera, J., Lombarte, A., Gordoa, A., Macpherson, E., 1990. Influence of Benguela upwelling on the structure of demersal fish populations off Namibia. Mar. Biol. 182, 175–182.

Matabos, M., Tunnicliffe, V., Juniper, S.K., Dean, C., 2012. A year in hypoxia: epibenthic community responses to severe oxygen deficit at a subsea observatory in a coastal inlet. PloS One 7, e45626.

Matabos, M., Bui, A.O.V., Mihaly, S., Aguzzi, J., Juniper, S.K., Ajayamohan, R.S., 2014. High-frequency study of epibenthic megafaunal community dynamics in Barkley Canyon: a multi-disciplinary approach using the NEPTUNE Canada network. J. Mar. Syst. 130, 56–68.

Matey, V., Richards, J.G., Wang, Y., Wood, C.M., Rogers, J., Davies, R., Murray, B.W., Chen, X.-Q., Du, J., Brauner, C.J., 2008. The effect of hypoxia on gill morphology and ionoregulatory status in the Lake Qinghai scaleless carp, *Gymnocypris przewalskii*. J. Exp. Biol. 211, 1063–1074.

McClatchie, S., Goericke, R., Cosgrove, R., Auad, G., Vetter, R., 2010. Oxygen in the Southern California Bight: multidecadal trends and implications for demersal fisheries. Geophys. Res. Lett. 37, L19602.

McIlwain, J.L., Harvey, E.S., Grove, S., Shiell, G., Al-Oufi, H., Al-Jardani, N., 2011. Seasonal changes in a deep-water fish assemblage in response to monsoon-generated upwelling events. Fish. Oceanogr. 20 (6), 497–516.

Mead, G., 1963. Observations on fishes caught over the anoxic waters of the Cariaco Trench, Venezuela. Deep-Sea Res. Oceanogr. Abstr. 10, 251–257.

Merrett, N., Marshall, N., 1980. Observations on the ecology of deep-sea bottom-living fishes collected off northwest Africa (08°–27°N). Prog. Oceanogr. 9, 185–244.

Mettett, N.R., Haedrich, R.L., 1997. Deep-Sea Demersal Fish and Fisheries, first ed. Chapman and Hall, London.

Milessi, A.C., Sellanes, J., Gallardo, V.A., Lange, C.B., 2005. Osseous skeletal material and fish scales in marine sediments under the oxygen minimum zone off northern and central Chile. Estuar. Coast. Shelf Sci. 64, 185–190.

Milliken, D.M., Houde, E.D., 1984. A new species of Bregmacerotidae (Pisces), *Bregmaceros cantori*, from the Western Atlantic Ocean. Bull. Mar. Sci. 35 (1), 11–19.

Mislan, K.A.S., Dunne, J.P., Sarmiento, J.L., 2015. The fundamental niche of blood-oxygen binding in the pelagic ocean. Oikos. http://dx.doi.org/10.1111/oik.02650.

Mittelstaedt, F., 1976. On the currents along the Northwest African coast south of 22°N. Dt. Hydrogr. Z. 29 (3), 97–117.

Moffitt, S.E., Hill, T.M., Ohkushi, K., Kennett, J.P., Behl, R.J., 2014. Vertical oxygen minimum zone oscillations since 20 ka in Santa Barbara Basin: a benthic foraminiferal community perspective. Paleoceanography 29, 44–57.

Moffitt, S.E., Hill, T.M., Roopnarine, P.D., Kennett, J.P., 2015a. Response of seafloor ecosystems to abrupt global climate change. PNAS 112 (15), 4684–4689.

Moffitt, S.E., Moffitt, R.A., Sauthoff, W., Davis, C.V., Hewett, K., Hill, T.M., 2015b. Paleoceanographic insights on recent oxygen minimum zone expansion: lessons for modern oceanography. PLoS One 10 (1), e0115246.

Montecino, V., Lange, C.B., 2009. The Humboldt Current System: ecosystem components and processes, fisheries, and sediment studies. Prog. Oceanogr. 83, 65–79.

Morrison, J.M., Codispoti, L.A., Gaurin, S., Jones, B., Magnhnani, V., Zheng, Z., 1998. Seasonal variation of hydrographic and nutrient fields during the US JGOFS Arabian Sea Process Study. Deep-Sea Res. II 45, 2053–2102.

Morrison, J., Codispoti, L., Smith, S., 1999. The oxygen minimum zone in the Arabian Sea during 1995. Deep-Sea Res. II 46, 1903–1931.

Mullins, H.T., Thompson, J.B., McDougall, K., Vercoutere, T.L., 1985. Oxygen-minimum zone edge effects: evidence from the central California coastal upwelling system. Geology 13, 491–494.

Murty, S.J., Bett, B.J., Gooday, A.J., 2009. Megafaunal responses to strong oxygen gradients on the Pakistan margin of the Arabian Sea. Deep-Sea Res. II 56, 472–487.

Nam, S.H., Kim, H.-J., Send, U., 2011. Amplification of hypoxic and acidic events by La Niña conditions on the continental shelf off California. Geophys. Res. Lett. 38, L22602.

Nam, S.H., Takeshita, Y., Frieder, C.A., Martz, T., Ballard, J., 2015. Seasonal advection of Pacific equatorial water alters oxygen and pH in the Southern California Bight. J. Geophys. Res. Oceans 120, 5387–5399.

Netburn, A.N., Koslow, J.A., 2015. Dissolved oxygen as a constraint on daytime deep scattering layer depth in the southern California current ecosystem. Deep-Sea Res. I 104, 149–158.

Nilsson, G.E., 2007. Gill remodeling in fish—a new fashion or an ancient secret? J. Exp. Biol. 210, 2403–2409.

Nilsson, G.E., 2010. Respiratory Physiology of Vertebrates. Life With and Without Oxygen. Cambridge University Press, Cambridge, pp. 1–334.

Nilsson, G.E., Ostlund-Nilsson, S., 2008. Does size matter for hypoxia tolerance in fish? Biol. Rev. Camb. Philos. Soc. 83, 173–189.

Nishida, T., Sivasubramaniam, K., 1986. Atlas of Deep Water Demersal Fishery Resources in the Bay of Bengal. Bay of Bengal programme: development of small-scale fisheries, UN FAO, pp. 1–17.

Norris, R.D., Turner, S.K., Hull, P.M., Ridgwell, A., 2013. Marine ecosystem responses to Cenozoic global change. Science 341, 492–498.

Norse, E.A., Brooke, S., Cheung, W.W.L., Clark, M.R., Ekeland, E., Froese, R., Gjerde, K.M., Haedrich, R.L., Heppell, S.S., Morato, T., Morgan, L.E., Pauly, D., Sumaila, R., Watson, R., 2012. Sustainability of deep-sea fisheries. Mar. Pol. 36, 307–320.

Patterson, C., 1993. An overview of the early fossil record of acanthomorphs. B. Mar. Sci. 52 (1), 29–59.

Paulmier, A., Ruiz-Pino, D., 2009. Oxygen minimum zones (OMZs) in the modern ocean. Prog. Oceanogr. 80, 113–128.

Paulmier, A., Ruiz-Pino, D., Garçon, V., Farías, L., 2006. Maintaining of the Eastern South Pacific Oxygen Minimum Zone (OMZ) off Chile. Geophys. Res. Lett. 33, L20601.

Paulmier, A., Ruiz-Pino, D., Garçon, V., 2011. CO_2 maximum in the oxygen minimum zone (OMZ). Biogeosciences 8, 239–252.

Peden, A.E., Corbett, C.A., 1973. Commensalism between a liparid fish, *Careproctus sp*., and the lithodid box crab, *Lopholithodes foraminatus*. Can. J. Zool. 51 (5), 555–556.

Peña-Izquierdo, J., van Sebille, E., Pelegri, J.L., Sprintall, J., Mason, E., Llanillo, P.J., Machin, F., 2015. Water mass pathways to the North Atlantic oxygen minimum zone. J. Geophys. Res. Oceans 120. http://dx.doi.org/10.1002/2014JC010557.

Perry, S., 2011. Respiratory responses to hypoxia in fish. In: Farrell, A.P. (Ed.), Encyclopedia of Fish Physiology: From Genome to Environment. Academic Press, Amsterdam, pp. 1751–1756.

Piontkovski, S., Al-Oufi, H., 2014. Oxygen Minimum Zone and fish landings along the Omani Shelf. J. Fish. Aquat. Sci. 9, 294–310.

Piontkovski, S., Al-Gheilani, H.M.H., Jupp, B.P., Al-Azri, A.R., Al-Hashmi, K.A., 2012. Interannual changes in the Sea of Oman ecosystem. Open Mar. Biol. J. 6, 38–52.

Pollock, M., Clarke, L., Dube, M., 2007. The effects of hypoxia on fishes: from ecological to physiological effects. Environ. Rev. 14, 1–14.

Pörtner, H.O., Knust, R., 2007. Climate change affects marine fishes through the oxygen limitation of thermal tolerance. Science 315, 95–97.
Pörtner, H.O., Peck, M.A., 2010. Climate change effects on fish and fisheries: towards a cause- and -effect understanding. J. Fish Biol. 77, 1745–1779.
Pörtner, H.O., Bennett, A.F., Bozinovic, F., Clarke, A., Lardies, M.A., Lucassen, M., Pelster, B., Schiemer, F., Stillman, J.H., 2006. Trade-offs in thermal adaptation: the need for a molecular to ecological integration*. Physiol. Biochem. Zool. 79 (2), 295–313.
Pörtner, H.O., Schulte, P.M., Wood, C.M., Schiemer, F., 2010. Niche dimensions in fishes: an integrative view. Physiol. Biochem. Zool. 83 (5), 808–826.
Powers, D., 1980. Molecular ecology of teleost fish hemoglobins: strategies for adapting to changing environments. Am. Zool. 20, 139–162.
Powers, D.A., Greaney, G.S., Place, A.R., 1979. Physiological correlation between lactate dehydrogenase genotype and haemoglobin function in killifish. Nature 277, 240–241.
Prakash, S., Nair, T.M.B., Bhaskar, T.V.S.U., Prakash, P., Gilbert, D., 2012. Oxycline variability in the central Arabian Sea: an argo-oxygen study. J. Sea Res. 71, 1–8.
Prince, E.D., Goodyear, C.P., 2006. Hypoxia-based habitat compression of tropical pelagic fishes. Fish. Oceanogr. 15, 451–464.
Prince, E.D., Luo, J., Goodyear, C.P., Hoolihan, J.P., Snodgrass, D., Orbesen, E.S., Serafy, J.E., Ortiz, M., Schirripa, M.J., 2010. Ocean scale hypoxia-based habitat compression of Atlantic istiophorid billfishes. Fish. Oceanogr. 19, 448–462.
Quiroga, E., Sellanes, J., Arntz, W.E., Gerdes, D., Gallardo, V.A., Hebbeln, D., 2009. Benthic megafaunal and demersal fish assemblages on the Chilean continental margin: the influence of the oxygen minimum zone on bathymetric distribution. Deep-Sea Res. II 56, 1112–1123.
R Core Team, 2012. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, ISBN: 3-900051-07-0.
Raman, A.V., Damodaran, R., Levin, L.A., Ganesh, T., Rao, Y.K.V., Nanduri, S., Madhusoodhanan, R., 2015. Macrobenthos relative to the oxygen minimum zone on the East Indian margin, Bay of Bengal. Mar. Ecol. 36, 679–700.
Rankin, J.C., Jensen, F.B., 1993. Fish Ecophysiology. Chapman and Hall, London, pp. 1–421.
Redfield, A.C., Ketchum, B.H., Richards, F.A., 1963. The influence of organisms on the composition of sea-water. In: Hill, M.N. (Ed.), The sea, vol. 2. Interscience, New York, pp. 26–77.
Revsbech, N.P., Larsen, L.H., Gundersen, J., Dalsgaard, T., Ulloa, O., Thamdrup, B., 2009. Determination of ultra-low oxygen concentrations in oxygen minimum zones by the STOX sensor. Limnol. Oceanogr. Methods 7, 371–381.
Rex, M.A., Etter, R.J., 2010. Deep-Sea Biodiversity: Pattern and Scale. Harvard University Press, Cambridge, MA. 354 pp.
Richards, J., 2009. Metabolic and molecular responses of fish to hypoxia. Fish Physiol. 27, 443–485.
Richards, J., 2010. Metabolic rate suppression as a mechanism for surviving environmental challenge in fish. Prog. Mol. Subcell. Biol. 49, 113–139.
Richards, J.G., 2011. Physiological, behavioral and biochemical adaptations of intertidal fishes to hypoxia. J. Exp. Biol. 214, 191–199.
Robb, T., Abrahams, M.V., 2003. Variation in tolerance to hypoxia in a predator and prey species: an ecological advantage of being small? J. Fish Biol. 62, 1067–1081.
Roel, B.A., 1987. Demersal communities off the west coast of South Africa. Afr. J. Marine Sci. 5, 575–584.
Roel, B.A., Rucabado, J., Lloris, D., Lleonart, J., 1985. Las comunidades de peces demersales del afloramiento de Africa occidental (Sahara y Namibia). In: Bas, C., Margalef, R., Rubies, P. (Eds.), Simposio internacional sobre las areas de afloramiento mas importantes

del oueste africano (Cabo Blanco y Benguela). Instituto Investigaci6nes Pesqueras, Barcelona, pp. 691–700 (in spanish).

Roesner, A., Hankeln, T., Burmester, T., 2006. Hypoxia induces a complex response of globin expression in zebrafish (*Danio rerio*). J. Exp. Biol. 209, 2129–2137.

Roesner, A., Mitz, S.A., Hankeln, T., Burmester, T., 2008. Globins and hypoxia adaptation in the goldfish, *Carassius auratus*. FEBS J. 275, 3633–3643.

Rogers, A.D., 2000. The role of the oceanic oxygen minima in generating biodiversity in the deep sea. Deep-Sea Res. II 47, 119–148.

Rosenberg, R., Arntz, W.E., Chuman de Flores, E., Flores, L.A., Carbjal, G., Finger, I., Tarazona, J., 1983. Benthos biomass and oxygen deficiency in the upwelling system off Peru. J. Mar. Sci. 41, 263–279.

Rummer, J.L., Roshan-Moniri, M., Balfry, S.K., Brauner, C.J., 2010. Use it or lose it? Sablefish, *Anoplopoma fimbria*, a species representing a fifth teleostean group where bNHE associated with the red blood cell adrenergic stress response has been secondarily lost. J. Exp. Biol. 213, 1503–1512.

Rummer, J.L., McKenzie, D.J., Innocenti, A., Supuran, C.T., Brauner, C.J., 2013. Root effect hemoglobin may have evolved to enhance general tissue oxygen delivery. Science 340, 1327–1329.

Sadorus, L.L., Mantua, N.J., Essington, T., Hickey, B., Hare, S., 2014. Distribution patterns of Pacific halibut (*Hippoglossus stenolepis*) in relation to environmental variables along the continental shelf waters of the US West Coast and southern British Columbia. Fish. Oceanogr. 23 (3), 225–241.

Salvanes, A.G.V., Utne-Palm, A.C., Currie, B., Braithwaite, V.A., 2011. Behavioural and physiological adaptations of the bearded goby, a key fish species of the extreme environment of the northern Benguela upwelling. Mar. Ecol. Prog. Ser. 425, 193–202.

Sankaranarayanan, V.N., Qasim, S.Z., 1968. The influence of some hydrographical factors on the fisheries of the Cochin area. Bull. Nat. Inst. Sci. India 38, 846–853.

Schlitzer, R., 2015. Ocean Data View. http://odv.awi.de.

Schurmann, H., Steffensen, J.F., 1992. Lethal oxygen levels at different temperatures and the preferred temperature during hypoxia of the Atlantic cod, *Gadus morhua*. J. Fish Biol. 41, 927–934.

Secor, D.H., Gunderson, T.E., 1998. Effects of hypoxia and temperature on survival, growth, and respiration of juvenile Atlantic Sturgeon, *Acipenser oxyrinchus*. Fish. Bull. 96 (3), 603–613.

Seibel, B.A., 2011. Critical oxygen levels and metabolic suppression in oceanic oxygen minimum zones. J. Exp. Biol. 214, 326–336.

Seibel, B.A., Walsh, P.J., 2003. Biological impacts of deep-sea carbon dioxide injection inferred from indices of physiological performance. J. Exp. Biol. 206, 641–650.

Sellanes, J., Quiroga, E., Neira, C., Gutiérrez, D., 2007. Changes of macrobenthos composition under different ENSO cycle conditions on the continental shelf off central Chile. Cont. Shelf Res. 27, 1002–1016.

Sellanes, J., Neira, C., Quiroga, E., Teixido, N., 2010. Diversity patterns along and across the Chilean margin: a continental slope encompassing oxygen gradients and methane seep benthic habitats. Mar. Ecol. 31, 111–124.

Semenza, G.L., 1998. Hypoxia-inducible factor 1: master regulator of O_2 homeostasis. Curr. Opin. Genet. Dev. 8 (5), 588–594.

Send, U., Nam, S., 2012. Relaxation from upwelling: the effect on dissolved oxygen on the continental shelf. J. Geophys. Res. 117, C04024.

Seshappa, G., 1953. Observations on the physical and biological features of the inshore sea bottom along the Malabar coast. Proc. Nat. Inst. Sci. India 19, 257–279.

Shaffer, G., Olsen, S.M., Pedersen, J.O.P., 2009. Long-term ocean oxygen depletion in response to carbon dioxide emissions from fossil fuels. Nat. Geosci. 2, 105–109.

Shepard, M.P., 1955. Resistance and tolerance of young speckled trout (*Salve linus fontinalis*) to oxygen lack, with special reference to low oxygen acclimation. J. Fish. Res. Board Can. 12, 387–446.

Sibert, E.C., Hull, P.M., Norris, R.D., 2014. Resilience of Pacific pelagic fish across the Cretaceous/Palaeogene mass extinction. Nat. Geosci. 7, 667–670.

Sielfeld, W., Vargas, M., 1999. Review of marine fish zoogeography of Chilean Patagonia (42°-57°S). Sci. Mar. 63, 451–463.

Slater, R.D., Kroopnick, P., 1984. Controls on dissolved oxygen distribution and organic carbon deposition in the Arabian Sea. In: Haq, B.U., Milliman, J.D. (Eds.), Geology and Oceanography of the Arabian Sea and Coastal Pakistan, pp. 305–312.

Smale, M.J., Roel, B., Badenhorst, A., Field, J.G., 1993. Analysis of the demersal community of fish and cephalopods on the Agulhas Bank, South Africa. J. Fish Biol. 43, 169–191.

Sollid, J., De Angelis, P., Gundersen, K., Nilsson, G.E., 2003. Hypoxia induces adaptive and reversible gross morphological changes in crucian carp gills. J. Exp. Biol. 206, 3667–3673.

Somerton, D.A., Donaldson, W., 1998. Parasitism of the golden king crab, *Lithodes aequispinus*, by two species of snailfish, genus *Careproctus*. Fish. Bull. 96, 871–884.

Speers-Roesch, B., Mandic, M., Groom, D.J.E., Richards, J.G., 2013. Critical oxygen tensions as predictors of hypoxia tolerance and tissue metabolic responses during hypoxia exposure in fishes. J. Exp. Mar. Biol. Ecol. 449, 239–249.

Sperling, E.A., Frieder, C.F., Raman, A.V., Girguis, P.R., Levin, L.A., Knoll, A.H., 2013. Oxygen, ecology, and the Cambrian radiation of animals. PNAS 110 (33), 13446–13451.

Sperling, E.A., Frieder, C.A., Levin, L.A., 2016. Biodiversity response to natural gradients of multiple stressors on continental margins. Proc. R. Soc. B. 283, 20160637.

Stein, D.L., Drazen, J.C., Schlining, K.L., Barry, J.P., Kuhnz, L., 2006. Snailfishes of the central California coast: video, photographic and morphological observations. J. Fish Biol. 69, 970–986.

Stramma, L., Johnson, G.C., Sprintall, J., Mohrholz, V., 2008. Expanding oxygen-minimum zones in the tropical oceans. Science 320, 655–658.

Stramma, L., Schmidtko, S., Levin, L.A., Johnson, G.C., 2010. Ocean oxygen minima expansions and their biological impacts. Deep-Sea Res. I 57, 587–595.

Stramma, L., Prince, E.D., Schmidtko, S., Luo, J., Hoolihan, J.P., Visbeck, M., Wallace, D.W.R., Brandt, P., Kortzinger, A., 2011. Expansion of oxygen minimum zones may reduce available habitat for tropical pelagic fishes. Nat. Clim. Change 2, 33–37.

Stromme, T., Saetersdal, G., 1988. Final report: surveys of the fish resources on the Pacific Shelf from Colombia to Southern Mexico, 1987. pp. 1–94. NORAD/UNDP/FAOPROGRAMME.

Thiel, H., 1978. Benthos in upwelling regions. In: Boje, R., Tomczak, M. (Eds.), Upwelling Ecosystems. Springer-Verlag, Berlin, pp. 124–138.

Thomas, S., 1983. Changes in blood acid-base balance in trout (*Salmo gairdneri* Richardson) following exposure to combined hypoxia and hypercapnia. J. Comp. Physiol. 152, 53–57.

Tiano, L., Garcia-Robledo, E., Dalsgaard, T., Devol, A.H., Ward, B.B., Ulloa, O., Canfield, D.E., Revsbech, N.P., 2014. Oxygen distribution and aerobic respiration in the north and south eastern tropical Pacific oxygen minimum zones. Deep-Sea Res. I 94, 173–183.

Tiedke, J., Thiel, R., Burmester, T., 2014. Molecular responses of estuarine fish to hypoxia: a comparative study with ruffe and flounder from field and laboratory. PLoS One 9 (3), e90778.

Torres, J.J., Grigsby, M.D., Clarke, M.E., 2012. Aerobic and anaerobic metabolism in oxygen minimum layer fishes: the role of alcohol dehydrogenase. J. Exp. Biol. 215, 1905–1914.

Utne-Palm, A.C., Salvanes, A.G.V., Currie, B., Kaartvedt, S., Nilsson, G.E., Braithwaite, V.A., Stecyk, J.A.W., Hundt, M., van der Bank, M., Flynn, B., Sandvik, G.K., Klevjer, T.A., Sweetman, A.K., Brüchert, V., Pittman, K., Peard, K.R., Lunde, I.G., Strandabø, R.A.U., Gibbons, M.J., 2010. Trophic structure and community stability in an overfished ecosystem. Science 329, 333–336.

Van Assendelft, O.W., 1970. Spectrophotometry of Haemoglobin Derivatives. Royal Vangorcum, Assen, Netherlands. 152 pp.

Vaquer-Sunyer, R., Duarte, C.M., 2008. Thresholds of hypoxia for marine biodiversity. PNAS 105, 15452–15457.

Vaquer-Sunyer, R., Duarte, C.M., 2011. Temperature effects on oxygen thresholds for hypoxia in marine benthic organisms. Glob. Change Biol. 17, 1788–1797.

Vetter, R.D., 1996. Bathymetric demography and niche separation of thornyhead rockfish: *Sebastolobus alascanus* and *Sebastolobus altivelis*. Can. J. Fish. Aquat. Sci. 53, 600–609.

Vetter, R.D., Lynn, E.A., 1997. Bathymetric demography, enzyme activity patterns, and bioenergetics of deep-living scorpaenid fishes (genera *Sebastes* and *Sebastolobus*): paradigms revisited. Mar. Ecol. Prog. Ser. 155, 173–188.

Vetter, R.D., Lynn, E.A., Garza, M., Costa, A.S., 1994. Depth zonation and metabolic adaptation in Dover sole, *Microstomus pacificus* and other deep-living flatfishes: factors that affect the sole. Mar. Biol. 120, 145–159.

Vornanen, M., Stecyk, J.A.W., Nilsson, G.E., 2009. The anoxia-tolerant crucian carp (*Carassius carassius L.*). In: Richards, J.G., Farrell, A.P., Brauner, C.J. (Eds.), Fish physiology. In: Hypoxia, vol. 27. Elsevier, Amsterdam, pp. 397–441.

Weeks, S.J., Currie, B., Bakun, A., Peard, K.R., 2004. Hydrogen sulphide in the Atlantic Ocean off southern Africa, implications of a new view based on SeaWIFS satellite imagery. Deep-Sea Res. I 51, 153–172.

Wells, R.M.G., 2009. Blood-gas transport and hemoglobin function: adaptations for functional and environmental hypoxia. Fish Physiol. 27, 255–299.

White, B.N., 1988. Oceanic anoxic events and allopatric speciation in the deep sea. Biol. Oceanogr. 5, 243–259.

Whitney, F.A., Freeland, H.J., Robert, M., 2007. Persistently declining oxygen levels in the interior waters of the eastern subarctic Pacific. Prog. Oceanogr. 75, 179–199.

Wishner, K., Levin, L., Gowing, M., Mullineaux, L., 1990. Involvement of the oxygen minimum in benthic zonation on a deep seamount. Nature 346, 57–59.

Wishner, K., Ashjian, C., Gelfman, C., 1995. Pelagic and benthic ecology of the lower interface of the Eastern Tropical Pacific oxygen minimum zone. Deep-Sea Res. I 42, 93–115.

Wood, S., Johansen, K., 1972. Adaptation to hypoxia by increased HbO_2 affinity and decreased red cell ATP concentration. Nat. New Biol. 237, 278–279.

Woodhead, P.M., Hamukuaya, H., O'Toole, M.J., McEnroe, M., 1998. Effects of oxygen depletion in shelf waters on hake populations off central and northern Namibia. In: Shannon, V., O'Toole, M.J. (Eds.), International Symposium, Environmental Variability in the South East Atlantic. National Marine Information and Research Centre, Namibia.

Wosnitza-Mendo, C., Espino, M., 1986. The impact of El Niño on recruitment of the Peruvian hake (*Merluccius gayi peruanus*). Meeresforsch 31, 47–51.

Wu, R.S.S., 2002. Hypoxia: from molecular responses to ecosystem responses. Mar. Pollut. Bull. 45, 35–45.

Wu, R., 2009. Effects of hypoxia on fish reproduction and development. Fish Physiol. 27, 79–141.

Wyrtki, K., 1962. The oxygen minima in relation to ocean circulation. Deep-Sea Res. I 9, 11–23.

Wyrtki, K., 1966. Oceanography of the eastern equatorial Pacific Ocean. Oceanogr. Mar. Biol. 4, 33–68.

Yang, T.H., Lai, N.C., Graham, J.B., Somero, G.N., 1992. Respiratory, blood and heart enzymatic adaptations of *Sebastolobus alascanus* (Scorpaenidae: Teleostei) in the oxygen minimum zone: a comparative study. Biol. Bull. 183, 490–499.

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CHAPTER 3

Deep-sea demersal fish communities in the Gulf of California and their relationship with temperature, oxygen, latitude, and depth

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Abstract

Understanding the vulnerability of deep-sea communities to climate change is challenging due to the difficulties of conducting community-level manipulative experiments in the deep sea. A natural laboratory approach, based on comparisons of community structure across oceanographic gradients, can be a valuable tool. The Gulf of California presents an ideal system for examining relationships between faunal patterns and environmental conditions because deep-sea conditions change from warm and oxygen-rich in the north to cold and severely hypoxic in the south. The MBARI remotely-operated vehicle (ROV) *Doc Ricketts* was used to conduct seafloor video transects at depths of ~200-1400 m in the northern, central and southern Gulf. Demersal fish community composition, density, and diversity were compared to environmental conditions. We tested the hypothesis that climate-relevant variables (temperature and oxygen) have more explanatory power than static variables (latitude and depth) in explaining variation in fish community structure. Temperature best explained variance in density, while oxygen best explained variance in diversity. Both density and diversity declined with decreasing oxygen, but diversity declined at a higher oxygen threshold (~7 μmol kg^{-1}). Remarkably high density fish communities were observed living under suboxic conditions (< 5 μmol kg^{-1}). Using an earth systems global climate model forced under an RCP8.5 scenario, we found that by 2081-2100 the entire Gulf of California seafloor is expected to experience a mean temperature increase of 1.08 +/- 1.07°C and modest deoxygenation. We expect projected changes in temperature and oxygen will be accompanied by changes in deep-sea demersal fish communities and reduced species diversity.

Introduction

Climate change is leading to warming ocean temperatures, decreasing pH, and decreasing oxygen concentrations (Bopp et al. 2013, Pörtner et al. 2014, Breitburg et al. 2018), including in the deep sea (Mora et al. 2013, Sweetman et al. 2017). Consequently, there is a critical need to understand organismal and ecosystem sensitivities to climate variables. While carefully-controlled manipulative laboratory experiments provide important insight into the physiological sensitivities of animals, they have several limitations. Specifically, experiments are usually short relative to the life of the animal, represent an acute change, and focus only on the physiological responses while de-coupling ecological relationships that play an important role in fitness. Deep-sea animals present an additional challenge, due to the difficulties of recovering healthy animals from depth and performing experiments under appropriate pressures.

On continental margins, steep natural gradients in climate-relevant variables exist with depth. By sampling communities across spatial and vertical physicochemical gradients of interest, researchers can examine how environmental conditions correlate with differences in community ecology. This approach, termed the natural laboratory approach, can also allow for the identification of important thresholds, both for community metrics and for individual species, which can later be tested using manipulative, controlled laboratory experiments and applied to predictive climate change models (Sperling et al. 2016).

Oceanography of the Gulf of California

The broad range of hydrographic conditions in the Gulf of California make it an ideal study system for utilizing a natural laboratory approach to explore the relationship between climate variables and the structure of marine communities. Conditions change from a warm, oxygen-rich environment in the northern Gulf to a cold, severely-hypoxic environment in the southern Gulf. These regions decouple environmental temperature, oxygen, and depth across relatively short latitudinal (~1126 km) and vertical (~1400 m) distances. In comparison, similar changes in environmental conditions would not be captured even across a much larger latitudinal range from northern Washington State to the Pacific tip of Baja California.

The Gulf of California has some of the world's greatest environmental extremes for a body of water, including a large seasonal temperature flux, a pronounced oxygen minimum zone (OMZ), and an extreme tidal range in the upper Gulf (Roden 1964, Álvarez-Borrego 1983). These large differences in temperature and oxygen between the north and south were first described during the 1939 *E.W. Scripps* Expedition (Sverdrup 1941). Due to widespread upwelling of nutrient-rich water, the Gulf is also a very productive body of water (Espinosa-Carreón & Escobedo-Urías 2017). The oceanography of the Gulf has been extensively reviewed (Roden 1964, Álvarez-Borrego 2010) and here will be briefly described as it relates to this study.

The Gulf of California is relatively young, first appearing in the late Miocene (8.3-6.5 Ma) as the result of a tectonic structural rift (Ledesma-Vásquez & Carreno 2010), and is characterized today by a series of basins and sills (van Andel 1964). Alluvial deposits from the Colorado River have filled the northern part of the Gulf, resulting in a relatively shallow, smooth concave seafloor (Moser et al. 1971). The Salsipuedes Basin (also known as the Ballenas Channel) is an exception and represents a deep basin in the northern Gulf. It is characterized by high temperatures, salinities, and oxygen at great depths due to mixing by strong tidal currents and isolation from the rest of the deep Gulf of California by a submarine ridge (Sverdrup 1941, Roden 1964, Álvarez-Borrego 1983). Due to the isolation of the Salsipuedes Basin, dramatic differences in temperature and oxygen are evident, compared to the same depths south of the submarine ridge (Sverdrup 1941, Roden 1964).

The water in the central and southern regions of the Gulf is in communication with the Pacific and has the properties of Equatorial Pacific water (Sverdrup 1941, Roden 1964). The southern Gulf of California has one of the most extreme and thick oxygen minimum zones (OMZs) ($O_2 < 22.5$ μmol kg^{-1}) in the world, with severely hypoxic conditions extending from shallower than 100 m to deeper than 1200 m, and nearly anoxic conditions are found within the OMZ core (Hendrickx & Serrano 2014). The core of the OMZ is defined as the region where the lowest oxygen levels are observed; oxygen levels increase shallower and deeper than this core region.

Ichthyofauna of the Gulf of California

The Gulf of California ichthyofauna is composed of a mixture of northern and southern eastern Pacific species, as well as several both widespread and endemic species (Walker 1960, Hastings et al. 2010). Overall, the fish fauna of the Gulf is mainly tropical or Panamic (Walker 1960), with 87% of known Gulf fish species reported from areas south of the Gulf in the eastern tropical Pacific (Hastings et al. 2010). The Macrofauna Golfo project, a ten-year effort to compile comprehensive species data for the Gulf of California identified 911 species of fishes living within the Gulf, including 3 myxinids, 87 species of cartilaginous fish, and 821 species of ray-finned fishes (Hastings et al. 2010). Several studies have described shallow water and shelf fish communities in the Gulf (Walker 1960, Thomson & Eger 1966, Thomson et al. 2000, Hastings et al. 2010) and deep-sea midwater fish communities

(Lavenberg & Fitch 1966, Robison 1972, Brewer 1973, De la Cruz-Agüero & Galván-Magaña 1992). However, the ecology of the deep-sea demersal fish community remains virtually undescribed in the English scientific literature though several valuable Spanish language references exist (López-Martínez et al. 2012, Del Moral-Flores et al. 2013, Mejía-Mercado et al. 2014, Zamorano et al. 2014).

Relationship between Oceanographic Variables and Community Characteristics

Understanding how oceanographic conditions affect species distributions and community structure is a key goal of ecological studies, and is especially timely now that environmental conditions are rapidly changing due to anthropogenic activities. In this study, we seek to differentiate the explanatory power of "static" variables such as depth and latitude in explaining trends in demersal fish community structure, from "climate-relevant" variables such as temperature and oxygen that are changing with climate change (Pörtner et al. 2014). If static variables are more highly correlated with community trends, then deep-sea communities may be relatively insensitive to climate change. However, if climate-relevant variables are more highly correlated with existing community trends, then deep-sea communities may show strong responses to changing environmental conditions in the future.

Depth, latitude, temperature, and oxygen all have the potential to influence the structure of deep-sea demersal fish communities in the Gulf of California. Faunal differences between the northern, central, and southern Gulf have been identified by the Macrofauna Golfo project (Brusca & Hendrickx 2008, Hastings et al. 2010) and are likely to also be evident in deep-sea communities. Hydrostatic pressure, which is the only environmental variable directly related to depth, may explain depth zonation trends due to pressure adaptation limits across species (Carney 2005, Brown & Thatje 2014). Demersal fishes show depth-related declines in metabolic enzyme activity that cannot be explained solely as a function of mass or habitat temperature (Drazen et al. 2015). However, the explanatory power of depth may be reduced on upwelling margins with strong hydrographic gradients (Sperling et al. 2016).

Temperature is considered by some to be most strongly associated with species zonation (Carney 2005), due in part to the strong influence of temperature on metabolic rates, termed the Q_{10} effect. Temperature and diversity may also be related through the *metabolic niche hypothesis*, which posits that warmer temperature environments may positively influence diversity by allowing a greater range of energetic lifestyles (Clarke & Gaston 2006). In the Barents Sea, temperature and depth were found to both be significant explanatory variables for trends in demersal fish density and diversity, with density positively related to temperature, while diversity was negatively correlated with temperature (Johannesen et al. 2012).

Oxygen minimum zones (OMZs) are known to influence the composition and diversity of demersal fish communities (Gallo & Levin 2016), however research for the Gulf of California is limited. Along the US West Coast, demersal fish catch and species richness have been found to exhibit significant and positive relationships with near-bottom oxygen concentrations (Keller et al. 2015), with an apparent threshold effect observed under hypoxic conditions, where small decreases in oxygen were associated with large decreases in total catch and species richness (Keller et al. 2017). The oxygen conditions found in the southern and central Gulf of California are some of the most extreme in the world, and are known to exclude most invertebrate species (Zamorano et al. 2007, Hendrickx & Serrano 2014). On average, demersal fish have been found to have higher oxygen requirements than benthic invertebrates (Vaquer-Sunyer & Duarte 2008), so we hypothesize that most demersal fish will be excluded from suboxic benthic environments ($O_2 < 5$ µmol kg^{-1}) in the Gulf, where the core of the OMZ intercepts the margin.

In this study, we make use of the strong hydrographic differences in the Gulf of California, to assess the relative explanatory power of these environmental variables in explaining variation in deep-sea demersal fish composition, density, and diversity. We hypothesize that “climate-relevant” variables will have higher explanatory power than “static” variables in explaining community trends.

The objectives of this research are to: 1) describe the bathymetric and latitudinal zonation of the deep-sea demersal fish community in the Gulf of California; 2) identify which environmental variables best describe variance in fish density, diversity, and community composition and identify threshold responses if they exist; 3) determine if demersal fish are excluded from certain habitats in the Gulf due to the extreme hypoxic conditions; and 4) consider the response of the fish community to climate change model projections for the Gulf of California.

Materials and Methods

On the 4th leg of the MBARI Gulf of California 2015 research cruise on the *R/V Western Flyer*, the remotely operated vehicle (ROV) *Doc Ricketts* was used to conduct eight dives at five locations to study benthic and demersal communities: Salsipuedes Basin, San Pedro Mártir Basin, Isla Tortuga, Cerralvo Trough, and Cabo Pulmo (listed respectively from the most northern to the most southern location in the Gulf) (Fig. 3.1, Table 3.1). The ROV was equipped with a CTD, transmissometer, and oxygen optode, and temperature, pressure, salinity, and oxygen data were collected continuously during all dives. The ROV was equipped with seven cameras, and video footage was continuously recorded from the science camera with lasers used for scale. The video footage was annotated post-cruise using the Video Annotations and Reference System (VARS) (Schlining & Stout 2006). With the use of the ROV manipulator arm and suction hose, 40 fish specimens were collected to aid in species identification of the fish observed in the transects. However, not all unique fish species observed during dives were captured. Fish specimens were immediately frozen or preserved in either ethanol or formaldehyde and were identified by HJ Walker at the Scripps Institution of Oceanography Pelagic Vertebrates Collection.

Morphological Species Identification

To assist with species identification of the collected specimens, as well as images from the video footage, we used the following identification keys for the following groups: ogcocephalids (Bradbury 1999), ophidiiformes (Nielsen et al. 1999), scyliorhinids (Springer 1979), batrachoidids (Walker & Rosenblatt 1988), and others from the eastern tropical Pacific (Fischer et al. 1995a,b). We have high certainty that identification of all collected specimens is correct, however, it is likely that during the annotation of the video, certain cryptic species may have been encountered which may not be correctly identified. The species richness determined from the video analysis should thus be considered conservative, and the true number of unique species is likely a modest amount higher. To reduce error in species annotations, the first author conducted the video annotation, and the second author checked all annotations. All collected specimens were deposited in the Scripps Institution of Oceanography Vertebrates Collection.

Molecular Species Identification

To confirm species identifications, small tissue samples were collected from captured specimens that were either frozen or fixed in 95% ethanol. To take the tissue samples, a small piece of skin on the dorsal side was removed and a section of underlying white muscle (~5-10 mg) was excised. Ethanol-preserved samples were first washed several times with molecular-grade water to remove excess ethanol. A Chelex preparation was used to break down the tissues and release DNA (Walsh et al. 2013). This included adding 180 μL of a 10% Chelex solution to each tissue sample, vigorously vortexing the samples twice for 30 seconds at a time, boiling samples at 100°C on a hot plate for 10 min, and then putting samples on ice. A 1 μL aliquot was collected from each extraction and used in a PCR reaction.

Mitochondrial cytochrome oxidase c subunit 1 gene and 16S ribosomal rRNA gene were amplified for molecular identification of collected specimens. For most the specimens, COI VF1 forward primer (5′-TTCTCAACCAACCACAAAGACATTGG-3') and COI VR1 reverse primer (5′-TAGACTTCTGGGTGGCCAAAGAATCA-3′) (deWaard et al. 2007) were used for the CO1 gene, and 16Sar forward primer (5'-CGCCTGTTATCAAAAA CAT-3') and 16Sbr reverse primer (5'-CCGGTCTGAACTCAGATCACGT-3') (Palumbi 1996) were used for the 16S gene. For the rockfish, *Sebastes*-specific CO1 primers, modified from Ward et al. (2005) by J. Hyde (NOAA SWFSC) were used (F: 5'-TCWACCAACCA CAAAGAYAT YGGCAC-3', R: 5'-TARACTTCWGGGTGRCCRAAGAATCA-3'). Following amplification, an aliquot was run out on a gel, and the remaining PCR product was cleaned using a Sephadex G50 fine spin column and then quantified on a Nanodrop spectrophotometer. Samples were sequenced by Retrogen Inc (San Diego, CA). Recovered sequences were manually edited in Sequencher and compared to other sequences entered into NCBI GenBank for species matches by BLAST searches.

Transect Design

Video footage was collected during all dives, representing 60 hours of video footage total, and all available footage was annotated for fish observations. As the ROV transited upslope from depths of ~1400-200 m, a series of standardized ~100 m long benthic transects were conducted to allow for a quantitative analysis of differences in fish density, diversity, and community composition. To allow for sizing, parallel lasers were turned on during all video transects and were 29 cm apart. Transects used in this study to quantify the fish community were separated by close-up transects that are not quantified in this study. A total of 88 transects were conducted, with ~7-21 transects conducted per dive (Table 3.1). We acknowledge some pseudoreplication, in that transects obtained from a single dive are not entirely independent. No quantitative transects were obtained during Dive 733 in the Salsipuedes Basin due to extremely strong current conditions and poor visibility, but noteworthy qualitative observations are reported.

Fish densities (fish m^{-2}) were calculated for all transects by dividing the number of fish observed in each transect by the area traversed during each transect. Transect length was determined by calculating the distance between the start and end coordinates of each transect and using the hypotenuse cumulative distance formula. For each transect, several screenshots were taken that were representative of the field of view for that transect. These screenshots were then used for sizing by calculating the horizontal field of view in ImageJ using the known distance between laser points (29 cm) as a reference. The field of view was then averaged across all images taken for that transect, and the average field of view was multiplied by the distance traversed to calculate an area for each transect. The average horizontal field of view for all transects was 3.57 m +/- 0.72 m (SD), and ranged between 2.31 and 6.37 m. Fish were only counted if they were within the image frame when they passed the lasers (midpoint of the frame). If fish were originally within the image frame but swam out due to potential ROV avoidance prior to passing the midline of the frame, they were still counted. Behavioral avoidance or attraction to the ROV was rarely observed.

Data Analysis and Statistics

For each transect, fish community composition, density, and diversity were determined. Shannon-Wiener diversity (H_{ln}) was calculated as a metric of community diversity. We used Similarity Percentage analysis (SIMPER) in the multivariate statistical analysis software package PRIMER v.6 (Clarke & Gorley 2006) to evaluate differences in community composition both within and between regions using a Bray Curtis similarity matrix on square-root transformed fish count data. SIMPER was also used to assess contributions of specific taxa to community similarity across regions. A cluster analysis, using group-average linkage, was performed using the same resemblance matrix used for the SIMPER analysis to visualize grouping of transects by community similarity. Analysis of similarities (ANOSIM) in PRIMER v.6 was used to conduct pairwise tests of significance across regions. Dives were categorized as northern (Dives 733 and 735), central (Dives 731, 732, 734, and 736), or southern (Dives 737 and 738) in accordance with the biogeographic province regions identified by the Macrofauna Golfo project (Brusca & Hendrickx 2010, Hastings et al. 2010).

The R statistical package “vegan” (Oksanen et al. 2017) was used for all subsequent multivariate analyses. To visualize differences in community similarity and how these related to environmental variables, we used a non-metric multidimensional scaling (nMDS) ordination technique based on a Bray-Curtis dissimilarity matrix, using square-root transformed fish count data from each transect (n=87). To determine how environmental variables correlated with differences in community composition, we employed a canonical correspondence analysis (CCA) (ter Braak 1986) on square-root transformed fish count data from each transect (n = 87). A CCA was used because species abundances often have a unimodal relationship to environmental variables for which a CCA approach is suitable (ter Braak & Verdonschot 1995). We tested the amount of inertia in our species distribution matrix that was explained by four environmental factors: temperature, oxygen, depth, and latitude. Variance inflation factors (VIFs) were checked and all were below 12. The significance of the CCA model, environmental variables, and selected axes were then tested with an ANOVA.

Generalized additive models (GAMs) were used to explore the relationship between environmental variables and the density and diversity of demersal fish communities. GAMs were chosen because they are better able to model nonlinear relationships than traditional regression analysis due to the use of non-parametric smoothers (Hastie & Tibshirani 1986) and have been used successfully to model the relationship between near-bottom environmental conditions and demersal fish catch per unit effort (CPUE) and species richness (Keller et al. 2017). Near-bottom ROV measurements of temperature, dissolved oxygen, bottom depth, and latitude were included as explanatory environmental variables in the model. We only selected environmental variables that we hypothesized could have a relevant physiological and ecological influence on fish communities, so did not include salinity (which only ranged between 34.5-35.0 psu). The response variables of interest were fish density (fish m^{-2}) and fish assemblage diversity (H'). To meet the assumptions of normality, density data were first log-transformed. To do so, one transect that had a fish density of zero, was modified to a fish density of 0.00001 fish m^{-2}. No transformation was needed for the diversity data. The "mgcv" R package (Wood 2017) was used for the GAM analyses, and thin plate regression splines were used to fit the data.

The same model structure was initially applied to both density and diversity data:

$$\text{Log(Density)} = s1(\text{Latitude}) + s2(\text{Temperature}) + s3(\text{Oxygen}) + s4(\text{Depth})$$

$$\text{Shannon's } H' = s1(\text{Latitude}) + s2(\text{Temperature}) + s3(\text{Oxygen}) + s4(\text{Depth})$$

Variables that were found to be non-significant ($p > 0.05$) were removed if the model performance was improved following removal of the non-significant variables. Akaike's information criteria (AIC) was used to evaluate a suite of models and select the most parsimonious model, based on the lowest AIC value. Model fit was also evaluated through percent deviance explained and generalized cross-validation (GCV). Component plots of the GAM results were visualized using the "visreg" package in R (Breheny & Burchett 2017).

When strong threshold responses were observed from the GAM outputs, we used a broken-stick model in R-package "segmented" (Muggeo 2008) to identify the environmental thresholds of interest. Threshold responses were identified when an abrupt change in density or diversity was observed corresponding to a small change in the environmental variable of interest.

Climate Model Projections for the Gulf of California

The availability of regional climate projections for the Gulf of California is limited, with studies focusing more on upper water column changes (Lluch-Cota et al. 2010). To explore benthic impacts, we used a fully coupled, 3-D earth system model, Max Planck Institute's (MPI) ESM-MR (Giorgetta et al. 2013), to project changes in bottom temperature and dissolved oxygen under a representative concentration pathway RCP8.5 scenario, representing unchecked emissions growth. We choose MPI-ESM-MR because it has the highest spatial resolution (802 x 404) among all models within the Coupled Models Intercomparison Project Phase 5 (CMIP5), and therefore, was suitable for our regional-scale analysis. All climate projection data were download from the Earth System Grid Federation (ESGF) Peer-to-Peer (P2P) enterprise system (https://esgf-node.llnl.gov). Monthly projected temperatures were first averaged by year and then the yearly temperature and dissolved oxygen were averaged between 1951 and 2000 and between 2081 and 2100. We retained the bottom-most grids among the depth layers of decadal averages and then interpolated the raster layers to 10 arc-minute (approximately 0.167 arc-degree) grids by inverse distance weighting. The interpolated raster layers (georeferenced by latitude and longitude) were projected to cylindrical equal-area projection before cell statistics computation (e.g. mean, standard deviation, etc.). The geostatistical analyses used R packages "raster" (Hijmans 2016), "gstat" (Gräler et al. 2016), "sp" (Bivand et al. 2013) and "maptools" (Bivand & Lewin-Koh 2017).

Results

Environmental differences between the northern, central, and southern Gulf of California

The oceanography of the Gulf of California, hereafter referred to as the Gulf, varies dramatically between the northern and southern region. Profiles generated from the environmental sensors on the ROV (Fig. 3.1) show that the stations at the southern end of the Gulf (Cabo Pulmo and Cerralvo Trough) were characterized by a thick and intense oxygen minimum zone (OMZ), where oxygen levels drop below 22.5 μmol kg^{-1} by ~100 m and do not recover above these low levels until ~1250 m. In these locations, the OMZ core is situated between 300-700 m and the conditions are nearly anoxic, with oxygen concentrations <1 μmol kg^{-1}. The lowest oxygen concentrations encountered were 0.5 μmol kg^{-1} during dive 738 off Cabo Pulmo. Temperature decreases with increasing depth and temperatures range between ~6-14 °C in the OMZ. At the central Gulf stations, the OMZ (O_2 < 22.5 μmol kg^{-1}) begins at deeper depths (~275 m) and extends deeper (~1400 m) than at the southern stations. The core region is thinner (600-700 m), but conditions are still nearly anoxic in the core (<1 μmol kg^{-1}). The temperature profile is like that of southern stations and the temperature range of the OMZ is ~3-12 °C.

In contrast to the southern and central region, the northern Gulf is characterized by a warmer, more oxygenated water column that is well-mixed due to strong tides that propagate through the narrow and deep Salsipuedes Basin. Profiles collected during the ROV dive show a well-mixed water column below 250 m, with almost no change in oxygen concentration or temperature between 250-1500 m (Fig. 3.1). Oxygen concentrations are >30 μmol kg^{-1} and temperatures are between 11-12°C across this depth range. At 1000 m, temperatures were

~7°C warmer and oxygen conditions were ~26 µmol kg^{-1} higher in the northern Gulf, than at similar depths in the central and southern Gulf.

Gulf of California Deep-Sea Demersal Fish Community

Forty-eight demersal fish species were observed during the ROV dives (Table 3.2, Appendix Supp. 1). However, this number is likely conservative as cryptic species may have been present that are indistinguishable using ROV video alone. For example, several deep-water macrourid species were grouped as *Macrouridae spp.* due to the difficulty of distinguishing grenadier species using ROV video alone. These include *Coryphaenoides capito* and *Nezumia liolepis,* and may include *Nezumia convergens* and *Coryphaenoides anguliceps* which were captured along with *C. capito* and *N. liolepis* by Zamorano et al. (2014).

With the use of the ROV manipulator arm and suction hose, 40 fish specimens were collected. Based on the morphological and genetic information, we could confirm that these represented 20 distinct species (indicated in Table 3.2). Selected images of collected specimens are provided (Appendix Supp. 2). We successfully sequenced 70% of the species collected (14/20) for mitochondrial cytochrome oxidase c subunit 1 (CO1) gene, but only 30% (6/20) for 16S ribosomal rRNA gene (16S). We were consistently unable to sequence the collected macrourids for either CO1 or 16S: specimens of all three macrourid species collected (*Nezumia liolepis*, *Coryphaenoides capito*, *Coelorinchus scaphopsis*) failed to amplify in the PCR reaction.

Northern Gulf of California

High current conditions encountered during dive 733 in the Salsipuedes Basin only allowed for qualitative observations. The community observed on this dive was composed of *Sebastes cortezi, Eptatretus sinus*, *Parmaturus xaniurus*, and *Hydrolagus colliei*. At this site, *S. cortezi* was observed at deeper depths than expected (1126-1448 m). Fishes were observed either hiding among the rocks (*E. sinus* and *S. cortezi*) or swimming actively against the strong current (*P. xaniurus* and *H. colliei*).

The quantitative transects for the northern region are restricted to those collected during dive 735. Similar to dive 733, the deep-water community (> 700 m) here was characterized by *S. cortezi* (Fig. 3.2 D), *E. sinus* (Fig. 3.2 C), *P. xaniurus*, and *H. colliei*. *Symphurus spp.* were observed here at deeper depths than expected and had a broad depth range (289-1010 m). One was collected allowing us to confirm the species identification as *Symphurus oligomerus* (Table 3.2). *Sebastes spp.* were also observed across a broad depth range during this dive (242-1009 m), and included *S. cortezi* and *S. exsul*. *E. sinus* was also observed across a broad depth range (390-1080 m). Shallower than 786 m, the macrourid (*Coelorinchus scaphopsis*) was observed in open sandy areas and became a common member of the fish community (~50% community composition) (Fig. 3.2 B). At the shallowest depths (200-400 m), the fish community was dominated by *C. scaphopsis* (~48%), *Pontinus furcirhinus* (~22%) (Fig. 3.2 A), and *Physiculus rastrelliger* (9%). Rare species observed during this dive include *Paralabrax auroguttatus*, *Gnathophis cinctus*, *Ophichthus frontalis*, and others shown in Table 3.2.

Central Gulf of California

Four dives (731, 732, 734, and 736) in two locations, near Isla Tortuga and San Pedro Island, were used to characterize the central Gulf deep-sea demersal fish community. The deep-water community (>1000 m) was dominated by *Bathypterois sp.* (41%) (Fig. 3.2 H), *Macrouridae spp*. (36%), and *Lycenchelys spp.* (10%). At intermediate depths (600-1000 m), the central community was dominated by *Cherublemma emmelas* (~43%) and *Cephalurus cephalus* (~40%) (Fig. 3.2 G). Unlike the northern Gulf, *E. sinus* was absent in deep-water, but was present at shallower depths (<500 m). Shallower than 500 m, *P. rastrelliger* (~18%) (Fig. 3.2 E), *P. furcirhinus* (~16%), *Sebastes spp.* (~15%), *E. sinus* (~15%), and *Bathycongrus macrurus* (~10%) (Fig. 3.2 F) dominated the fish community. Rarer species (<10%) included *Dibranchus spp.*, *Eknomoliparis chirichignoae*, *Paraliparis rosaceus*, *Liopropoma longilepis*, *Sebastes macdonalldi*, *Xeneretmus ritteri, Chilara taylori*, and others (Table 3.2). A previous record of *C. taylori* from the Gulf of California was considered doubtful (Nielsen et al. 1999), but the three observations of *C. taylori* confirm that this species' range extends into the central Gulf.

We did observe some noteworthy differences in the fish communities in the central region. While during dive 734, *C. scaphopsis* were common members (~36%) of the shallow (200-400 m) community, they were rare (< 5%) during dive 736 and were absent in the more southern dives 731 and 732. Therefore, there may be a latitudinal break in the distribution of *C. scaphopsis* between 27-28°N. Dive 736 also differed from the other three dives in the central region by the high abundance of *E. sinus* (~36%), *Sebastes spp.* (~31%), *P. xaniurus* (~11%), and *H. colliei (*~7%) observed in shallower areas (300-400 m). This difference in community composition may be influenced by the benthic habitat encountered during this dive, which was primarily a boulder field.

While *Sebastes spp.* are thought to be relatively hypoxia intolerant (McClatchie et al. 2010), in the central Gulf, *S. cortezi* was observed living in deep-water areas under severely hypoxic conditions (1.83-7.61 µmol kg^{-1}). To our knowledge, these represent the lowest oxygen records for a rockfish species.

Southern Gulf of California

Similar to the central Gulf, the deep-water community (>1000 m) in the southern Gulf was dominated by *Macrouridae spp.* (29%) (Fig. 3.2 K), *Bathypterois sp.* (~26%), and *Lycenchelys spp.* (16%). Rarer species included *Dibranchus spp.* (10%) (Fig. 3.2 L), *Eretmichthys pinnatus* (8%), and *Dibranchus spinosus* (6%). At shallower depths (400-900 m), *C. emmelas* dominated the fish community (63%) (Fig. 3.2 J), and co-occurred with *Macrouridae spp.* (~19%) and *D. spinosus* (~6%) within the deeper portion of its depth range (700-900 m). Midwater myctophids and bathylagids were also observed swimming directly into the seafloor between (400-700 m). Shallower than 400 m, the demersal fish community was dominated by *B. macrurus* (38%), *Porichthys mimeticus* (23%), and *Pontinus sierra* (~15%) (Fig. 3.2 I). *C. scaphopsis*, a very common member of the shallow water community in the more northern sites, was completely absent in the south. Similarly, *Sebastes spp.* were completely absent in the south.

Community Similarity for the Northern, Central, and Southern Gulf of California

Similarities and differences in community assemblages were visualized using a nMDS plot (Fig. 3.3), shown with overlain environmental contours in Supplementary Item 3 (Appendix). Demersal fish communities differed significantly by region (ANOSIM, Global R

= 0.17, $p < 0.01$) and all pairwise comparisons were also found to be significant (ANOSIM, $p < 0.01$). The northern assemblages group together and show no overlap with any of the southern assemblages. Overall, the central Gulf has the highest community heterogeneity. Assemblages in the southern Gulf also show high heterogeneity, though they are more homogeneous than fish assemblages in the central Gulf. Central communities cluster with both northern and southern communities, but northern and southern communities are distinctly separate (Fig. 3.3, Appendix Supp. 4).

By analyzing the quantitative transects with SIMPER, we found that community similarity was highest (35%) for the northern Gulf, lowest (15%) for the central Gulf, and intermediate for the southern Gulf (27%). For the northern sites, *S. cortezi* and *C. scaphopsis* contributed the most (79%) to community similarity. *C. emmelas* and *Macrouridae spp.* contributed the most to community similarity (55%) for the southern region. Southern and northern demersal fish communities had very high average dissimilarity (99%) and only shared three species: *E. sinus*, *Lophiodes caulinaris*, and *P. rastrelliger*. Average dissimilarity between northern and central communities was 89%; similar to the dissimilarity between central and southern communities (88%). The species that contributed the greatest to the dissimilarity between northern and central sites were *C. scaphopsis* and *S. cortezi* which were more abundant in the northern transects. The species that contributed the greatest to the dissimilarity between the central and southern sites were *C. emmelas* and *Macrouridae spp.* which were more abundant in the southern transects.

Relationship between Environmental Variables and Demersal Fish Community Composition, Density, and Diversity

To address how environmental conditions contributed to the observed differences in community similarity, we utilized a canonical correspondence analysis (CCA). We found that temperature, oxygen, depth, and latitude were all highly related to differences in community composition ($p < 0.001$) (Appendix Supp. 5), and the resultant model was statistically significant ($p < 0.001$) and able to constrain 25.7% of the inertia in the species matrix. We suspect that other abiotic factors not considered in the model, such as benthic habitat type, may be particularly important in explaining the remaining variance in community composition.

In addition to understanding how environmental variables relate to community composition, we were also interested in how fish community density and diversity relate to environmental conditions. Using generalized additive models (GAMs), we found that the tested explanatory variables (oxygen, temperature, depth, and latitude) could explain a high amount of the variance for both density and diversity trends, but that the importance of specific environmental variables differed for these two community metrics.

For density, we found that temperature, latitude, and oxygen were all significant explanatory variables ($p < 0.001$), able to explain 59% of the variance in fish community density (Table 3.3). In contrast, depth was not a significant predictor of density trends ($p = 0.91$) (Table 3.3). Fish density was higher in lower latitudes and density exhibited a threshold response to environmental oxygen with fish density decreasing once environmental oxygen became too low (Fig. 3.4). Temperature had the highest explanatory power, and could explain 32% of the variance in fish densities, followed by latitude, and finally oxygen, which alone only explained ~4% of the variance (Table 3.3). Component plots show the predicted relationship between the explanatory variables and fish density for the resultant model (Fig.

3.4), and component plots with two predictors were made to visualize a possible interaction between temperature and oxygen (Appendix Supp. 6).

Similar to the results for density, we found that depth had no explanatory power for trends in community diversity ($p = 0.56$) (Table 3.4). In contrast, while temperature had the highest explanatory power for trends in fish density, it had limited explanatory power for trends in fish diversity ($p = 0.39$). The most parsimonious model ($\Delta AIC=0$), included only oxygen and latitude as explanatory variables, and could explain 57% of the variance in fish community diversity. Oxygen had the highest explanatory power and could explain 52% of the variance in fish community diversity. Component plots for oxygen and latitude are shown (Fig. 3.5). Diversity showed a strong threshold response to environmental oxygen with diversity decreasing sharply once oxygen levels became too low.

Since both fish density and diversity showed a nonlinear relationship with oxygen and appeared to exhibit a threshold response, we used a segmented regression model to identify the oxygen concentration under which strong changes in fish density and diversity were observed. In both cases, the segmented regression model identified a statistically significant threshold ($p = 0.05$ for density and $p < 0.001$ for diversity). The oxygen threshold for diversity (6.96 +/- 1.06 μmol kg^{-1}) was twice as high as the threshold for density (3.14 +/- 1.31 μmol kg^{-1}); below these oxygen thresholds, fish density and diversity sharply declined (Fig. 3.6).

Demersal Fish Tolerance to Severe Hypoxia

Conditions were suboxic (<5 μmol kg^{-1}) for nearly half (43/88) of the transects conducted. Despite the severely hypoxic conditions, demersal fish were observed during 87 of

88 transects. The only transect where no fish were observed took place at intermediate depth (354 m) off Cabo Pulmo (Dive 738), and conditions were nearly anoxic (O_2 = 0.74 µmol kg^{-1}) and relatively warm (10.15°C). During all other transects, fish were observed and more than one fish species was present in 90% of transects. The highest density demersal fish community (3.26 fish m^{-2}) was observed during Dive 737 in the Cerralvo Trough at 774 m, under cold (5.94°C) and severely hypoxic (O_2 = 1.61 µmol kg^{-1}) conditions. Nearby transects also had fish densities ~4 times higher (0.46 fish m^{-2}) than the average fish density observed across all the transects in the study (0.11 fish m^{-2}), showing that the Cerralvo Trough supported high fish densities despite the presence of severely hypoxic conditions. Therefore, suboxic environments in the Gulf do not appear to exclude demersal fish.

Two species appear to be specialized to live in the suboxic Gulf environment. These are the ophidiid, *C. emmelas*, and the scyliorhinid, *C. cephalus*. They were consistently observed living under the most extreme hypoxic conditions encountered during this study and neither were observed in the northern Gulf where severely hypoxic conditions are not present. Other species were also present in these suboxic communities, including *D. spinosus* and *N. liolepis*, however they were rarer and their distribution extended into habitats that were deeper and more oxygen-rich (Table 3.2).

Climate Change Projections for the Gulf of California Seafloor

By 2081 to 2100, the Gulf of California seafloor is projected to experience warming up to 3.4°C with a mean temperature increase of 1.08 +/- 1.07°C (Fig. 3.7 A). The strongest warming is projected to occur in the northern Gulf (2.85 +/- 0.52°C), followed by the central (0.87 +/- 0.49°C) and southern Gulf (0.50 +/- 0.68°C). In addition to the projected warming, most of the Gulf seafloor may experience modest deoxygenation with a mean decrease of dissolved oxygen of 0.21 μmol kg^{-1} by 2081 to 2100. However, the standard deviation is almost 16 times the mean, suggesting large spatial variability in dissolved oxygen changes (Fig. 3.7 B). Regionally, the northern Gulf is likely to have the largest variability. Dissolved oxygen may decrease up to 11.55 μmol kg^{-1} at the northern tip of the Gulf near the mouth of the Colorado River but increase up to 15.85 μmol kg^{-1} in the Delfín Basin north of the Isla Ángel de la Guarda. The near-bottom dissolved oxygen concentration in the central and southern Gulf is expected to decline by 0.5 μmol kg^{-1} on average with relatively large standard deviations of approximately 2 to 3 times the mean.

By 2081 to 2100, approximately 14% of the Gulf seafloor will likely have oxygen conditions below the threshold found in this study to correlate with decreases in fish density (black contour line, Fig. 3.7 B). Similarly, 16% of the Gulf seafloor will likely have oxygen conditions below the threshold found in this study to correlate with decreases in fish diversity (red contour line, Fig. 3.7 B). The percentage and coverage of these low oxygen areas were found to be almost identical between 1951 to 2000 and 2081 to 2100 projections with little to no change in dissolved oxygen concentration (Fig. 3.7 B). Despite the stability in size and oxygen concentration, it is worth noting that temperatures in these low oxygen areas are projected to increase by 0.42+/-0.16°C (Fig. 3.7 A).

Discussion

This study provides the first descriptions of the deep-sea demersal fish community in the Gulf of California accompanied by genetic verification, environmental analyses, and climate change projections. It demonstrates that temperature and oxygen have more explanatory power than latitude and depth in explaining variation in fish community composition, density, and diversity. Here we briefly consider how the results of this study compare to previously described bathymetric and latitudinal zonation trends, discuss unique features of the Gulf of California fish community, consider study limitations, and discuss the study implications for predicting climate change impacts.

Latitudinal differences in community composition, density and diversity have previously been described for the Gulf of California. Larval assemblages collected by zooplankton hauls in the northern and central Gulf differed significantly between the northern "island" assemblage and the central "oceanic" assemblage, with the northern assemblage characterized by lower larval abundance and species richness (Ávalos-García et al. 2003). Similarly, overall fish species richness for the Gulf is reported to be twice as high in the south than in the north (Hastings et al. 2010). Our results (Figs. 3.3, 3.4, 3.5) lend support to some, but not all, of these general latitudinal patterns. Deep-sea demersal fish community composition was found to relate to latitude, with significant grouping by region and high community dissimilarity across regions. Trends in density with latitude were also consistent, with average fish densities found to be ~5 times higher in the southern Gulf than in the northern Gulf. However, latitude had less explanatory power than temperature for community density trends (Table 3.3).

In contrast to Hastings et al. (2010), we did not find large differences in fish diversity or species richness between the northern and southern Gulf. Average species richness was slightly higher for the southern Gulf (4.3 species per transect) compared to the northern Gulf (3.5 species per transect), but average Shannon diversity was very similar. Latitude only explained 11% of the variance in fish community diversity (Table 3.4). Previous studies on biogeographic patterns in the Gulf have suggested that differences in diversity between the north and south may be partially driven by the high seasonal temperature variability of the northern Gulf (Roden 1964, Álvarez-Borrego 2010), but this may influence shallow communities more than the deep communities (>200 m) studied here.

Depth (i.e. hydrostatic pressure) was not a significant explanatory factor for demersal fish density and diversity (Tables 3.3 and 3.4). In areas like the Salsipuedes Basin in the northern Gulf, where relatively warm, well-oxygenated conditions are found deep, Parker (1964) noted that virtually no stratification of macroinvertebrates was found: macroinvertebrates generally found from 150-200 m occurred here at depths to 1500 m. Similarly, we observed very limited zonation in the Salsipuedes Basin and found *Sebastes cortezi*, *Eptatretus sp.*, and *Symphurus oligomerus* occupying a broad depth range.

In contrast to the more limited role of latitude and depth in explaining variation in the demersal fish community, we found that oxygen and temperature had high explanatory power. In previous studies, oxygen was found to best explain mollusk community density and diversity trends in the Gulf, compared to depth, epibenthic temperature, sediment texture and organic matter content (Zamorano et al. 2007). While we also found that oxygen had the highest explanatory power for variation in fish diversity, temperature was more strongly correlated with trends in fish density, explaining 32% of the variance.

Both fish density and diversity exhibited a threshold relationship with oxygen, with density and diversity decreasing sharply below a specific oxygen threshold (Fig. 3.6). For the Eastern Pacific macrofauna community, diversity was found to decline sharply at oxygen levels below 7.5 μmol kg^{-1} (Sperling et al. 2016), therefore the oxygen threshold identified here for fish diversity ($O_2 \sim 7 +/- 1$ μmol kg^{-1}) is remarkably similar. In the southern Gulf, oxygen conditions were lower than this identified threshold for 70% of our transects. Consequently, we may not have observed higher fish diversity in the southern Gulf compared to the northern Gulf, in contrast to Hastings et al. (2010), because the negative effect of hypoxia may counteract latitudinal diversity trends for the deep-sea communities in the Gulf.

We found that the threshold response for diversity occurred at an oxygen level twice higher than that for density (Fig. 3.6), suggesting that diversity is more sensitive to low oxygen conditions than density. We hypothesize that this difference may be due to the following succession of hypoxia impacts. Most fish species are intolerant of severely hypoxic conditions; thus, diversity decreases as these species are excluded. These areas then become food-rich, predator-refuges and support high densities of the few tolerant species. Once oxygen levels become too limiting to support even the most highly hypoxia-adapted species, fish density also decreases. It should be noted that this study looks at density and not biomass, which may show a different threshold response with oxygen. Thresholds for decreases in fish diversity and density occurred at much lower oxygen levels than the definition for the OMZ ($O_2 < 22.5$ µmol kg^{-1}), suggesting the need for ecological definitions for oxygen thresholds that correlate with community changes.

Consistent with this, “edge effects” were first used to describe high-density aggregations of benthic marine taxa at the “edge” (i.e. upper and lower boundary) of the OMZ (Mullins et al. 1985, Levin 2003, Jeffreys et al. 2012). In this study, we observed high density aggregations of fish, dominated by *C. emmelas*, within the OMZ, and not at the OMZ “edge”. Similarly, high-density mollusk communities have also been reported in the Gulf at oxygen concentrations of ~5.6 µmol kg^{-1} (0.13 ml L^{-1}) (Zamorano et al. 2007). Fish densities were highest in the Cerralvo Trough (~3.26 fish/m^2, $O_2 = 1.6$ µmol kg^{-1}), where the Trough may have additionally enhanced fish densities, but were also elevated off Cabo Pulmo (~0.24 fish/m^2, O_2 = 1.6 μmol kg^{-1}). Off Hawaii, submarine canyons were found to enhance the abundance of deep-sea demersal fish, however, the enhancing effect was offset when oxygen concentrations fell below ~30 μmol kg^{-1} (0.7 ml L^{-1}) (De Leo et al. 2012). In contrast, in this study, fish densities only decreased when oxygen was below ~3 μmol kg^{-1} (Fig. 3.6). Decreased diversity and high dominance of hypoxia-tolerant species are a consistent characteristic of OMZ communities (Wishner et al. 1990, Levin 2003, Gooday et al. 2010, Gallo & Levin 2016) and these results support this pattern.

While temperature had high explanatory power for explaining variation in demersal fish density in the Gulf, the relationship was not straightforward to interpret. At the lower end of the temperature range (~3-6°C), fish density was positively correlated with temperature. This relationship is consistent to that observed for demersal fish assemblages in the Arctic-Atlantic transition zone across this temperature range (Johannesen et al. 2012). However, at warmer temperatures in the Gulf, this positive correlation appeared to break down, and a noteworthy drop in fish density was observed during transects at temperatures between ~9-11°C (Fig. 3.4). These communities with lower fish densities were encountered as the ROV moved upslope through the OMZ core and temperatures began to increase, but oxygen conditions remained suboxic.

We hypothesize that this decrease in fish density may be due to the interaction of temperature and oxygen in limiting suitable fish habitat. The *oxygen and capacity limited thermal tolerance* (OCLTT) hypothesis (Pörtner et al. 2017) posits that increases in metabolic rate with temperature increase oxygen demand, and can decrease fitness when metabolic demand exceeds oxygen supply capacity. This mismatch between oxygen demand and the capacity for oxygen supply has been implicated in the decrease in abundance of the eelpout, *Zoarces viviparous*, as water temperatures warmed (Pörtner & Knust 2007). When our GAM results are examined using a combined component plot for oxygen and temperature (Appendix Supp. 6), a negative relationship between temperature and fish density is observed at temperatures above ~9.5°C, under low oxygen conditions ($O_2 < 10$ µmol kg^{-1}). It is noteworthy that the only transect in which fish were not observed was characterized by relatively warm (10.15°C) and suboxic ($O_2 = 0.74$ µmol kg^{-1}) conditions. Since fish were observed in several transects where oxygen conditions were lower ($O_2 = 0.52$-0.69 µmol kg^{-1}), but temperatures were colder (7.1-9.0°C), we hypothesize that the combination of warm and nearly anoxic conditions may have excluded fish from this habitat.

Our results suggest that in areas where strong depth zonation has been observed for margin communities, researchers should explore if oxygen and temperature conditions can explain the observed "depth-related" patterns. Sampling across multiple horizontal and vertical scales is necessary to deal with the issue of covariance between depth and temperature. We also note that the local bathymetry and substrate type influenced the ease of observing zonation, with zonation more evident in soft sediment environments compared to rocky reef areas.

Unique Features of the Gulf of California Fish Community

The extensive severely hypoxic conditions present in the Gulf make it a good model system for the study of deep-sea communities living on the metabolic edge. Seventy-seven demersal fish species have previously been described living under severely hypoxic conditions ($O_2 < 22.5$ µmol kg^{-1}) (Gallo & Levin 2016). This study adds an additional 18 species, raising the number of demersal fish species globally known to live in OMZ conditions to 95 (Appendix Supp. 7). This number is likely conservative as many OMZ margins remain poorly studied, but is still a small fraction of the global estimate for deep-sea demersal fishes (3000-4000) (Koslow et al. 1997). Newly added species from this study are: *Dibranchus spinosus*, *Dibranchus hystrix*, *Coryphaenoides capito*, *Bathypterois sp.*, *Eretmichthys pinnatus*, *Bathycongrus macrurus*, *Eptatretus sinus*, *Paraliparis rosaceus*, *Lophiodes caulinaris*, *Lycenchelys spp.*, *Merluccius sp.*, *Physiculus rastrelliger*, *Pontinus furcirhinus*, *Porichthys mimeticus*, *Sebastes cortezi*, *Symphurus spp.*, *Serranidae sp.*, and *Derepodichthys alepidotus*. *C. emmelas* and *C. cephalus* had previously been described living under severely hypoxic conditions in the Gulf (Aguirre-Villaseñor & Castillo-Velázquez 2011, Aguirre-Villaseñor & Salas-Singh 2012). High hypoxia tolerance in the pelagic fish community has also been reported in the Gulf of California, with high larval species richness and abundance described in severely hypoxic areas (Davies et al. 2015).

Several studies have focused on how the OMZ relates to distributions of invertebrates in the Gulf. This study allows a comparison of how fish hypoxia tolerance compares to trends observed for the invertebrate community. While many invertebrates are excluded from the Gulf's severely hypoxic habitats, tolerant species that commonly occur in the OMZ include: the stomatopod shrimp, *Squilla*, galatheid crabs, *Pleuroncodes* and *Munida*, and bivalves, *Dacrydium pacificum* and *Lucinoma heroica*, (Parker 1964, Zamorano et al. 2007). However, even galatheid crabs are impacted by oxygen levels below 4 μmol kg^{-1} (0.1 ml L^{-1}) in the Gulf, and no species of galatheids were recorded living in areas where oxygen content was less than ~2 μmol kg^{-1} (0.05 ml L^{-1}) (Hendrickx & Serrano 2014). In contrast, this study finds that several demersal fish species, including *C. emmelas*, *C. cephalus*, and *D. spinosus*, are capable of living in areas where oxygen content is less than 2 μmol kg^{-1}, suggesting that fish in the Gulf may be more hypoxia tolerant than most crustaceans.

During this study, we observed midwater fish interacting with the seafloor under severely hypoxic conditions. At intermediate depths (~400-800 m) in the southern Gulf, we observed small pelagic fish rapidly swimming down and crashing headfirst into the sediment, before swimming away. Most commonly, these appear to be the deep-sea smelt, *Leuroglossus stilbius*, however we also observed several myctophid individuals interacting with the sediment. Midwater fish that are widespread and abundant in the southern and central Gulf are *Triphoturus mexicanus, Vinciguerria lucetia*, *Diogenichthys laternatus*, and *Leuroglossus stilbius* (Moser et al. 1971). This behavior was most common in the nearly anoxic areas ($O_2 <$ 1 μmol kg^{-1}) in the southern Gulf, and we did not observe this behavior in either the central or northern Gulf. It is unclear if the fish are feeding on the sediment or if they are physiologically impaired by the extreme conditions and exhibiting this odd behavior as a result.

While pleuronectids and paralichthyids are common demersal fish community members along the US West Coast (Keller et al. 2010, 2012) and the Pacific coast of Baja California (Rodríguez-Romero et al. 2008), they were not observed during this study. The only Pleuronectiformes observed were soleids. Consistent with these observations, eggs from pleuronectids were not found in the ichthyoplankton off Cabo Pulmo and paralichthyid species present in the ichthyoplankton all have adult distributions shallower than this study (<200 m) (Ahern et al. 2018). It is unclear why these flatfish appear to be absent from the deep-sea demersal fish community in the Gulf.

A previous study on the Gulf of California ichthyoplankton found that *Sebastes spp.* larvae are concentrated in the northern part of the Gulf and are absent in the southern Gulf (Moser et al. 1971). These results are consistent with our findings that adult *Sebastes spp.* only occur in the northern and central region of the Gulf and are entirely absent from the southern Gulf. Moser et al. (1971) hypothesized that temperature differences were responsible for the observed distribution of *Sebastes* larvae, with the larvae preferring cold water regions around the large islands in the northern Gulf. Examination of the habitat of *Sebastes spp.* found in this study suggests that the previously observed larval distributions are likely explained by the distributions of the adults, since rockfish are live-bearing.

Study Constraints

This study presents a snapshot of the deep-sea demersal fish community in the Gulf of California in late March 2015. However, neither environmental conditions nor biological communities are static. The northern Gulf of California experiences significant seasonality, with shallow-water temperatures ranging by 15°C between January and August (Parker 1964). Temporal oxygen variability has been described for the deep Salsipuedes Basin (Álvarez-Borrego 1983) and the southern Gulf (Roden 1964). The abundance and distribution of midwater and larval fish species in the Gulf is known to vary interannually and seasonally (Moser et al. 1971, Ávalos-García et al. 2003, Sánchez-Velasco et al. 2009). Larvae of several demersal species included in this study (*C. scaphopsis*, *P. rastrelliger*, *C. emmelas*, *Pontinus spp*., *B. macrurus*, and *S. oligomerus*) showed seasonal and interannual changes in abundance in response to La Niña and El Niño events (Sánchez-Velasco et al. 2004). It is unknown if the deep-sea demersal fish community also responds to the pronounced environmental variability in the Gulf, but this would be a valuable area of research in the future.

This study focuses on adult fish that can easily be observed with the ROV. Consequently, we miss the early life stages which are often pelagic and typically found in shallower waters. Understanding the influence of environmental variables on these early life stages is also important in determining how species will fare under climate change scenarios. Studies on larval fish assemblages in the Gulf have found clear relationships between larval assemblages and oceanographic variables (Ávalos-García et al. 2003, Davies et al. 2015). Larvae of demersal fish are often captured and reported in these ichthyoplankton datasets, however are not focused on because they represent a minor component of the community compared to dominant pelagic and midwater species (Moser et al. 1971).

While we did not measure carbonate system parameters in this study, pH conditions are highly positively correlated with oxygen conditions for the Gulf (Álvarez-Borrego 1983). Within the core of the OMZ, where oxygen values are lowest, very low pH values (between 7.63 and 7.66) have been reported (Gaxiola-Castro et al. 1978). In the central and southern Gulf, the water becomes rapidly undersaturated with respect to calcite (300 m) and aragonite (70 m) (Gaxiola-Castro et al. 1978, Álvarez-Borrego 1983). Since oxygen and pH are highly correlated, we cannot state that the relationships found between fish community metrics and oxygen may not also be influenced by carbonate system parameters, and encourage future studies to explore this relationship.

Implications for Climate Change Impacts

Based on the climate change projections for 2100, benthic ecosystems in the deep Gulf of California will likely experience greater stress from warming temperatures than from declining oxygen levels. Regional differences in warming are predicted with the northern Gulf expected to experience the most warming, followed by the central and southern Gulf. The eastern Gulf of California may also experience greater warming and oxygen loss than the western Gulf (Fig. 3.7). The limited projected oxygen decline is somewhat surprising given that the spatial extent of suboxic areas is expected to be highly sensitive to climate-driven oxygen loss (Deutsch et al. 2011). One possible reason for this result may be the model uncertainty and the difficulty of capturing small oxygen changes in areas already low in dissolved oxygen. Despite the limited oxygen decline predicted by the climate model, fish communities may still experience oxygen stress, as warming increases metabolic rates and oxygen demand (Pörtner et al. 2017). Based on our results, communities in the central Gulf may be especially vulnerable to climate-driven metabolic constraints. Currently, oxygen conditions for ~41% of the seafloor area in the central Gulf are lower than the threshold found in this study to correlate with decreases in fish diversity ($O_2 \sim 7$ μmol kg^{-1}), and the central Gulf seafloor is projected to warm by 0.87 +/- 0.49°C by 2100.

Examining the temperature and oxygen niches of species may offer an opportunity to explore species-specific vulnerabilities to climate change and possible metabolic limits on species distributions based on combined temperature and oxygen stress. *C. scaphopsis*, a shallow-water grenadier (220-550 m) common in the northern and upper central Gulf, is absent in the southern and lower central Gulf where severely hypoxic conditions ($O_2 < 10$ μmol kg^{-1}) are present in shallow (200-500 m) areas. If *C. scaphopsis* is restricted to higher oxygen habitats due to a high metabolism, the combination of warming and oxygen loss projected for the northern and central Gulf may result in significant habitat compression for this species. The *metabolic index* has been proposed as a mechanistic framework for understanding marine species distributions, with contemporary distributions limited to areas where the environmental oxygen supply is at least 2-5 times greater than the animal's resting metabolic oxygen demand (Deutsch et al. 2015). Relating projected changes in the metabolic index for the Gulf of California with current environmental niches for demersal fish species may allow for valuable insight into organismal and ecosystem vulnerabilities to climate change.

Conclusions

Oxygen and temperature are highly correlated with trends in deep-sea demersal fish community structure in the Gulf of California. Consequently, climate changes to the oxygen and temperature regimes in the Gulf will likely lead to altered demersal fish community composition, density, and diversity. Near-bottom oxygen is the strongest factor explaining variation in demersal fish community diversity, while temperature has more explanatory power for trends in density. Warming is projected to be more pronounced for the Gulf of California than deoxygenation, and the influence of warming temperatures on metabolic rates may lead to additional oxygen stress for the fish community. Additional factors linked to ocean acidification were not examined but could also contribute to cumulative stress on fishes. We find that several demersal fish species exhibit remarkable hypoxia-tolerance, however, these species are currently of no fisheries value and economically valuable species, such as *Sebastes macdonaldi*, are excluded from severely hypoxic areas. Coupled observations of community trends across natural gradients with climate model projections provide a valuable tool for exploring ecosystem vulnerabilities to climate change. Additional laboratory and geochemical proxy approaches may help to verify the environment-community relationships documented here and generate further mechanistic understanding.

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Literature Cited

Aguirre-Villaseñor H, Castillo-Velázquez R (2011) New depth record of *Cherublemma emmelas*, black brotula (Ophidiiformes: Ophidiidae) from the Gulf of California, Mexico. *Revista Mexicana de Biodiversidad* 82: 713-715.

Aguirre-Villaseñor H, Salas-Singh C (2012) New records of the lollipop catshark *Cephalurus cephalus* (Scyliorhinidae) from the Gulf of California, Mexico. *Revista Mexicana de Biodiversidad* 83: 298-300.

Ahern ALM, Burton RS, Saldierna-Martínez RJ, Johnson AF, Harada AE, Erisman B, Aburto-Oropeza O, Arvizú DIC, Sánchez-Uvera AR, Gómez-Gutiérrez J (2018) Using molecular identification of ichthyoplankton to monitor spawning activity in a subtropical no-take Marine *Reserve. Mar. Ecol. Prog. Ser.* 592: 159-179.

Álvarez-Borrego S (1983) Chapter 17: Gulf of California. Estuaries and Enclosed Seas. Elsevier: 427-449.

Álvarez-Borrego S (2010) Chapter 2: Physical, Chemical and Biological Oceanography of the Gulf of California. The Gulf of California: Biodiversity and Conservation. University of Arizona Press. p. 24-48.

Ávalos-García C, Sánchez-Velasco L, Shirasago B (2003) Larval fish assemblages in the Gulf of California and their relation to hydrographic variability (Autumn 1997-Summer 1998). *Bull. Mar. Sci.* 72(1): 63-76.

Bivand R, Lewin-Koh N (2017) maptools: Tools for Reading and Handling Spatial Objects. R package version 0.9-2.

Bivand RS, Pebesma E, Gomez-Rubio V (2013) Applied spatial data analysis with R. Springer, NY.

Bopp L, Resplandy L, Orr JC, Doney SC, Dunne JP, Gehlen M, Halloran P, Heinze C, Ilyina T, Séférian R, Tjiputra J, Vichi M (2013) Multiple stressors of ocean ecosystems in the 21st century: projections with CMIP5 models. *Biogeosciences* 10: 6225-6245.

Bradbury MG (1999) A review of the fish genus *Dibranchus* with descriptions of new species and a new genus, *Solocisquama* (Lophiiformes, Ogcocephalidae). *Proceedings of the California Academy of Sciences* 51(5): 259-310.

Breheny P, Burchett W (2017). visreg: Visualization of Regression Models. R package version2.4-1.

Breitburg D, Levin LA, Oschlies A, Grégoire M, Chavez FP, Conley DJ, Garçon V, Gilbert D, Gutiérrez D, Isensee K, Jacinto GS, Limburg KE, Montes I, Navqi SWA, Pitcher GC, Rabalais NN, Roman MR, Rose KA, Seibel BA, Telszewski M, Yasuhara M, Zhang J (2018) Declining oxygen in the global ocean and coastal waters. *Science* 359(6371): eaam7240.

Brewer GD (1973) Midwater fishes from the Gulf of California and the adjacent eastern tropical Pacific. *Los Angeles County Museum Contributions in Science* 242: 1–47.

Brown A, Thatje S (2014) Explaining bathymetric diversity patterns in marine benthic invertebrates and demersal fishes: physiological contributions to adaptations of life at depth. *Biol. Rev. Camb. Philos. Soc.* 89(2): 406-426.

Brusca RC, Hendrickx ME (2008) The Gulf of California Invertebrate Database: The Invertebrate Portion of the Macrofauna Golfo Database. http://www.desertmuseum.org/center/seaofcortez/database.php.

Brusca RC, Hendrickx ME (2010) Chapter 4: Invertebrate biodiversity and conservation in the Gulf of California. The Gulf of California: Biodiversity and Conservation. University of Arizona Press. p. 72-95.

Carney RS (2005) Zonation of deep biota on continental margins. *Ocean. Mar. Biol. Ann. Rev.* 43: 211-278.

Clarke A, Gaston KJ (2006) Climate, energy and diversity. *Proc. R. Soc. B* 273: 2257-2266.

Clarke KR, Gorley RN (2006) PRIMER v6: User Manual/Tutorial. PRIMER-E Ltd., Plymouth (190 pp.).

Davies SM, Sánchez-Velasco L, Beier E, Godínez VM, Barton ED, Tamayo A (2015) Three-dimensional distribution of larval fish habitats in the shallow oxygen minimum zone in the Eastern Tropical Pacific Ocean off Mexico. *Deep-Sea Res. I* 101: 118–129.

De la Cruz-Agüero J, Galván-Magaña F (1992) Peces mesopelágicos de la costa occidental de Baja California Sur y del Golfo de California. Universidad Nacional Autónoma de México. *Anales del Instituto de Ciencias del Mar y Limnología* 19: 25–31.

Del Moral-Flores LF, González-Acosta AF, Espinosa-Pérez H, Ruiz-Campos G, Castro-Aguirre JL (2013) Annotated checklist of the ichthyofauna from the islands of the Gulf of California, with comments on its zoogeographic affinities. *Revista Mexicana de Bioversidad* 84: 184-214.

De Leo FC, Drazen JC, Vetter EW, Rowden AA, Smith CR (2012) The effects of submarine canyons and the oxygen minimum zone on deep-sea fish assemblages off Hawai'i. *Deep-Sea Res. I* 64: 54-70.

Deutsch C, Brix H, Ito T, Frenzel H, Thompson L (2011) Climate-forced variability of ocean hypoxia. *Science* 333: 336–339.

Deutsch C, Ferrel A, Seibel B, Pörtner H-O, Huey RB (2015) Climate change tightens a metabolic constraint on marine habitats. *Science* 348: 1132–1136.

deWaard JR, Ivanova NV, Hajibabei M, Hebert PDN (2007) Assembling DNA Barcodes. Methods in Molecular Biology. *Environmental Genomic* 410: 275–294.

Drazen JC, Friedman JR, Condon NE, Aus EJ, Gerringer ME, Keller AA, Clarke ME (2015) Enzyme activities of demersal fishes from the shelf to the abyssal plain. *Deep-Sea Res. I* 100: 117-126.

Espinosa-Carreón TL, Escobedo-Urías D (2017) South region of the Gulf of California large marine ecosystem upwelling, fluxes of CO2 and nutrients. *Environmental Development* 22: 42-51.

Fischer W, Krupp F, Schneider W, Sommer C, Carpenter KE, Niem VH (1995a) Guia FAO para la identificacion de especies para los fines de la pesca. Pacifico centro-oriental. Volumen II. Vertebrados – Parte 1. Roma, FAO. Vol II: 647-1200.

Fischer W, Krupp F, Schneider W, Sommer C, Carpenter KE, Niem VH (1995b) Guia FAO para la identificacion de especies para los fines de la pesca. Pacifico centro-oriental. Volumen III. Vertebrados – Parte 2. Roma, FAO. Vol III: 1201-1813.

Gallo ND, Levin LA (2016) Fish ecology and evolution in the world's oxygen minimum zones and implications of ocean deoxygenation. *Adv. Mar. Biol.* 1-82.

Gaxiola-Castro G, Álvarez-Borrego S, Schwartzlose RA (1978) Sistema del bióxido de carbano en el Golfo de California. *Ciencias Marinas* 5(2): 25-40.

Giorgetta MA, Jungclaus J, Reick CH, Legutke S, Bader J, Bottinger M, Brovkin V, Crueger T, Esch M, Fieg K, Glushak K, Gayler V, Haak H, Hollweg H-D, Ilyina T, Kinne S, Kornblueh L, Matei D, Mauritsen T, Mikolajewicz U, Mueller W, Notz D, Pithan F, Raddatz T, Rast S, Redler R, Roeckner E, Schmidt H, Schnur R, Segschneider J, Six KD, Stockhause M, Timmreck C, Wegner J, Widmann H, Wieners K-H, Claussen M, Marotzke J, Stevens B (2013) Climate and carbon cycle changes from 1850 to 2100 in MPI-ESM simulations for the Coupled Model Intercomparison Project phase 5. *J. Adv. Model. Earth Syst.*, 5: 572–597.

Gooday AJ, Bett BJ, Escobar E, Ingole B, Levin LA, Neira C, Raman AV, Sellanes J (2010) Habitat heterogeneity and its influence on benthic biodiversity in oxygen minimum zones. *Mar. Ecol.* 31: 125-147.

Gräler B, Pebesma E, Heuvelink G (2016) Spatio-Temporal Interpolation using gstat. *The R Journal* 8(1): 204-218.

Hastie TJ, Tibshirani RJ (1986) Generalized additive models. *Stat. Sci.* 1(3): 297-318.

Hastings PA, Findley LT, Van der Heiden AM (2010) Chapter 5: Fishes of the Gulf of California. The Gulf of California: Biodiversity and Conservation. University of Arizona Press. p. 96-118.

Hendrickx ME, Serrano D (2014) Effects of the oxygen minimum zone on squat lobster distributions in the Gulf of California, Mexico. *Cent. Eur. J. Biol.* 9(1): 92-103.

Hijmans RJ (2016) raster: Geographic Data Analysis and Modeling. R package version 2.5-8.

Jeffreys RM, Levin LA, Lamont PA, Woulds C, Whitcraft CR, Mendoza GF, Wolff GA, Cowie GL (2012) Living on the edge: single-species dominance at the Pakistan oxygen minimum zone boundary. *Mar. Ecol. Prog. Ser.* 470: 79-99.

Johannesen E, Høines AS, Dolgov AV, Fossheim M (2012) Demersal fish assemblages and spatial diversity patterns in the Arctic-Atlantic transition zone in the Barents Sea. *PLoS ONE* 7(4): e34924.

Keller AA, Ciannelli L, Wakefield WW, Simon V, Barth JA, Pierce SD (2015) Occurrence of demersal fishes in relation to near-bottom oxygen levels within the California Current large marine ecosystem. *Fish. Oceanogr.* 24(2): 162–176.

Keller AA, Ciannelli L, Wakefield WW, Simon V, Barth JA, Pierce S (2017) Species-specific responses of demersal fish to near-bottom oxygen levels within the California Current large marine ecosystems. *Mar. Ecol. Prog. Ser.* 568: 151-173.

Keller AA, Simon V, Chan F, Wakefield WW, Clarke ME, Barth JA, Kamikawa D, Fruh EL (2010) Demersal and invertebrate biomass in relation to an offshore hypoxic zone along the US West Coast. *Fish. Oceanogr.* 19(1): 76–87.

Keller A, Wallace J, Horness B (2012) Variations in eastern North Pacific demersal fish biomass based on the US west coast groundfish bottom trawl survey (2003–2010). *Fish. Bull.* 110: 205–222.

Koslow JA, Williams A, Paxton JR (1997) How many demersal fish species in the deep sea? A test of a method to extrapolate from local to global biodiversity. *Biodivers. Conserv.* 6: 1523-1532.

Lavenberg RJ, Fitch JE (1966) Annotated list of the fishes collected by mid-water trawl in the Gulf of California, March–April 1964. *California Fish and Game* 52: 92–110.

Ledesma-Vásquez J, Carreno AL (2010) Chapter 1: Origin, Age, and Geological Evolution of the Gulf of California. The Gulf of California: Biodiversity and Conservation. University of Arizona Press. p. 7-23.

Levin LA (2003) Oxygen minimum zone benthos: adaptation and community response to hypoxia. *Ocean. Mar. Biol. Ann. Rev.* 41: 1-45.

Lluch-Cota SE, Parés-Sierra A, Magaña-Rueda VO, Arreguín-Sánchez F, Bazzino G, Herrera-Cervantes H, Lluch-Belda D (2010) Changing climate in the Gulf of California. *Prog. Oceanogr.* 87: 114-126.

López-Martínez J, Acevedo-Cervantes A, Herrera-Valdivia E, Rodríguez-Romero J, Palacios-Salgado DS (2012) Composición taxonómica y aspectos zoogeográficos de peces de profundidad (90-540m) del Golfo de California, México. *Int. J. Trop. Biol.* 60(1): 347-360.

McClatchie S, Goericke R, Cosgrove R, Auad G, Vetter R (2010) Oxygen in the Southern California Bight: Multidecadal trends and implications for demersal fisheries. *Geophys. Res. Lett.* 37: L19602.

Mejía-Mercado BE, Balart-Páez E, Sosa-Nishizaki O, Hinojoso-Corona A (2014) Chapter 6: Registros de especies ícticas (Myxini, Chondrichthyes, y Actinopterygii). Explorando el mar profundo del Golfo de California: 2008-2014. CICESE, p. 206-226. ISBN: 978-607-95688-1-8.

Mora C, Wei C-L, Rollo A, Amaro T, Baco AR, Billett D, Bopp L, Chen Q, Collier M, Danovar R, Gooday AJ, Grupe BM, Halloran PR, Ingels J, Jones DOB, Levin LA, Nakano H, Norling K, Ramirez-Llodra E, Rex M, Ruhl HA, Smith CR, Sweetman AK, Thurber AR, Tjiputra JF, Usseglio P, Watling L, Wu T, Yasuhara M (2013) Biotic and human vulnerability to projected changes in ocean biogeochemistry over the 21st Century. *PLoS Biol* 11(10), e1001682.

Moser HG, Ahlstrom EH, Kramer D, Stevens EG (1971) Distribution and abundance of fish larvae in the Gulf of California. *CalCOFI Reports* 17: 112-128.

Muggeo VMR (2008). segmented: an R Package to Fit Regression Models with Broken-Line Relationships. R News, 8/1, 20-25.

Mullins HT, Thompson JB, McDougall K, Vercoutere TL (1985) Oxygen-minimum zone edge effects: evidence from the central California coastal upwelling system. *Geology* 13: 491–494.

Nielsen JG, Cohen DM, Markle DF, Robins CR (1999) Ophidiiform fishes of the world (Order Ophidiiformes): An annotated and illustrated catalogue of pearlfishes, cusk-eels, brotulas and other ophidiiform fishes known to date. *FAO Fisheries Synopsis* 125(18): 1-190.

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2017). vegan: Community Ecology Package. R package version 2.4-4.

Palumbi SR (1996) Nucleic acids II: the polymerase chain reaction. In: Hillis DM, Moritz C, Mable BK, editors. Molecular Systematics. Sinauer & Associates Inc, Sunderland, MA, USA. pp. 205–47.

Parker RH (1964) Zoogeography and ecology of macro-invertebrates of Gulf of California and continental slope of Western Mexico. Marine Geology of the Gulf of California – A Symposium. Mem. No. 3 pp. 331-376. Am. Assoc. Pet. Geol., Tulsa, Oklahoma.

Pörtner H-O, Bock C, Mark KC (2017) Oxygen- and capacity-limited thermal tolerance: bridging ecology and physiology. *J. Exp. Biol*. 220: 2685-2696.

Pörtner H-O, Karl DM, Boyd PW, Cheung WWL, Lluch-Cota SE, Nojiri Y, Schmidt DN, Zavialov PO (2014) Ocean systems. *IPCC AR5 WG2 Report*: 411-484.

Pörtner H-O, Knust R (2007) Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science* 315: 95-97.

Robison BH (1972) Distribution of the midwater fishes of the Gulf of California. *Copeia* 1972(3): 448–461.

Roden GI (1964) Oceanographic aspects of the Gulf of California. Marine Geology of the Gulf of California – A Symposium. Mem. No. 3 pp. 30-58. *Am. Assoc. Pet. Geol.*, Tulsa, Oklahoma.

Rodríguez-Romero J, Palacios-Salgado DS, López-Martínez J, Hernández-Vázquez J, Ponce-Díaz G (2008) Taxonomic composition and zoogeographic relations of demersal in the western coast of Baja California Sur, Mexico. *Int. J. Trop. Biol.* 56(4): 1765-1783.

Sánchez-Velasco L, Ávalos-García C, Renteria-Cano M, Shirasago B (2004) Fish larvae abundance and distribution in the central Gulf of California during strong environmental changes (1997-1998 El Niño and 1998-1999 La Niña). *Deep-Sea Res. II* 51: 711-722.

Sánchez-Velasco L, Lavín MF, Peguero-Icaza M, León-Chávez CA, Contreras-Catala F, Marinone SG, Gutiérrez-Palacios IV, Godínez VM (2009) Seasonal changes in larval fish assemblages in a semi-enclosed sea (Gulf of California). *Cont. Shelf Res.* 29: 1697-1710.

Schlining BM, Stout NJ (2006) MBARI's Video Annotation and Reference System. Proceedings of the Marine Technology Society/Institute of Electrical and Electronics Engineers Oceans Conference pp. 1–5.

Sperling EA, Frieder CA, Levin LA (2016) Biodiversity response to natural gradients of multiple stressors on continental margins. *Proc. R. Soc. B* 283: 20160637.

Springer, S (1979) A revision of the catsharks, Family Scyliorhinidae. NOAA Technical Report NMFS Circular 422: 1-153.

Sverdrup HU (1941) The Gulf of California: preliminary discussion on the cruise of the E.W. Scripps in February and March 1939. *6th Pac. Sci. Congr. Proc.* 161-166.

Sweetman AK, Thurber AR, Smith CR, Levin LA, Mora C, Wei C-L, Gooday AJ, Jones DOB, Rex M, Yasuhara M, Ingels J, Ruhl HA, Frieder CA, Danovaro R, Wurzberg L, Baco A, Grupe BM, Pasulka A, Meyer KS, Dunlop KM, Henry L-A, Roberts JM (2017) Major impacts of climate change on deep-sea benthic ecosystems. *Elem Sci Anth.* 5: 4.

ter Braak CJF (1986) Canonical correspondence analysis: A new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67(5): 1167-1179.

ter Braak CJF, Verdonschot PFM (1995) Canonical correspondence analysis and related multivariate methods in aquatic ecology. *Aquat. Sci.* 57(3): 255-289.

Thomson DA, Eger, WH (1966) Guide to the Families of the Common Fishes of the Gulf of California. University of Arizona Press, Tucson, AZ.

Thomson DA, Findley LT, Kerstitch AN (2000) Reef Fishes of the Sea of Cortez: The Rocky-Shore Fishes of the Gulf of California. University of Texas Press, Austin, TX.

van Andel TH (1964) Recent marine sediments of Gulf of California. P. 216-310. In T. H. van Andel and G. G. Shor. Jr. (eds..) Marine geology of the Gulf of California. *Am. Ass. Petroi. Geol., Memoir* (3): 1-408.

Vaquer-Sunyer R, Duarte CM (2008) Thresholds of hypoxia for marine biodiversity. *Proc. Natl. Acad. Sci.* 105, 15452–15457.

Walker BW (1960) The distribution and affinities of the marine fish fauna of the Gulf of California. *Syst. Zool.* 9(3/4): 123-133.

Walker HJ, Rosenblatt RH (1988) Pacific toadfishes of the Genus *Porichthys* (Batrachoididae) with descriptions of three new species. *Copeia* 1988(4): 887-904.

Walsh PS, Metzger DA, Higuchi R (2013) Chelex 100 as a medium for simple extraction of DNA for PCR-based typing from forensic material. *BioTechniques* 54(3): 134-139.

Ward RD, Zemlak TS, Innes BH, Last PR, Hebert PDN (2005) Barcoding Australia’s fish species. *Philos. Trans. R. Soc. Lon. B*, 360: 1847–1857.

Wishner K, Levin L, Gowing M, Mullineaux L (1990) Involvement of the oxygen minimum in benthic zonation on a deep seamount. *Nature* 346: 57–59.

Wood SN (2017) Generalized Additive Models: An Introduction with R. Chapman and Hall/CRC.

Zamorano P, Hendrickx ME, Toledano-Granados A (2007) Distribution and ecology of deep-water mollusks from the continental slope, southeastern Gulf of California, Mexico. *Mar. Biol.* 150(5): 883-892.

Zamorano P, Hendrickx ME, Méndez N, Goméz S, Serrano D, Aguirre H, Madrid J, Morales-Serna N (2014) La exploración de las aguas profundas del Pacífico mexicano: el proyecto TALUD. La Frontera Final: El Océano Profundo. Instituto Nacional de Ecología, Secretaría del Medio Ambiente y Recursos Naturales (SEMARNAT) 293 p: 105-147.

Tables

Table 3.1. Region, dive, date, location, annotated dive time, number of fish transects, and environmental information for each of the eight Gulf of California ROV dives analyzed in this study. Dives were conducted in the northern (N), central (C), and southern (S) Gulf of California and regions are abbreviated as such. The location coordinates provided correspond to the beginning of each dive. Environmental ranges represent the minimum and maximum value encountered for each parameter during the total annotated dive time for each dive.

Region/ Dive	Date	Location	Latitude	Longitude	Annotated Dive Time	No. of Fish Transects	Depth Range (m)	Temperature Range (°C)	Oxygen Range (μmol kg^{-1})	Salinity Range (psu)
C/731	21-Mar-15	Isla Tortuga	27.384269	-111.872958	4 h 20 min	7	1012 - 1358	3.28 - 4.58	6.48 - 18.96	34.55 - 34.59
C/732	22-Mar-15	Isla Tortuga	27.400906	-111.872560	9 h 01 min	12	200 - 952	4.70 - 12.96	1.22 - 40.18	34.54 - 34.88
N/733	23-Mar-15	Salsipuedes Basin	28.614186	-112.893840	2 h 16 min	No Transects	737-1505	11.73 - 11.27	30.79 - 39.40	34.79 - 34.82
C/734	24-Mar-15	San Pedro Martir Basin	28.353634	-112.348216	8 h 05 min	12	200 - 919	6.19 - 12.98	1.30 - 29.01	34.54 - 34.87
N/735	25-Mar-15	Salsipuedes Basin	29.053637	-113.261312	10 h 33 min	10	196 - 1081	11.56 - 14.29	25.48 - 91.98	34.80 - 35.02
C/736	26-Mar-15	San Pedro Island North	28.395416	-112.392707	9 h 26 min	16	377 - 854	6.20 - 9.84	1.30 - 28.57	34.54 - 34.73
S/737	28-Mar-15	Cerralvo Trough	24.216883	-109.786416	6 h 29 min	10	295 - 959	4.80 - 11.14	0.52 - 6.22	34.50 - 34.72
S/738	29-Mar-15	Cabo Pulmo	23.419939	-109.348321	9 h 55 min	21	200 - 1274	3.72 - 12.12	0.39 - 21.96	34.48 - 34.78

Table 3.2. Table of all demersal fish species observed during ROV dives, along with the dives and environmental conditions they were observed under. Entries in gray represent collected specimens that were identified in the lab and sequenced.

Species	Dives Observed During	Depth Range (m)	Temp Range (°C)	Oxygen Range (µmol kg^{-1})
Bathycongrus macrurus	732, 737, 738	298-544	7.32-11.61	0.65-12.19
Bathypterois sp.	731, 732, 737, 738	863-1356	3.32-5.07	4.12-21.74
Cataetyx rubrirostris	738	1253	3.78	20.31
Cephalurus cephalus	732, 734, 736, 737, 738	494-918	5.34-8.11	0.83-3.17
Cephalurus cephalus (GB #)	732	716	6.17	1.6
Cherublemma emmelas	732, 734, 736, 737, 738	325-955	4.71-10.46	0.52-7.33
Cherublemma emmelas (GB #)	732	577	7.31	1.52
Cherublemma emmelas (GB #)	736	798	6.43	1.43
Cherublemma emmelas (GB #)	737	853	5.13	4.08
Chilara taylori	732, 734	208-306	11.74-12.90	14.06-27.68
Coelorinchus scaphopsis	734, 735, 736	222-786	9.53-13.20	20.78-60.92
Coelorinchus scaphopsis	734	382	10.65	22.99
Coelorinchus scaphopsis	735	296	12.97	55.67
Coryphaenoides capito	732	921	5.02	4.08
Cottoidea sp.	732	203-260	12.74-12.96	31.89-39.70
Derepodichthys alepidotus (GB #)	738	1182	3.98	16.57
Dibranchus spp.	731, 732, 737, 738	733-1271	3.66-6.11	1.61-21.74
Dibranchus hystrix (GB #)	732	922	5.02	3.99
Dibranchus hystrix (GB #)	737	946	4.81	6.09
Dibranchus hystrix (GB #)	738	1184	3.96	16.75
Dibranchus spinosus	732, 737, 738	723-1243	3.83-6.06	1.30-19.44
Dibranchus spinosus (GB #)	738	1126	4.31	11.63
Eknomoliparis chirichignoae	731	1314	3.51	16.4
Eptatretus sinus	732, 733, 734, 735, 736, 737	263-1080	5.01-12.08	2.73-35.02
Eretmichthys pinnatus	731, 737, 738	867-1264	3.74-5.06	4.25-21.39
Gnathophis cinctus	735	285-302	13.16-13.44	60.05-67.47
Gnathophis cinctus (GB #)	735	285	13.44	67.47
Hydrolagus colliei	733, 735, 736	369-1020	9.50-13.11	19.74-58.62
Lestidiops sp.	732	294	11.87	17.09
Liopropoma longilepis	732, 735	199-261	12.81-13.82	29.42-79.10
Lophiodes caulinaris	732, 734, 735, 738	217-888	10.54-12.07	2.99-29.46
Lycenchelys sp. 1	731, 732, 737, 738	894-1355	3.31-4.88	5.55-21.00
Lycenchelys sp. (GB #)	738	1184	3.99	16.4
Lycenchelys sp. 2	731, 732, 737, 738	898-1355	3.32-5.03	4.03-21.91
Lycenchelys sp. 2 (GB #)	737	946	4.8	6.07
Macrouridae spp.	731, 732, 734, 735, 736, 737, 738	460-1355	3.33-11.64	0.82-29.94
Merluccius sp.	732, 736	339-457	8.16-11.51	5.29-28.51
Nemichthys sp.	737	411	9.57	0.87
Nettastomatidae sp.	738	1227-1254	3.78-3.87	18.70-20.65
Nezumia liolepis	738	934	4.79	6.51
Opichthus frontalis	735	681	11.81	31.24
Paralabrax auroguttatus	735	217	13.78	76.37
Paraliparis rosaceus	731, 738	935-1348	3.37-4.77	6.51-17.79
Paraliparis rosaceus	738	935	4.77	6.51
Parmaturus xaniurus	733, 734, 735, 736, 738	377-1173	4.11-11.59	1.43-26.60
Parmaturus xaniurus (GB #)	736	798	6.44	1.43
Physiculus rastrelliger	732, 734, 735, 736, 738	216-483	8.33-13.49	1.08-68.95
Physiculus rastrelliger (GB #)	732	443	9.08	3.12
Physiculus rastrelliger (GB #)	735	392	12.09	35.28
Pontinus furcirhinus	732, 734, 735	197-387	10.44-13.86	6.42-79.36
Pontinus furcirhinus (GB #)	734	333	11.12	24.82
Pontinus sierra	737, 738	202-301	11.05-12.11	1.82-5.08
Pontinus sierra (GB #)	737	301	11.05	1.82
Porichthys mimeticus	737, 738	223-229	11.56-11.82	3.08-3.69
Porichthys mimeticus (GB #)	737	250	11.56	3.08
Pronotogrammus eos	734	203-213	12.85-12.88	27.59-27.73
Raja sp. 1	735, 736	300-511	11.99-12.90	33.28-53.32
Raja sp. 2	735	276	13.17	60.79
Sebastes cortezi	733, 734, 735, 736	199-1448	7.26-14.26	1.82-91.12
Sebastes cortezi (GB #)	736	559	7.65	2.48
Sebastes exsul	735	199-662	11.83-13.86	31.15-79.67
Sebastes macdonalldi	734	232-287	11.98-12.68	26.82-27.34
Serranidae sp.	738	223-227	11.79-11.81	3.21-3.47
Squatinidae sp.	735	291	13.12	59.23
Symphurus spp.	732, 734, 735, 736	224-1010	7.89-12.98	2.69-55.28
Symphurus oligomerus	735	808	11.67	30.33
Synodus sp.	738	212	11.83	3.56
Triglidae sp.	732	264	12.76	33.76
Xeneretmus ritteri (GB #)	734	383	9.78	13.88
Zoarcidae sp.	731, 738	1160-1348	3.37-4.13	10.07-19.61

Table 3.3. Comparison of generalized additive models evaluated for assessing relationship between environmental variables and demersal fish density across 88 transects in the Gulf of California. The initial model included latitude (Lat), near-bottom temperature (T), near-bottom dissolved oxygen (Ox), and depth (Z). Non-significant variables were then removed and a suite of models were tested to select the best model (ΔAIC = 0). The generalized cross-validation (GCV), variance explained (r^2 adjusted), and significance of each covariate included in the model are also shown.

Equation	AIC	ΔAIC	GCV	r^2 (adj)	p-value (Lat)	p-value (T)	p-value (Ox)	p-value (Z)
Log(Density) = s1(Lat) + s2(T) + s3(Ox)	258.47	0.00	1.125	0.588	1.39E-06	1.73E-09	1.58E-05	N/A
Log(Density) = s1(Lat) + s2(T) + s3(Ox) + s4(Z)	259.93	1.46	1.151	0.584	6.00E-06	4.00E-09	1.79E-05	0.91
Log(Density) = s1(Ox) + s2(Lat) + s3(Z)	289.49	31.01	1.596	0.41	4.27E-06	N/A	1.60E-05	6.95E-04
Log(Density) = s1(T) + s2(Ox) + s3(Z)	290.14	31.66	1.581	0.385	N/A	1.99E-06	0.154	0.021
Log(Density) = s1(Lat) + s2(T)	290.84	32.37	1.586	0.371	0.045	2.55E-05	N/A	N/A
Log(Density) = s1(T) + s2(Lat) + s3(Z)	292.16	33.68	1.614	0.366	0.276	2.49E-05	N/A	0.329
Log(Density) = s1(T) + s2(Ox)	292.59	34.12	1.626	0.368	N/A	9.80E-06	0.163	N/A
Log(Density) = s1(T)	296.11	37.64	1.675	0.32	N/A	1.80E-05	N/A	N/A
Log(Density) = s1(Lat) + s2(Ox)	307.52	49.05	1.890	0.187	4.14E-04	N/A	1.33E-03	N/A
Log(Density) = s1(Lat)	317.40	58.92	2.112	0.079	0.037	N/A	N/A	N/A
Log(Density) = s1(Ox)	322.66	64.19	2.245	0.0361	N/A	N/A	0.336	N/A

Table 3.4. Comparison of generalized additive models evaluated for assessing relationship between environmental variables and demersal fish diversity (H') across 88 transects in the Gulf of California. The initial model included latitude (Lat), near-bottom temperature (T), near-bottom dissolved oxygen (Ox), and depth (Z). Non-significant variables were then removed and a suite of models was tested to select the best model (ΔAIC = 0). The generalized cross-validation (GCV), variance explained (r^2 adjusted), and significance of each covariate included in the model are also shown.

Equation	AIC	ΔAIC	GCV	r^2 (adj)	p-value (Lat)	p-value (T)	p-value (Ox)	p-value (Z)
Diversity (H') = s1(Lat) + s2(Ox)	65.76	0.00	0.123	0.573	0.018	N/A	1.14E-14	N/A
Diversity (H') = s1(Lat) + s2(T) + s3(Ox)	67.11	1.34	0.125	0.57	0.024	0.452	3.69E-14	N/A
Diversity (H') = s1(Lat) + s2(T) + s3(Ox) + s4(Z)	68.92	3.16	0.128	0.563	0.022	0.392	2.20E-12	0.5594
Diversity (H') = s1(Ox)	74.23	8.46	0.134	0.517	N/A	N/A	1.12E-12	N/A
Diversity (H') = s1(Lat)	126.80	61.04	0.243	0.112	0.031	N/A	N/A	N/A

Figures

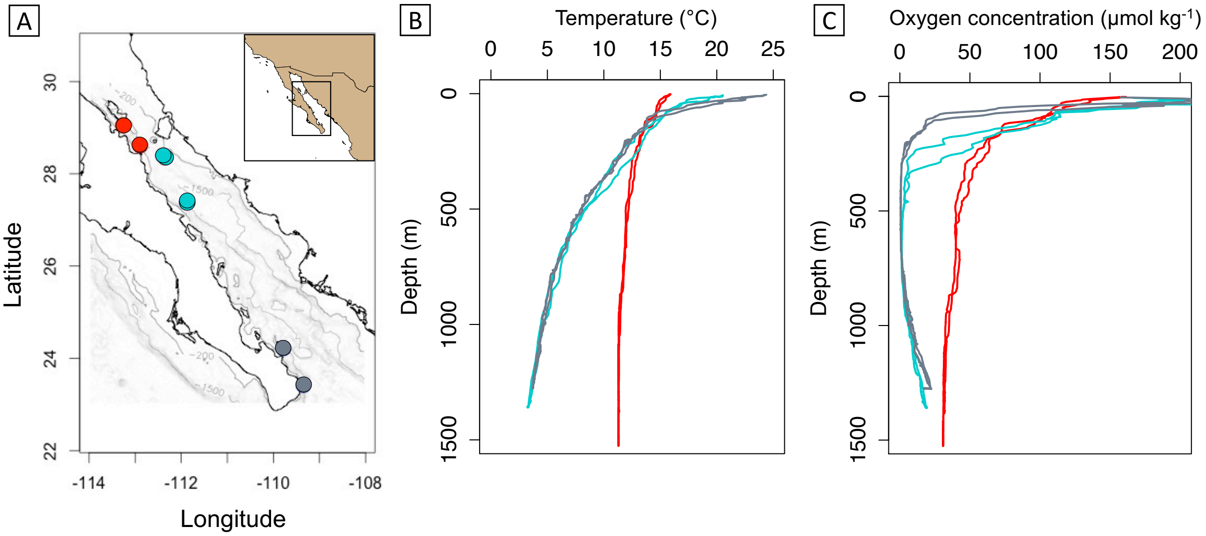


Figure 3.1. Dive locations and environmental profiles. A) Eight dives with the ROV *Doc Ricketts* were conducted in the Gulf of California. Dive locations are indicated as points and color-coded by region (northern = red, central = turquoise, southern = gray). The two points in the central region represent four dives, but locations are nearby making these independent dives difficult to see (Table 1). Dives were conducted upslope from depths of ~1400-200 m and the 200 and 1500 m isobaths for the Gulf of California are shown. The inset map shows the location of the Gulf of California relative to the US and Mexican Pacific coastline. Representative water column profiles for temperature (B) and oxygen (C) are shown for dives 733 (red, northern), 731 (turquoise, central), and 738 (gray, southern) to visualize differences in oceanographic conditions in these three regions.

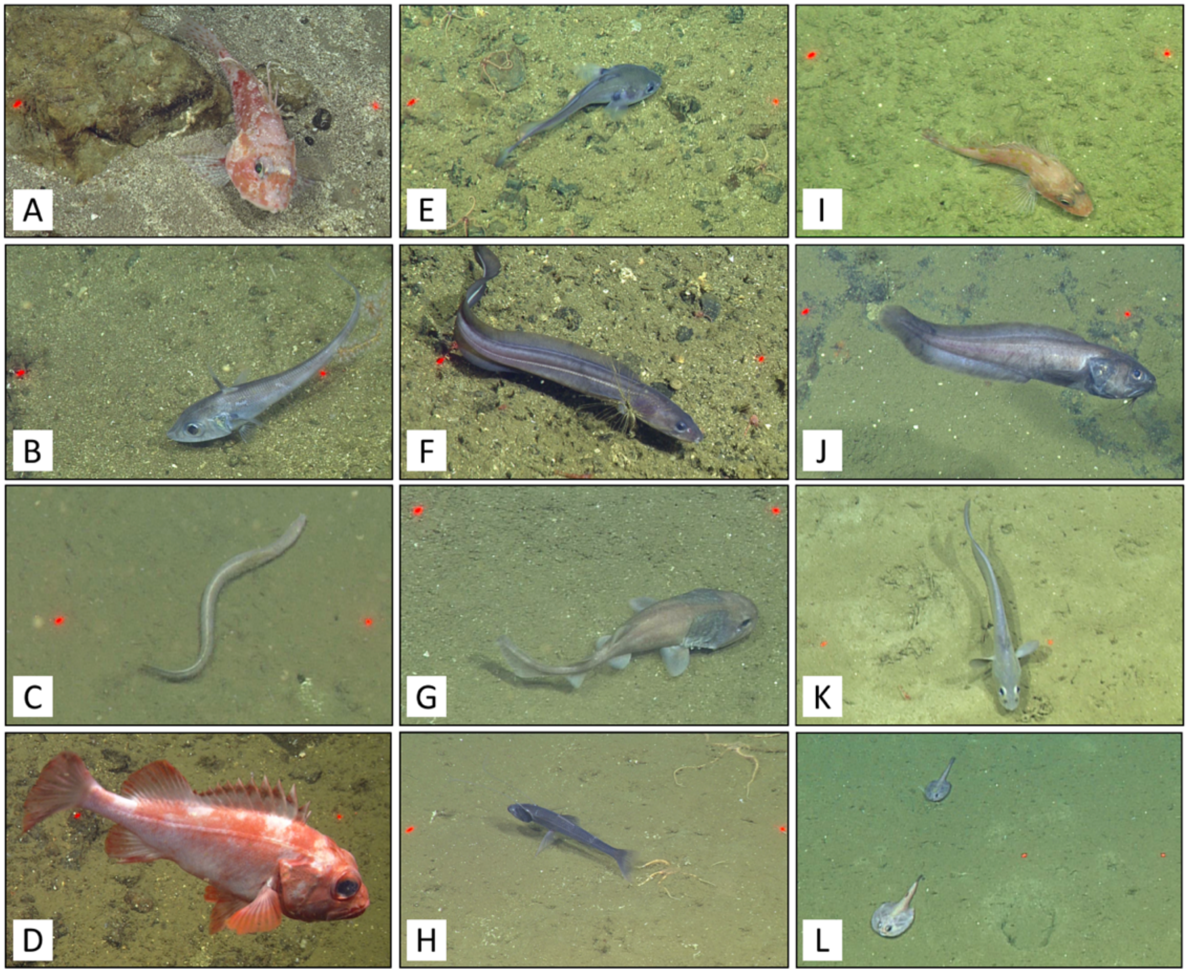


Figure 3.2. Common deep-sea demersal fish species in the northern (A-D), central (E-H), and southern (I-L) Gulf of California. The top row (A, E, J) represents species commonly found from 200-400 m, the second row (B, F, J) from 400-700 m, the third row (C, G, K) from 700-1000 m, and the fourth row (D, H, L) from deeper than 1000 m. Species pictured are: A) *Pontinus furcirhinus*, B) *Coelorinchus scaphopsis*, C) *Eptatretus sp.*, D) *Sebastes cortezi*, E) *Physiculus rastrelliger*, F) *Bathycongrus macrurus*, G) *Cephalurus cephalus*, H) *Bathypterois pectinatus*, I) *Pontinus sierra*, J) *Cherublemma emmelas*, K) *Coryphaenoides capito*, and L) *Dibranchus spinosus* (lower left) and *Dibranchus hystrix* (upper middle). A variety of species were selected to give a visual representation of the different species observed in the Gulf. Most of the pictured species were not restricted to only the region or depth range indicated in this figure, but are shown where they were encountered frequently. Lasers are provided for scale in each image. The distance between lasers is 29 cm.

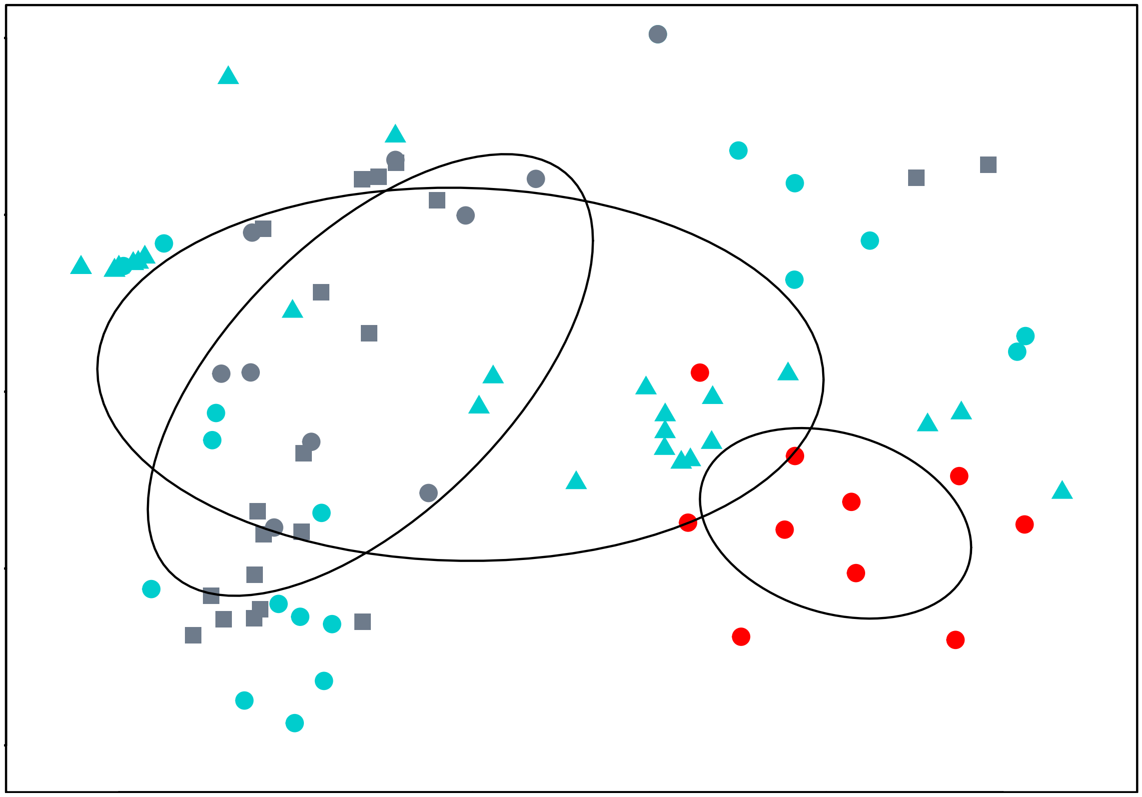


Figure 3.3. Multidimensional scaling plot of Bray-Curtis similarity matrix based on square-root transformed fish abundance data (2D stress is 0.08). Each point represents fish composition and counts in a ~100 m-long transect and colors indicate transects from the northern (red), central (turquoise), and southern (gray) Gulf of California. Ellipses represent grouping by region and show 50% confidence limits. Dives from different locations are differentiated by shape: red circles are transects from Dive 735 in the Salsipuedes Basin, turquoise circles are transects from Dives 731 and 732 off Isla Tortuga, turquoise triangles are transects from Dives 734 and 736 off Isla San Martir, grey circles are transects from Dive 737 off Isla Cerralvo, and grey squares are transects from Dive 738 off Cabo Pulmo. Additional nMDS plots with overlain environmental contours are provided in Supplementary Item 3.

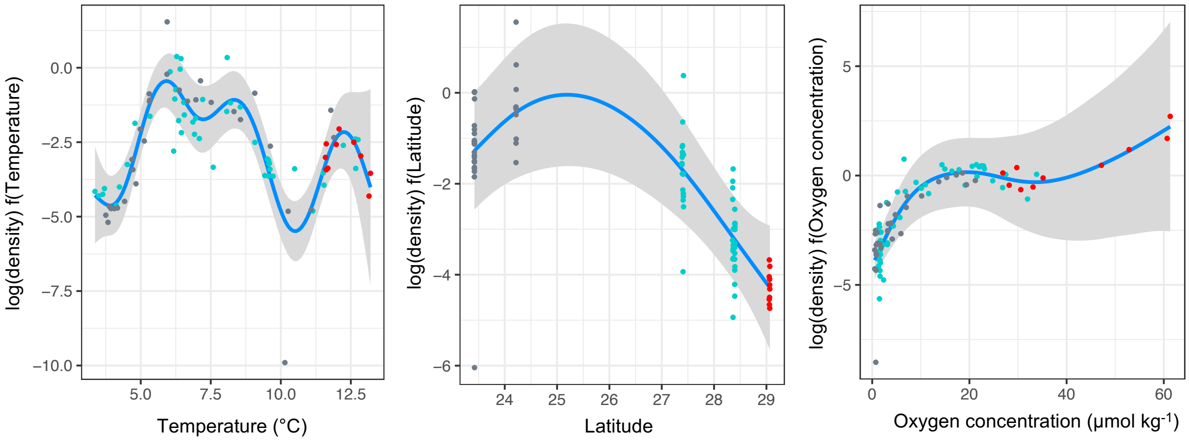


Figure 3.4. Deep-sea demersal fish density in the Gulf of California as a function of temperature (left), latitude (middle), and oxygen concentration (right). The generalized additive model with these explanatory variables could explain 59% of the variance in fish community density. The blue line represents the expected value with a confidence interval shown in gray, and points represent partial residuals for each of the 88 transects, colored by location where each transect was conducted (red = northern Gulf, turquoise = central Gulf, grey = southern Gulf). Temperature, latitude, and oxygen were all found to be significant explanatory variables for variation in fish density, while depth was not.

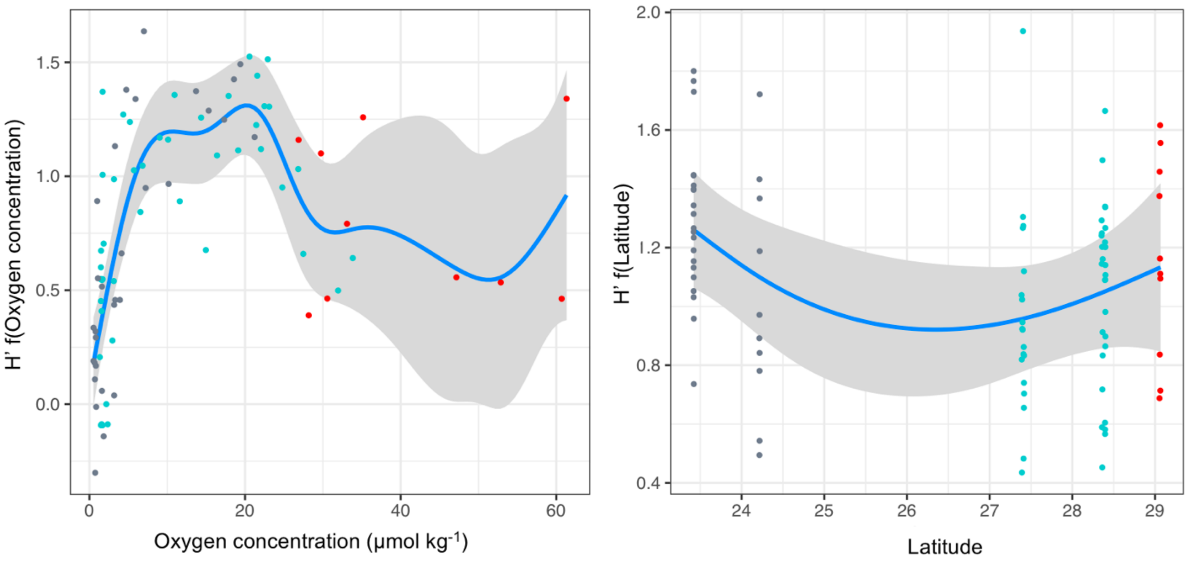


Figure 3.5. Gulf of California deep-sea demersal fish diversity (H') as a function of oxygen concentration (left) and latitude (right). The generalized additive model with these explanatory variables could explain 57% of the variance in fish community diversity. The blue line represents the expected value with a confidence interval shown in gray, and points represent partial residuals for each of the 88 transects, colored by location where each transect was conducted (red = northern Gulf, turquoise = central Gulf, grey = southern Gulf). Oxygen and latitude were found to be significant explanatory variables for variation in fish diversity, while depth and temperature were not. Oxygen concentration was the strongest predictor, able to explain ~52% of the variance in fish community diversity.

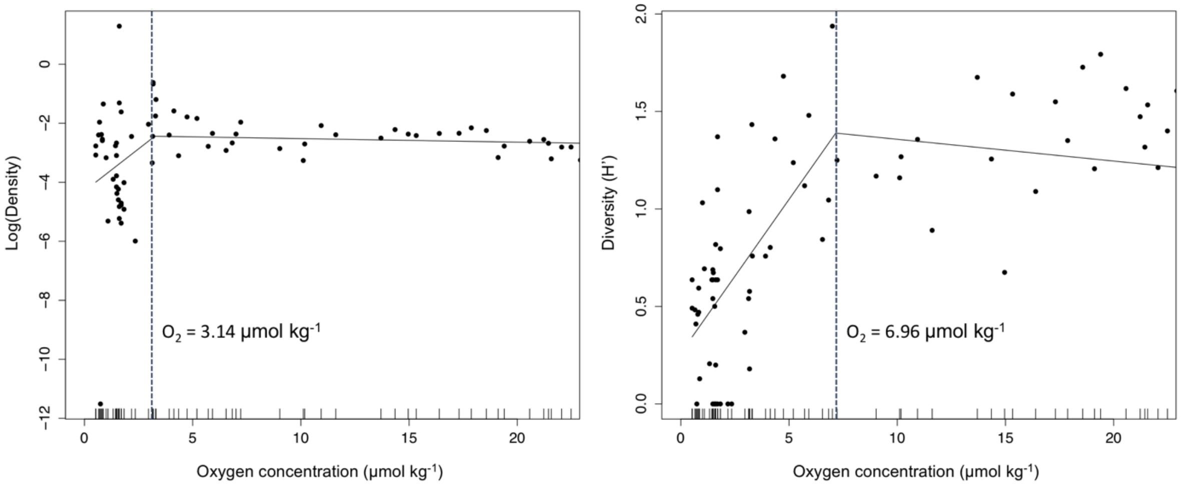


Figure 3.6. Gulf of California deep-sea demersal fish community density (left) and diversity (H') (right) as a function of near-bottom oxygen concentration. A segmented regression model identified threshold responses of fish density (left) ($p = 0.05$) and fish diversity (right) ($p < 0.001$) with near-bottom oxygen concentration. Points represent individual fish transects and the oxygen threshold identified by the model is indicated with a dashed line. Fish diversity begins to decline at a higher oxygen concentration than fish density suggesting that diversity is more sensitive to environmental oxygen conditions.

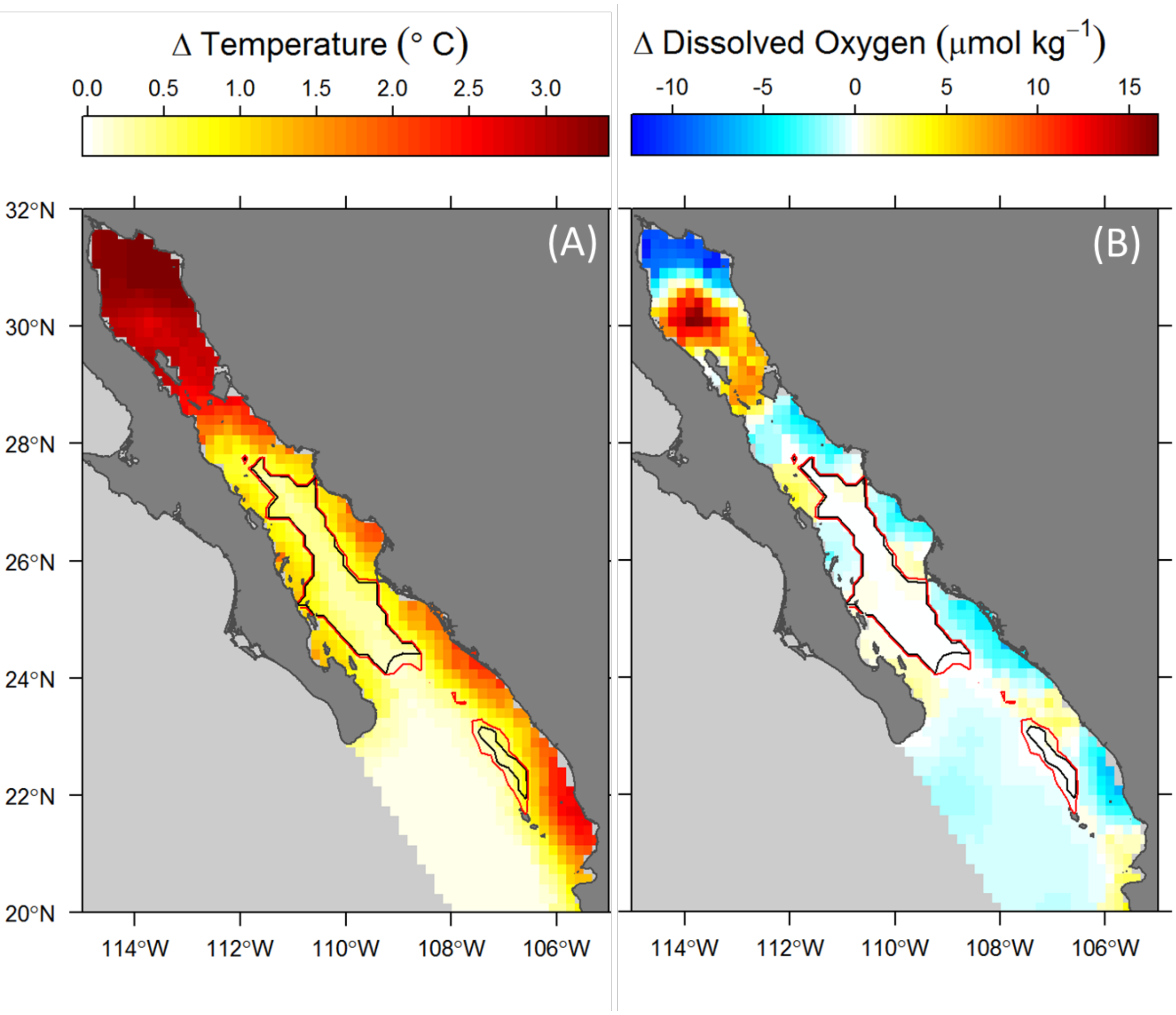


Figure 3.7. Projected changes for average seafloor temperature (A) and dissolved oxygen concentration (B) between 1951 to 2000 and 2081 to 2100 using the MPI ESM-MR model output for an RCP8.5 scenario. Warm colors indicate increases, cold colors indicate decreases, and white indicates no change. The black and red contour lines show the dissolved oxygen concentration of 3.14 and 6.96 µmol kg^{-1} by 2081 to 2100, corresponding to the thresholds identified for decreasing fish density and diversity, respectively. The southern bound of the northern Gulf of California is defined as the latitude 28°N, the central Gulf is between latitude 24°N and 28°N, and the southern Gulf is between latitude 20°N and 24°N.

Chapter 3 Appendix

Supplementary Material

Supplement 1 – Master guide to demersal fish species observed during the 2015 MBARI Gulf of California Expedition

Supplement 2 – Select images of collected fish specimens

Supplement 3 – nMDS plots showing fish community similarity with relation to environmental variables

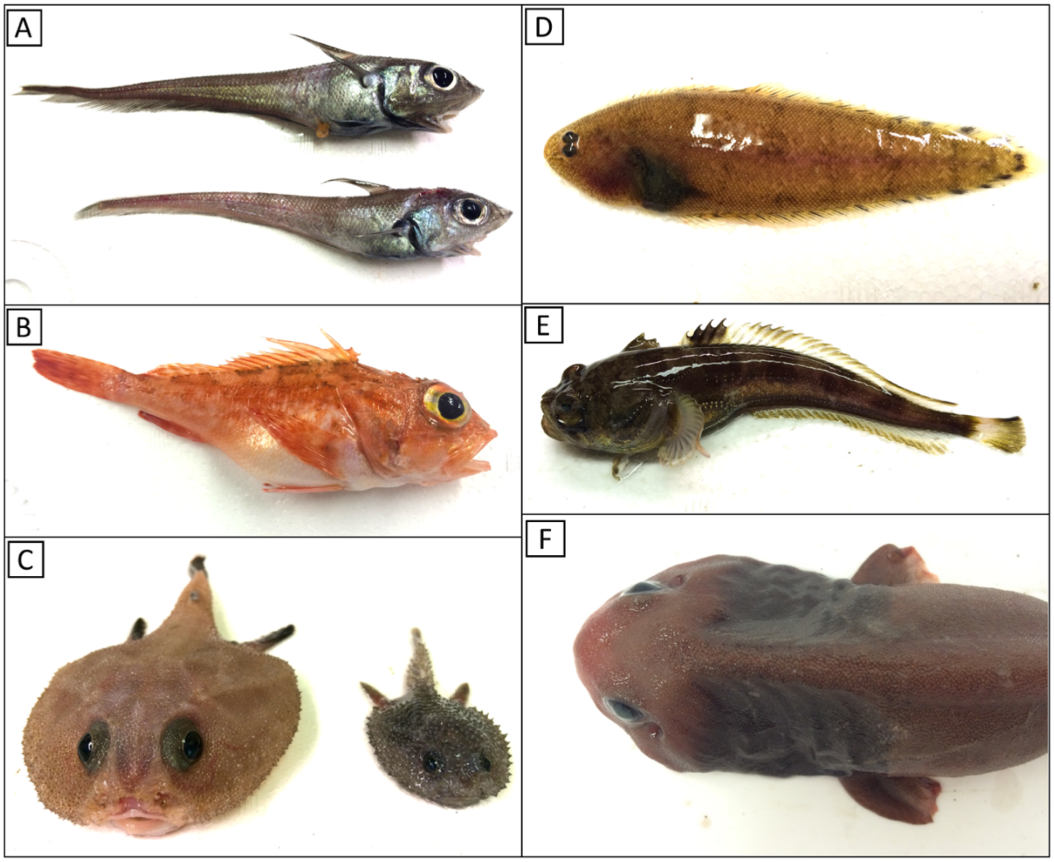
Supplement 4 – Cluster diagram showing fish community similarity with relation to environmental variables

Supplement 5 – Canonical correspondence analysis plot showing association between environmental variables and fish community composition

Supplement 6 – 2-dimensional component plot showing the combined influence of temperature and oxygen on demersal fish density

Supplement 7 – Expanded table showing demersal fish species capable of living in oxygen minimum zones (OMZs) with species from the Gulf of California added

Supplementary Item 2

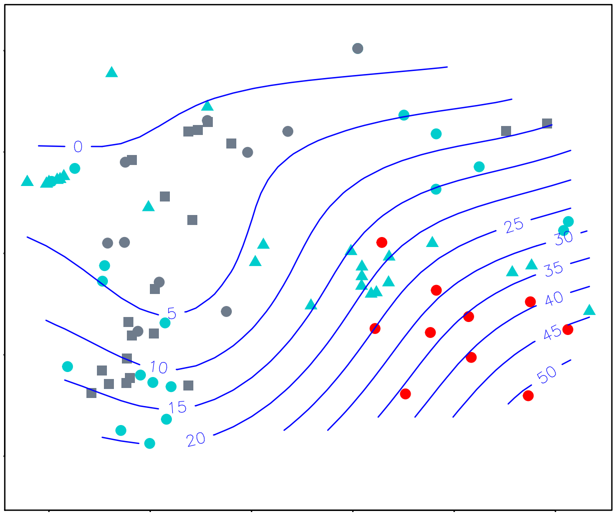


Collected specimens from the Gulf of California deep-sea demersal fish community, showing examples of several different species and orders. Photographs were taken of fresh, non-preserved specimens immediately after recovery from the ROV. Species are: A) *Coelorinchus scaphopsis*, a common macrourid in the northern Gulf, B) *Pontinus furcirhinus*, a scorpaenid common in the northern and central Gulf, C) two species of ogcocephalid, *Dibranchus spinosus* (left) and *Dibranchus hystrix* (right) that were both common in the southern Gulf, D) *Symphurus oligomerus*, a cynoglossid, common in the northern and central Gulf, E) *Porichthys mimeticus*, a batrachoidid common in shallower waters in the Southern Gulf, and F) the anterior-dorsal view of *Cephalurus cephalus*, a scyliorhinid common in the central and southern Gulf under low oxygen conditions. Note the very large gill chambers on the *C. cephalus* specimen.

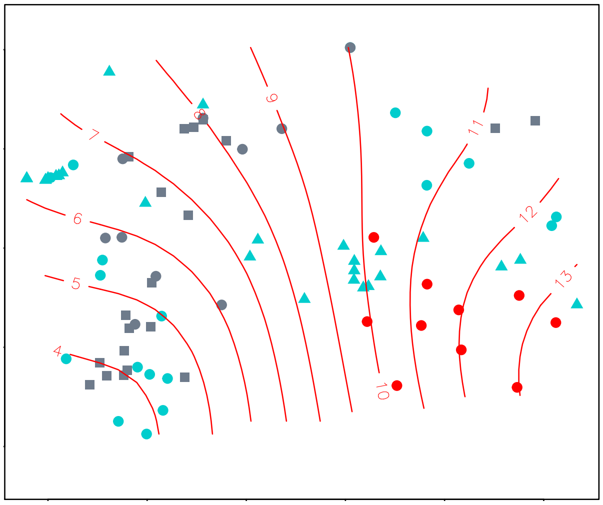
Supplementary Item 3

Multidimensional scaling plot of Bray-Curtis similarity matrix based on square-root transformed fish abundance data (2D stress is 0.08). Each point represents a ~100 m long fish transect and colors indicate transects from the northern (red), central (turquoise), and southern (grey) Gulf of California. Dives from different locations are differentiated by shape as well: red circles are transects from Dive 735 in the Salsipuedes Basin, turquoise circles are transects from Dives 731 and 732 off Isla Tortuga, turquoise triangles are transects from Dives 734 and 736 off Isla San Martir, grey circles are transects from Dive 737 off Isla Cerralvo, and grey squares are transects from Dive 738 off Cabo Pulmo. Overlain contour lines show near-bottom A) oxygen (μmol kg^{-1}), B) temperature (°C), and C) depth (m). Ordisurf fits a smooth surface for a given variable using thinplate splines (Wood 2003) in gam and plots the result on an ordination diagram, allowing for a visualization of how environmental parameters correlate with community similarities and differences. However, the contours should not be used to determine the exact environmental conditions for each plotted point, as these are not true values.

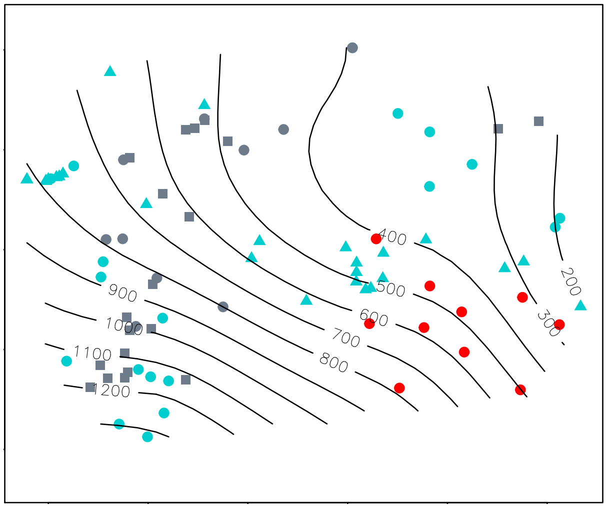
The northern assemblages group together and show no overlap with any of the southern assemblages, even when temperature is similar or transects are conducted at the same depth (see large difference in community assemblages at 400-600 m contours). When oxygen, temperature and depth conditions are similar at sites in the northern and central Gulf, the fish assemblages are also more similar and overlap in nMDS space (see red circles and turquoise triangles). Assemblages in the central Gulf show a great deal of heterogeneity overall, but seem to group into communities found in deeper, colder conditions (left side of the nMDS plots) and shallower, warmer conditions (right side of the nMDS plots). Assemblages in the southern Gulf also show a fair amount of heterogeneity, though are more homogeneous than fish assemblages in the central Gulf. In the southern Gulf, assemblages appear to group into those present under low oxygen, intermediate depth conditions (upper left of nMDS plots) and those present under higher oxygen, deeper conditions (lower left of nMDS plots). Overall, the central Gulf has the highest community heterogeneity, with the assemblages in shallow, warmer, and more oxygen-rich conditions more closely resembling those of the northern Gulf, and assemblages in deeper, colder and more hypoxic conditions resembling those of the southern Gulf.



A. Multidimensional scaling plot of Bray-Curtis similarity matrix based on square-root transformed fish abundance data with near-bottom oxygen contours overlain (μmol kg^{-1}).



B. Multidimensional scaling plot of Bray-Curtis similarity matrix based on square-root transformed fish abundance data with near-bottom temperature contours overlain (°C).

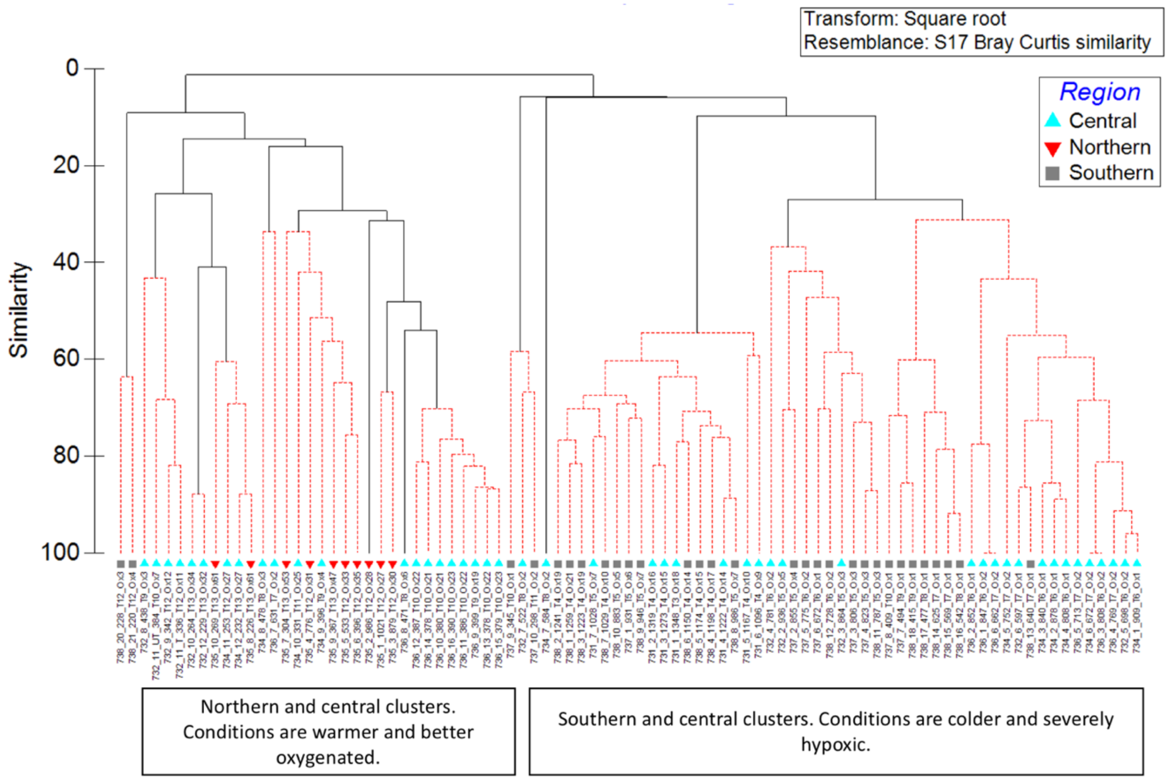


C. Multidimensional scaling plot of Bray-Curtis similarity matrix based on square-root transformed fish abundance data with depth contours overlain (m).

References

Wood, S.N. (2003) Thin plate regression splines. *J. R. Statist. Soc. B* 65, 95-114.

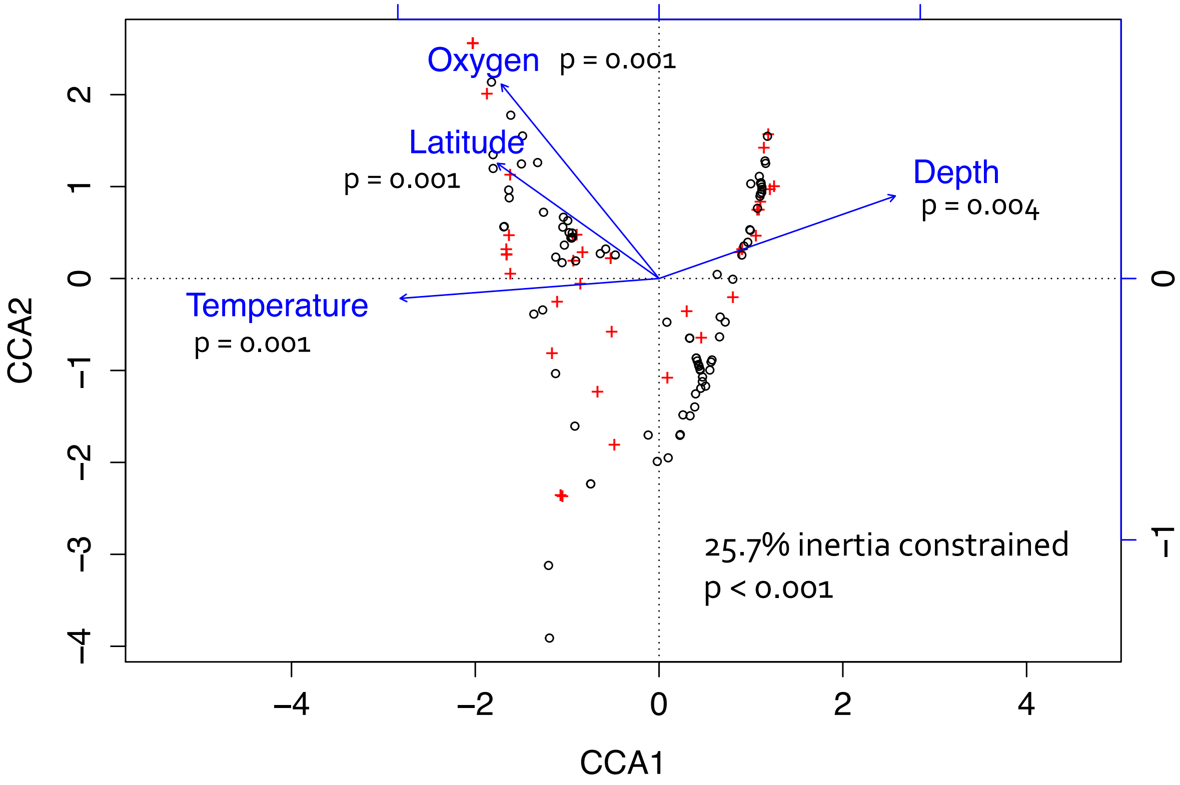
Supplementary Item 4



Grouping of demersal fish communities based on group-average linkage cluster analysis, together with a SIMPROF test, conducted in package PRIMER v.6. A Bray Curtis similarity matrix with square-root transformed fish count data was used as the resemblance matrix for the analysis. Solid lines represent statistically distinct groupings, while red dotted lines are not statistically significant. Each sample represents a demersal fish community from a ~100 m long benthic transect. Colors indicate transects from the northern (red), central (turquoise), and southern (grey) Gulf of California. Central stations group with both northern and southern stations, while southern and northern stations are statistically distinct. Central stations group with northern stations when conditions are warmer and better oxygenated, and group with southern stations when conditions are colder and severely hypoxic. Notation for each sample indicates the median environmental conditions encountered during each transect and follows the following formula:

Dive_Transect#_Depth_Temp_Ox. For example, the first sample on the left is the 20th transect of Dive 738, which had a median depth of 228 m, median temperature conditions of 12°C and median dissolved oxygen conditions of 3 μmol kg^{-1}. Environmental conditions are presented rounded to the nearest whole number for ease of visualization.

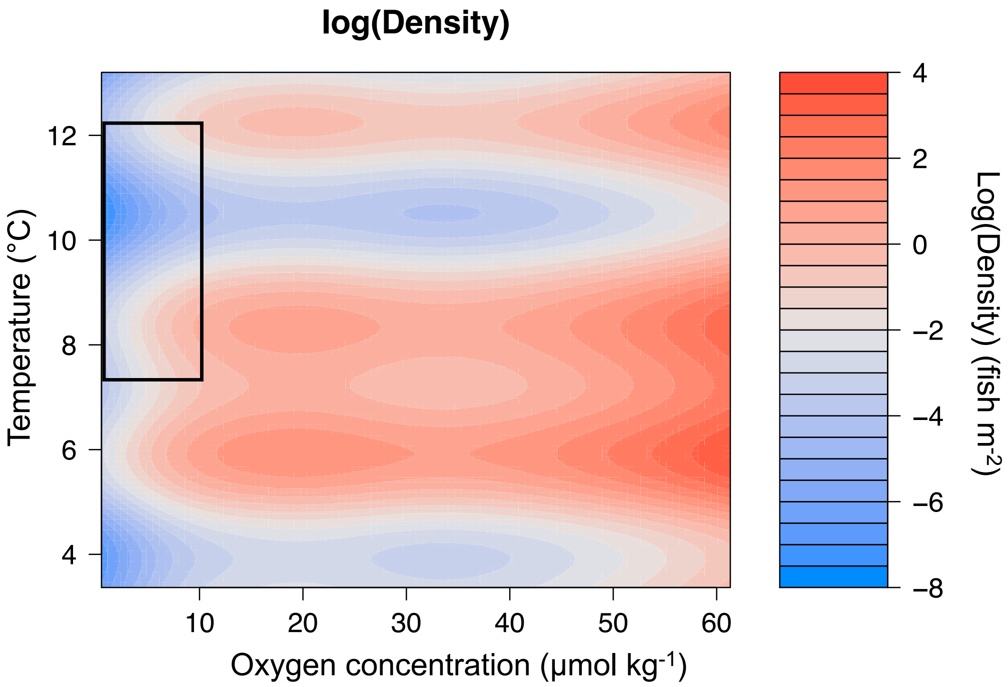
Supplementary Item 5



Ordination diagram visualizing the results of the canonical correspondence analysis. All four environmental variables included in the model (temperature, oxygen, latitude, and depth) were found to be significant ($p < 0.05$) and the model could constrain 25.7% of the inertia (ie. weighed variance) in the dataset. Red "+" denote species and black circles denote transects. Arrows show quantitative environmental variables.

Supplementary Item 6

Result of the Generalized Additive Model (GAM) for Gulf of California deep-sea demersal fish community density trends. The model with the greatest support was: Log(Density) = s1(Lat) + s2(T) + s3(Ox). Here we present a 2D component plots that shows log(density) as the response, in relation to both oxygen (x-axis) and temperature (y-axis). Warmer colors indicate higher density values, while cooler colors indicate lower density values. The area in the black box is highlighted to draw attention to the fact that under low oxygen conditions, fish density is predicted to be negatively impacted once temperatures are warmer than ~9.5°C. This suggests an interaction between oxygen and temperature leading to metabolic constraints on fish habitat.



Supplementary Item 7

Prior to this study, 77 demersal fish species globally were described from OMZ habitats (Gallo and Levin 2016). This study expands this list to 95 species. Newly added species, or species for whom new details were added, are indicated in gray.

	Common Name	Location	Depth Range (m)	Temp Range (°C)	Oxygen Range (µmol/kg)	Citations
Myxiniformes						
Myxinidae						
Eptatretus deani	Black hagfish	US Pacific margin (northeastern Pacific)	366-2743	3.6-6.4	13.1-58.2	N.D. Gallo unpublished, Day and Pearcy (1968)
Eptratretus sp.	Hagfish	Canada Pacific margin (northeastern Pacific)	890	3.6-4.0	10.5-15.3	Juniper et al. (2013)
Eptatretus sinus	Cortez hagfish	Gulf of California	263-1080	5.0-12.1	2.7-35.0	This study
Squaliformes						
Etmopteridae						
Etmopterus sp.	Lantern shark	Indian margin (Arabian Sea)	-	-	-	Hunter et al. (2011)
Centroscyllium ornatum	Ornate dogfish	Pakistan margin (Arabian Sea)	1000-1200	7.4-8.7	6.7-17.0	Murty et al. (2009)
Centrophoridae						
Centrophorus granulosus	Gulper shark	Yemen margin (Arabian Sea)	50-1440	5.2-12.9	13.3-212.7	Kukharev (2015)
Carcharhiniformes						
Scyliorhinidae						
Apristurus brunneus	Brown catshark	California margin (northeastern Pacific)	79-1448	2.9-5.4	13.1-70.9	N.D. Gallo unpublished
Parmaturus xaniurus	Filetail catshark	California margin to Gulf of California (northeastern Pacific)	88-1250	3.3-11.59	1.43-143.5	N.D. Gallo unpublished, This study
Cephalurus cephalus	Lollipop shark	Gulf of California	275-927	5.3-9.4	0.8-6.1	Aguirre-Villaseñor and Salas-Singh (2012), This study
Halaelurus spp.	Tiger catshark	Yemen margin (Arabian Sea)	-	-	13.3	Kukharev (2015)
Cephalurus sp. cf.	Catshark	Chilean margin (southeastern Pacific)	313-327	10.9-11.5	3.0-3.84	J. Sellanes (UCN) unpublished
Proscylliidae						
Eridacnis radcliffei	Pygmy ribbontail catshark	Yemen margin (Arabian Sea)	71-766	-	13.3-174.9	Kukharev (2015)
Rajiformes						
Arhynchobatidae						
Bathyraja interrupta	Sandpaper skate	Oregon margin (northeastern Pacific)	64-1500	3.1-8.3	13.1-273.4	Day and Pearcy (1968)
Bathyraja trachura	Roughtail skate	Oregon margin (northeastern Pacific)	213-2550	1.6-7.0	18.4-156.2	Day and Pearcy (1968)
Bathyraja sp.	Skate	Indian margin (Arabian Sea)	-	-	-	Hunter et al. (2011)
Pleuronectiformes						
Pleuronectidae						
Microstomus pacificus	Dover sole	US Pacific margin (northeastern Pacific)	10-1370	2.9-11.5	13.1-318.9	Friedman et al. (2012), Day and Pearcy (1968)
Embassichthys bathybius	Deep-sea sole	US and Canada Pacific margin (northeastern Pacific)	125-1800	2.4-6.4	13.1-54.3	N.D. Gallo unpublished, Day and Pearcy (1968), Juniper et al. (2013)
Lyopsetta exilis	Slender sole	US and Saanich Inlet (northeastern Pacific)	25-800	4.2-8.7	14.0-244.6	Matabos et al. (2012), Chu and Tunnicliffe (2015)
Paralichthyidae						

Hippoglossina macrops	Bigeye flounder	Chilean margin (southeastern Pacific)	34-580	10.6-16.5	22-83.5	J. Sellanes (UCN) unpublished
Bothidae						
Monolene maculipinna	Pacific deepwater flounder	Costa Rica to Peru (eastern tropical Pacific)	205-384	13.0-27.5	16.2-175.4	Bianchi et al. (1991)
Soleidae						
Austroglossus microlepis	West coast sole	Namibia to South Africa (southeastern Atlantic)	100-400	7.8-14.5	16.0-218.9	Hamukuaya et al. (2001)
Symphurus spp.	Tonguefish	Gulf of California	224-1010	7.9-13.0	2.69-55.28	This study
Anguilliformes						
Nettastomatidae						
Facciolella equatorialis	Dogface witch-eel	California margin (northeastern Pacific)	500-1000	6.2-8.2	9.2-47.7	N.D. Gallo unpublished
Nettastoma sp.	Duckbill eel	Yemen margin (Arabian Sea)	-	-	13.3	Kukharev (2015)
Congridae						
Congridae sp.	Conger eel	Indian margin (Arabian Sea)	-	-	-	Hunter et al. (2011)
Congridae sp.	Conger eel	Pakistan margin (Arabian Sea)	1200	7.4	13.4-17.0	Murty et al. (2009)
Bathycongrus macrurus	Shorthead conger	Gulf of California	298-544	7.32-11.61	0.65-12.19	This study
Synaphobranchidae						
Synaphobranchus sp.	Cutthroat eel	Indian margin (Arabian Sea)	-	-	-	Hunter et al. (2011)
Serrivomeridae						
Serrivomer sp.	Sawtooth eel	Pakistan margin (Arabian Sea)	1100	8	9.4-11.2	Murty et al. (2009)
Notacanthiformes						
Halosauridae						
Halosaurus sp.	Halosaur	Pakistan margin (Arabian Sea)	1200	7.4	13.4-17.0	Murty et al. (2009)
Notocanthidae						
Notocanthus sp.	Deep-sea spiny eel	Pakistan margin (Arabian Sea)	1100	8	9.4-11.2	Murty et al. (2009)
Aulopiformes						
Synodontidae						
Saurida tumbil	Greater lizardfish	Pakistan margin (Arabian Sea)	4-700	11.0-26.6	4.9-206.5	Murty et al. (2009)
Saurida undosquamis	Brushtooth lizardfish	Yemen margin (Arabian Sea)	1-350	11.3-28.3	13.3-210.9	Kukharev (2015)
Harpadon squamosus	Lizardfish	Yemen margin (Arabian Sea)	-	-	13.3	Kukharev (2015)
Ipnopidae						
Bathypterois sp.	Tripodfish	Gulf of California	863-1356	3.3-5.1	4.1-21.7	This study
Beryciformes						
Trachichthyidae						
Hoplostethus spp.	Roughy	Yemen margin (Arabian Sea)	-	-	13.3	Kukharev (2015)
Perciformes						
Stichaeidae						

Cherublemma emmelas	Black brotula	Baja California to Northern Chile (eastern tropical Pacific)	15-902	4.7-20.4	0.5-219.6	Aguirre-Villaseñor and Castillo-Velázquez (2011), Bianchi et al. (1991), Stromme and Saetersdal (1988), This study
Holcomycteronus sp.	Cusk-eel	Indian margin (Arabian Sea)	-	-	-	Hunter et al. (2011)
Brotulotaenia sp.	Cusk-eel	Pakistan margin (Arabian Sea)	1000-1200	7.4-8.7	6.7-17.0	Murty et al. (2009)
Genypterus maculatus	Black cusk-eel	Chilean margin (southeastern Pacific)	82-328	9.2-11.8	17.9-50.9	Chilean Fisheries Development Program, FIP2004-09
Genypterus blacodes	Rock ling	Chilean margin (southeastern Pacific)	58-450	7.2-11.3	21.7-110.4	Chilean Fisheries Development Program, FIP2004-09
Eretmichthys pinnatus	Cusk-eel	Gulf of California	867-1264	3.7-5.1	4.2-21.4	This study
Gadiformes						
Macrouridae						
Nezumia liolepis	Smooth grenadier	Volcano 7 (eastern equatorial Pacific), US Pacific margin (northeastern Pacific), Gulf of California	450-1660	4.5-6.5	3.5-43.8	Friedman et al. (2012), Wishner et al. (1990, 1995), Levin et al. (1991), This study
Coryphaenoides acrolepis	Strong-scaled rattail	Oregon margin (northeastern Pacific)	300-3700	1.7-6.9	18.8-158.8	Day and Pearcy (1968)
Coryphaenoides pectoralis	Pectoral rattail	Oregon margin (northeastern Pacific)	140-3500	1.8-4.6	17.1-256.4	Day and Pearcy (1968)
Coryphaenoides sp.	Grenadier	Indian margin (Arabian Sea)	-	-	-	Hunter et al. (2011)
Coryphaenoides capito	Bighead grenadier	Gulf of California	921	5	4.1	This study
Trachyrincus villegai	Grey grenadier	Northern Peru to Central Chile (southeastern Pacific)	250-980	-	2.6	Quiroga et al. (2009)
Merlucciidae						
Merluccius productus	North Pacific hake	US Pacific margin (northeastern Pacific), Saanich Inlet	3-1000	1.6-23.0	13.1-241.1	Chu and Tunnicliffe (2015)
Merluccius angustimanus	Panama hake	Mexico-Columbia (eastern tropical Pacific)	2-523	15.4-21.1	17.5-222.7	Bianchi et al. (1991), Stromme and Saetersdal (1988)
Merluccius capensis	Cape hake	Angola to South Africa (southeastern Atlantic)	20-512	6.1-19.8	10.9-236.7	Hamukuaya et al. (2001), Mas-Reira et al. (1990), Woodhead et al. (1996)
Merluccius gayi gayi	Whiting	Chilean margin (southeastern Pacific)	58-450	6.4-12.3	16.8-253.0	Chilean Fisheries Development Program, FIP2004-09
Merluccius sp.	Hake	Gulf of California	339-457	8.2-11.5	5.3-28.5	This study
Bregmacerotidae						
Bregmaceros bathymaster	East Pacific codlet	Gulf of California (eastern tropical Pacific)	32-500	7.6-15.4	9.2-31.5	Davies et al. (2015)
Bregmaceros cantori	Striped codlet	Cariaco Trench, Venezuela to Brazil (western Atlantic)	450-846	14.2-26.9	4.0-222.7	Baird et al. (1973), Milliken and Houde (1984), Love et al. (2004)

Plectobranchus evides	Bluebarred prickleback	Saanich Inlet (northeastern Pacific)	84-368	7.6-8.6	7.9-205.6	Chu and Tunnicliffe (2015), Matabos et al. (2012)
Agonidae						
Xeneretmus latifrons	Blacktip poacher	US Pacific margin, Saanich Inlet (northeastern Pacific)	18-486	4.6-8.7	7.4-244.6	Chu and Tunnicliffe (2015), Matabos et al. (2012)
Bathyagonus nigripinnis	Blackfin starsnout poacher	Canada Pacific margin (northeastern Pacific)	18-1290	3.0-8.3	10.5-201.7	Juniper et al. (2013)
Zoarcidae						
Zoarcid sp.	Eelpout	Canada Pacific margin (northeastern Pacific)	890	3.6-4	10.5-15.3	Juniper et al. (2013)
Lycenchelys spp.	Eelpout	Gulf of California	894-1355	3.3-5.0	4.0-21.9	This study
Derepodichthys alepidotus	Cuskpout	Gulf of California	1182	3.98	16.57	This study
Serranidae						
Diplectrum macropoma	Mexican sand perch	Mexico to Peru (eastern tropical Pacific)	1-220	16.6-16.8	17.5-120.3	Bianchi et al. (1991)
Serranidae sp.	Serranid	Gulf of California	223-227	11.8	3.2-3.5	This study
Trichiuridae						
Trichiurus nitens	Pacific cutlassfish	Mexico to Peru (eastern tropical Pacific)	160-250	13	17.5	Bianchi et al. (1991)
Lepturacanthus spp.	Hairtail	Yemen margin (Arabian Sea)	-	-	13.3	Kukharev (2015)
Gobiidae						
Sufflogobius bibarbatus	Bearded goby	Namibia and South Africa (southeastern Atlantic)	10-340	7.8-14.5	10.0-218.8	Hamukuaya et al. (2001), Mas-Reira et al. (1990), Utne-Palm et al. (2010), Salvanes et al. (2011)
Carangidae						
Trachurus trachurus capensis	Horse mackerel	Gulf of Guinea to South Africa (southeastern Atlantic)	0-500	5.4-22.0	16-252.0	Hamukuaya et al. (2001)
Carangidae sp.	Carangid	Pakistan margin (Indian Ocean)	300	14.8	4.9-5.4	Murty et al. (2009)
Epigonidae						
Epigonus sp.	Deepwater cardinalfish	Pakistan margin (Arabian Sea)	140	18.2	4.9	Murty et al. (2009)
Acropomatidae						
Synagrops adeni	Aden splitfin	Yemen margin (Arabian Sea)	60-600	-	13.3	Kukharev (2015)
Percophidae						
Bembrops caudimacula	Opal fish	Yemen margin (Arabian Sea)	160-505	14.4-17.4	13.3-192.3	Kukharev (2015)
Centrolophidae						
Psenopsis cyanea	Indian ruff	Yemen margin (Arabian Sea)	179-400	-	15.5-55.5	Kukharev (2015)
Scombridae						
Scomber australasicus	Japanese mackerel	Yemen margin (Arabian Sea)	9-494	7.7-24.0	13.3-279.7	Kukharev (2015)
Ophidiiformes						
Bythitidae						
Cataetyx rubrirostris	Rubynose brotula	US Pacific margin (northeastern Pacific)	288-1000	4.9	9.0-20.6	N.D. Gallo unpublished
Ophidiidae						

Bregmaceros sp.	Codlet	Indian margin (Arabian Sea)	540	12.1	0.34	Hunter et al. (2011)
Bregmaceros sp.	Codlet	Pakistan margin (Indian Ocean)	300	14.8	4.9-5.4	Murty et al. (2009)
Moridae						
Physiculus roseus	Rosy cod	Yemen margin (Arabian Sea)	277-510	-	13.3	Kukharev (2015)
Physiculus rastrelliger	Hundred fathom mora	Gulf of California	216-483	8.3-13.5	1.1-69.0	This study
Osmeriformes						
Argentinidae						
Argentina aliceae	Alice argentina	Nicaragua to Peru (eastern tropical Pacific)	73-300	13.8-17.1	16.2-46.4	Bianchi et al. (1991)
Cottiformes						
Liparidae						
Careproctus melanurus	Blacktail snailfish	US Pacific margin (northeastern Pacific)	89-2286	1.8-7.2	13.1-133.0	Friedman et al. (2012), Day and Pearcy (1968), Stein et al. (2006)
Liparidae sp.	Snailfish	Indian margin (Arabian Sea)	540	12.1	0.34	Hunter et al. (2011)
Paraliparis rosaceus	Pink snailfish	Gulf of California	935-1348	3.4-4.8	6.5-17.8	This study
Scorpaeniformes						
Scorpaenidae						
Pontinus sierra	Speckled scorpionfish	Gulf of CA to Panama (eastern tropical Pacific)	15-307	11.1-13.6	1.8-20.1	Bianchi et al. (1991), This study
Pontinus furcirhinus	Red scorpionfish	Gulf of California	197-387	10.4-13.9	6.4-79.4	This study
Sebastidae						
Sebastolobus alascanus	Shortspine thornyhead	US Pacific margin (northeastern Pacific)	54-1600	3.5-7.8	13.1-171.9	Friedman et al. (2012), Day and Pearcy (1968)
Sebastolobus altivelis	Longspine thornyhead	US Pacific margin (northeastern Pacific)	201-1757	2.7-8.6	13.1-112.4	Friedman et al. (2012), Day and Pearcy (1968)
Sebastolobus sp.	Thornyhead	Canada Pacific margin (northeastern Pacific)	890	3.6-4	10.5-15.3	Juniper et al. (2013)
Sebastes cortezi	Cortez rockfish	Gulf of California	199-1448	7.3-14.3	1.8-91.1	This study
Anoplopomatidae						
Anoplopoma fimbria	Sablefish	US and Canada Pacific margin (northeastern Pacific)	175-2740	1.8-14.6	13.1-318.9	Friedman et al. (2012), Day and Pearcy (1968), Juniper et al. (2013)
Triglidae						
Chelidonichthys capensis	Gurnard	Southeastern Atlantic and Western Indian Ocean	10-390	6.1-20.5	16-222.3	Hamukuaya et al. (2001), Mas-Reira et al. (1990)
Peristediidae						
Satyrichthys adeni	Yellowfinned searobin	Yemen margin (Arabian Sea)	71-378	7.9-17.3	13.3-213.1	Kukharev (2015)
Batrachoidiformes						
Batrachoididae						
Aphos porosus	Banded toadfish	Chilean margin (southeastern Pacific)	11-120	14.8-16.5	22-84.4	J. Sellanes (UCN) unpublished
Porichthys mimeticus	Mimetic midshipman	Gulf of California	223-229	11.6-11.8	3.1-3.7	This study
Lophiiformes						

Ogcocephalidae						
Dibranchus spinosus	Batfish	Gulf of California	723-1243	3.8-6.1	1.3-19.4	This study
Dibranchus hystrix	Batfish	Gulf of California	922-1184	3.9-5.0	4.0-16.7	This study
Lophiidae						
Lophiodes caulinaris	Spottedtail angler	Gulf of California	217-888	10.5-12.1	3.0-29.5	This study

CHAPTER 4

Home sweet suboxic home: Remarkable hypoxia tolerance in two demersal fish species in the Gulf of California

Natalya D. Gallo, Lisa A. Levin, Maryanne Beckwith, and James P. Barry

Extremophiles – organisms that live in extreme environments – invite us to question our assumptions about the requirements for life. Fish, as a group, are thought to be relatively hypoxia intolerant due to their high metabolic requirements (Vaquer-Sunyer and Duarte 2008), however, the cusk-eel, *Cherublemma emmelas*, and the catshark, *Cephalurus cephalus*, appear to thrive in one of the most extreme low oxygen marine habitats in the world – the Gulf of California. Here, we describe the behavior and habitat of these extraordinary species that live under conditions commonly thought to be uninhabitable by fish.

During MBARI's Gulf of California Expedition (March 21-29, 2015), eight dives were conducted during daytime hours (~7 am-7 pm) with the remotely operated vehicle (ROV) *Doc Ricketts*. The ROV conducted seafloor transects from depths of ~200-1400 m, representing a total of 60 hours of seafloor video footage that was annotated for fish observations. The ROV was equipped with environmental sensors, including dissolved oxygen, allowing all fish observations to be paired with corresponding environmental data. ROVs are considered a good method for studying deep-sea fish communities, as they do not typically affect demersal fish behavior or abundances (Ayma et al. 2016).

The Gulf of California has a thick oxygen minimum zone (OMZ) in the central and southern Gulf, with severely hypoxic conditions extending from ~100 m to over 1300 m deep, and suboxic conditions ($O_2 < 5$ μmol kg^{-1}) present for over 500 m of the water column (Hendrickx and Serrano 2014). Despite the extensive hypoxic conditions, we observed high densities of demersal fishes (3.26 fish m^{-2}) living where oxygen conditions were 1.61 μmol kg^{-1} (pO_2 = 0.12 kPa) (Fig. 4.1 A).

While most aerobic organisms are excluded from suboxic areas due to insufficient oxygen supply (Hofmann et al. 2011), the ophidiid, *Cherublemma emmelas* (Fig. 4.1 B, D), and the scyliorhinid, *Cephalurus cephalus* (Fig. 4.1 C), appear to thrive in the suboxic Gulf environment. The peak distribution for both species was at oxygen levels between 1.5-2 μmol kg^{-1} O_2 (pO_2 = 0.1-0.15 kPa) (Fig. 4.2), corresponding to depths between 600-900 m, where they were present in both soft sediment and rocky bottom areas. *C. emmelas* was the most abundant demersal fish species observed in our study, as well as captured during the TALUD cruises in the Gulf (Zamorano et al. 2014). We also observed the macrourid, *Nezumia liolepis*, and the ogcocephalid, *Dibranchus spinosus*, living under suboxic conditions, however, their range extended into more oxygenated areas, where *C. emmelas* and *C. cephalus* were absent.

To appreciate how extreme these observations are, a recent meta-analysis of fish hypoxia tolerance found that the mean critical oxygen threshold (P_{crit}) for fishes was 5.15 +/- 2.21 kPa, and ranged from 1.02-16.2 kPa (Rogers et al. 2016). At oxygen levels below P_{crit}, an animal can no longer maintain a stable rate of oxygen uptake. Similarly, previous studies have reported the P_{crit} of hypoxia-tolerant fishes ranging from 0.80-5.33 kPa (Nilsson 2010). Therefore, the oxygen conditions we describe these Gulf of California fishes living under are several times lower than the critical oxygen limits for even the most hypoxia-tolerant fishes known, and are ~27 times lower than the mean oxygen habitat for hypoxia-tolerant fishes in the N. Pacific (Chu and Tunnicliffe 2015).

C. emmelas individuals were even observed in areas where sheared sediment slopes revealed laminated sediments (O_2 < 1 μmol kg^{-1}, pO_2 <0.08 kPa), suggesting that in the recent past oxygen conditions were too low to support bioturbation activity by infauna. These fish were observed swimming over a featureless, depauperate sediment seafloor, resembling a moonscape. While some benthic macrofauna live in areas with laminated sediments (Calvert 1964), prior to this study, fish were not expected to tolerate hypoxic conditions this severe.

Thus, areas with laminated sediments in the paleo-oceanographic record could also potentially have hosted highly adapted fish communities.

Most studies on hypoxia-tolerant species come from environments that experience periodic, and not chronic, hypoxia. The best-studied vertebrate models – the crucian carp (Fagernes et al. 2017) and the freshwater turtle (Jackson 2002) – live in seasonally ice-covered ponds. Other fishes including hypoxia-tolerant tide pool sculpins (Mandic et al. 2009) and hypoxia-tolerant flatfish in fjords (Chu et al. 2018), make use of daily or seasonal oxygen variability to survive oxygen conditions lower than their lethal limits.

In contrast, the OMZ environment that *C. emmelas* and *C. cephalus* live in is relatively stable, compared to shallower systems. Suboxic conditions are extensive in the southern Gulf (~700 m thick), so frequent migration into more oxygenated waters is an unlikely strategy, and neither *C. emmelas* nor *C. cephalus* are known to migrate. Both species were abundant in suboxic areas and absent from areas with higher oxygen levels, suggesting a preference for these conditions. Previous trawl-based studies also report *C. emmelas* and *C. cephalus* living under severely hypoxic conditions (Aguirre-Villaseñor and Castillo-Velázquez 2011, Aguirre-Villaseñor and Salas-Singh 2012).

The adaptations that allow *C. emmelas* and *C. cephalus* to thrive under suboxic conditions are poorly known. Three categories of strategies are consistently used by hypoxia-tolerant animals: reduced oxygen demand, increased capacities for oxygen uptake and storage, and greater use of anaerobic pathways (Nilsson 2010). Both *C. emmelas* and *C. cephalus* appear to have increased their oxygen uptake ability through enlargement of gill surface area for gas exchange. The large head and expanded gills of *C. cephalus* (Fig. 4.1 C) have previously been noted as a hypoxia adaptation (Compagno 1984), and *C. emmelas* specimens collected in this study had large, bright red gills. Increased gill surface area appears to be a very common hypoxia adaptation, and among vertebrates, salamanders also develop enlarged external gills under hypoxic conditions (Iwami et al. 2007). *C. emmelas* has thin and weakly developed bones (Nielsen et al. 1999), which may also reduce energetic requirements. Both species are small; we observed individuals of *C. emmelas* ranging from ~8-30 cm in length, and *C. cephalus* from ~8-40 cm. We also suspect that both species have very low metabolic rates and high hemoglobin-O_2-binding affinity, as has been found in other hypoxia-tolerant fish (Mandic et al. 2009), but no physiological measurements are available. Both species would be excellent candidates for an in-depth study of hypoxia adaptations, as was recently done for the hypoxia-tolerant bearded goby on the Namibian margin (Salvanes and Gibbons 2018).

While *C. emmelas* and *C. cephalus* individuals were mainly observed actively swimming in this study, more than 20 observations were made of *C. emmelas* individuals resting with their heads buried in the sediment (Fig. 4.1 B) or, in one instance, pushed under a large bone on the seafloor. Individuals were alive and able to swim away when disturbed. These fish did not appear to be actively feeding, and no opercular movements were observed. It is unclear if fish were anchoring against the current. While no current measurements were taken, a weak current can be observed in the video based on particle motion. This behavior (ie. head burial) appeared more commonly for individuals living in areas at the lower end of their oxygen niche ($O_2 < 1$ μmol kg^{-1}, pO_2 <0.08 kPa), suggesting that it may be a behavioral adaptation for hypoxia tolerance, but runs counter to the expectation for fish to maximize water flow over their gills under hypoxic conditions.

The observations of *C. emmelas* and *C. cephalus* reported here suggest that demersal fish have the potential for much higher hypoxia tolerance than previously appreciated. *C. emmelas* and *C. cephalus* have ranges that extend throughout the Eastern Tropical Pacific, which contains the greatest volume of suboxic water in the world (Deutsch et al. 2011). These conditions likely created strong selective pressure for the evolution of extreme hypoxia tolerance in these species. While previous studies have focused predominantly on hypoxia tolerance of bony fishes, our observations suggest that the potential for hypoxia tolerance is similar for cartilaginous and bony fishes, since *C. cephalus* is cartilaginous, and *C. emmelas* is bony.

While there are terms for other extremophiles (e.g. high salinity = halophile, high temperature = hyperthermophile), there is no term for an aerobic organism specialized for extremely low oxygen environments. We propose the term "ligooxyphile" (leego-oxy-phile), from the Greek roots for "little oxygen lover" to describe aerobic animals that are extremophiles of low oxygen habitats. Apart from *C. emmelas* and *C. cephalus*, the Gulf of California is home to other ligooxyphiles, including the codlet, *Bregmaceros bathymaster* (Davies et al. 2015), and the gastropods, *Lucinoma heroica* and *Dacrydium pacificum* (Zamorano et al. 2007).

Understanding tolerance ranges of species to hypoxia takes on new relevance as the world's low oxygen zones expand (Breitberg et al. 2018). As climate change tightens metabolic constraints on marine species due to the combination of warming and oxygen loss (Deutsch et al. 2015), species that are already highly adapted to metabolically challenging conditions may expand their habitats (Sato et al. 2017). Irrespective of their status as climate change winners or losers, these remarkable species have much to teach us about the aerobic limits for life. Comparing the adaptations and tolerances of ligooxyphiles across low oxygen systems (e.g. oxygen minima, caves, ice-covered ponds, fjords) can provide insights into ecological endpoints, and may even provide some inference concerning the potential for life in extraterrestrial low-oxygen, oceanic systems, such as Europa (Hand et al. 2007).

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Literature Cited

Aguirre-Villaseñor, H., and Castillo-Velázquez, R. 2011. New depth record of *Cherublemma emmelas*, black brotula (Ophidiiformes: Ophidiidae) from the Gulf of California, Mexico. *Revista Mexicana de Biodiversidad* 82:713-715.

Aguirre-Villaseñor, H., and Salas-Singh, C. 2012. New records of the lollipop catshark *Cephalurus cephalus* (Scyliorhinidae) from the Gulf of California, Mexico. *Revista Mexicana de Biodiversidad* 83:298-300.

Ayma, A., Aguzzi, J., Canals, M., Lastras, G., Bahamon, N., Mecho, A., Company, J.B. 2016. Comparison between ROV video and Agassiz trawl methods for sampling deep water fauna of submarine canyons in the Northwestern Mediterranean Sea with observations on behavioural reactions of target species. Deep-Sea Res. I 114: 149-159.

Breitburg, D., Levin, L.A., Oschlies, A., Grégoire, M., Chavez, F.P., Conley, D.J., Garçon, V., Gilbert, D., Gutiérrez, D., Isensee, K., Jacinto, G.S., Limburg, K.E., Montes, I., Navqi, S.W.A., Pitcher, G.C., Rabalais, N.N., Roman, M.R., Rose, K.A., Seibel, B.A., Telszewski, M., Yasuhara, M., and Zhang, J. 2018. Declining oxygen in the global ocean and coastal waters. *Science* 359(6371):eaam7240.

Calvert, S.E. 1964. Factors affecting distribution of laminated diatomaceous sediments in Gulf of California. In T. H. Van Andel and G. G. Shor Jr. (eds.), Marine Geology of the Gulf of California: A Symposium, pp. 311–330.

Chu, J.W.F., and Tunnicliffe, V. 2015. Oxygen limitations on marine animal distributions and the collapse of epibenthic community structure during shoaling hypoxia. *Glob. Change Biol.* 21(8): 2989–3004.

Chu, J.W.F., Curkan, C., Tunnicliffe, V. 2018. Drivers of temporal beta diversity of a benthic community in a seasonal hypoxic fjord. R. Soc. open sci 5: 172284.

Compagno, L.J.V. 1984. FAO species catalogue. Vol. 4. Sharks of the World. An annotated and illustrated catalogue of shark species known to date. FAO Fisheries Synopsis No. 125, 4:1–655.

Davies, S.M., Sánchez-Velasco, L., Beier, E., Godínez, V.M., Barton, E.D., and Tamayo, A. 2015. Three-dimensional distribution of larval fish habitats in the shallow oxygen minimum zone in the Eastern Tropical Pacific Ocean off Mexico. *Deep-Sea Res. I* 101:118–129.

Deutsch, C., Brix, H., Ito, T., Frenzel, H., Thompson, L. 2011. Climate-forced variability of ocean hypoxia. Science 333: 336-339.

Deutsch, C., Ferrel, A., Seibel, B., Pörtner, H.-O., and Huey, R.B. 2015. Climate change tightens a metabolic constraint on marine habitats. *Science* 348:1132–1136.

Fagernes, C.E., Stensløkken, K.-O., Røhr, A.K., Berenbrink, M., Ellefsen, S., and Nilsson, G.E. 2017. Extreme anoxia tolerance in crucian carp and goldfish through neofunctionalization of duplicated genes creating a new ethanol-producing pyruvate decarboxylase pathway. *Scientific Reports* 7:7884.

Hand, K.P., Carlson, R.W., and Chyba, C.F. 2007. Energy, chemical disequilibrium, and geological constraints on Europa. *Astrobiology* 7(6):1006-1022.

Hendrickx, M.E., and Serrano, D. 2014. Effects of the oxygen minimum zone on squat lobster distributions in the Gulf of California, Mexico. *Cent. Eur. J. Biol.* 9(1):92-103.

Hofmann, A.F., Peltzer, E.T., Walz, P.M., and Brewer, P.G. 2011. Hypoxia by degrees: establishing definitions for a changing ocean. *Deep-Sea Res. I* 58:1212–1226.

Iwami, T., Kishida, O., Nishimura, K. 2007. Direct and indirect induction of a compensatory phenotype that alleviates the cost of an inducible defense. PLoS ONE 2(10): e1084.

Jackson, D.C. 2002. Hibernating without oxygen: Physiological adaptations of the painted turtle. *J. Physiol.* 543(3):731-737.

Levin, L.A. 2003. Oxygen minimum zone benthos: adaptation and community response to hypoxia. *Ocean. Mar. Biol. Ann. Rev.* 41:1-45.

Mandic, M., Todgham, A.E., Richards, J.G. 2009. Mechanisms and evolution of hypoxia tolerance in fish. Proc. R. Soc. B 276: 735-744.

Nielsen, J.G., Cohen, D.M., Markle, D.F., and Robins, C.R. 1999. Ophidiiform fishes of the world (Order Ophidiiformes): An annotated and illustrated catalogue of pearlfishes, cusk-eels, brotulas and other ophidiiform fishes known to date. FAO Fisheries Synopsis 125(18):1-190.

Nilsson, G.E. 2010. Respiratory physiology of vertebrates: Life with and without oxygen. Cambridge University Press, New York, 334 pgs.

Rogers, N.J., Urbina, M.A., Reardon, E.E., McKenzie, D.J., Wilson, R.W. 2016. A new analysis of hypoxia tolerance in fishes using a database of critical oxygen level (P_{crit}). Conservation Physiology 4(1): 1-19.

Salvanes A.G.V., and Gibbons, M.J. 2018. Adaptation to hypoxic environments; bearded gobies *Sufflogobius bibarbatus* in the Benguela upwelling system. *J. Fish Biol.* 92(3): 752-772.

Sato, K.N., Levin, L.A., Schiff, K. 2017. Habitat compression and expansion of sea urchins in response to changing climate conditions on the California continental shelf and slope (1994-2013). Deep-Sea Res. II 137: 377-389.

Vaquer-Sunyer, R., and Duarte, C.M. 2008. Thresholds of hypoxia for marine biodiversity. *Proc. Natl. Acad. Sci.* 105:15452–15457.

Zamorano, P., Hendrickx, M.E., and Toledano-Granados, A. 2007. Distribution and ecology of deep-water mollusks from the continental slope, southeastern Gulf of California, Mexico. *Mar. Biol.* 150(5):883-892.

Zamorano, P., Hendrickx, M.E., Méndez, N., Goméz, S., Serrano, D., Aguirre, H., Madrid, J., and Morales-Serna, N. 2014. La exploración de las aguas profundas del Pacífico mexicano: el proyecto TALUD. La Frontera Final: El Océano Profundo. Instituto Nacional de Ecología, Secretaría del Medio Ambiente y Recursos Naturales (SEMARNAT) 293 p:105-147.

Figures

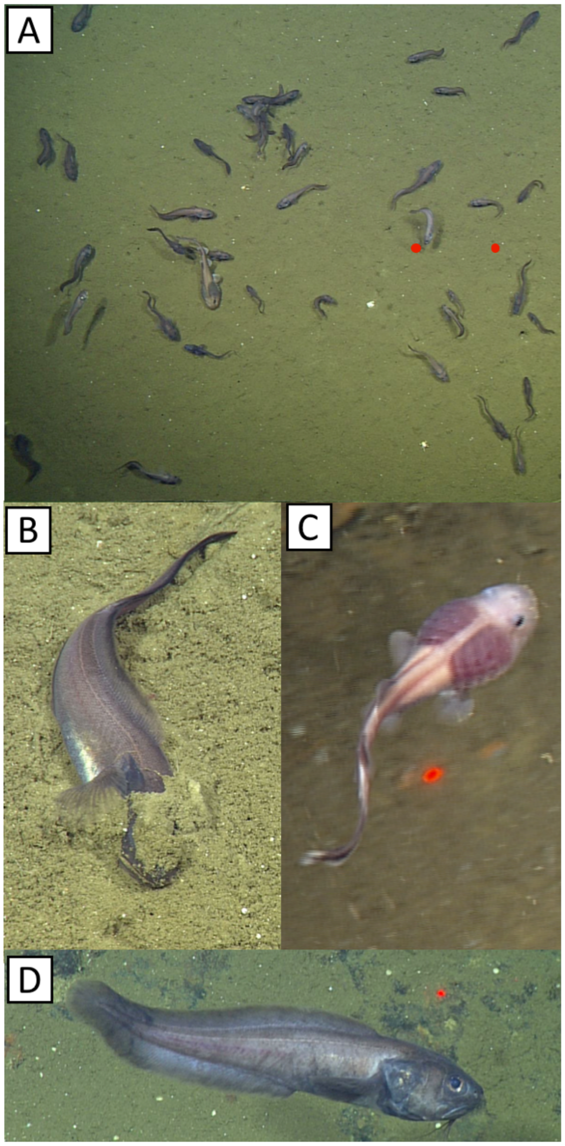

Figure 4.1. High density fish aggregations (3.26 fish m^{-2}) of *Cherublemma emmelas* and *Cephalurus cephalus* were observed in the Gulf of California under suboxic conditions (pO$_2$ = kPa, [O$_2$] = 1.61 µmol kg^{-1}) at 774 m. Red lasers are shown for scale on the right of the image and are 29 cm apart. B. *C. emmelas* individuals were periodically observed with their heads buried in the sediment. C. The lighter coloration of a juvenile *C. cephalus* clearly reveals the extensive gill chambers that allow for increased oxygen uptake in this species and inspire its charismatic common name, "lollipop shark". D. *C. emmelas* were typically observed swimming. Additional video to supplement these images is available at: https://drive.google.com/open?id=1nepIOakzJcCNZXdYGDy7dJc6EEOgZ7Pi. *Dibranchus spinosus* and *Nezumia liolepis* are also observed in the video footage.

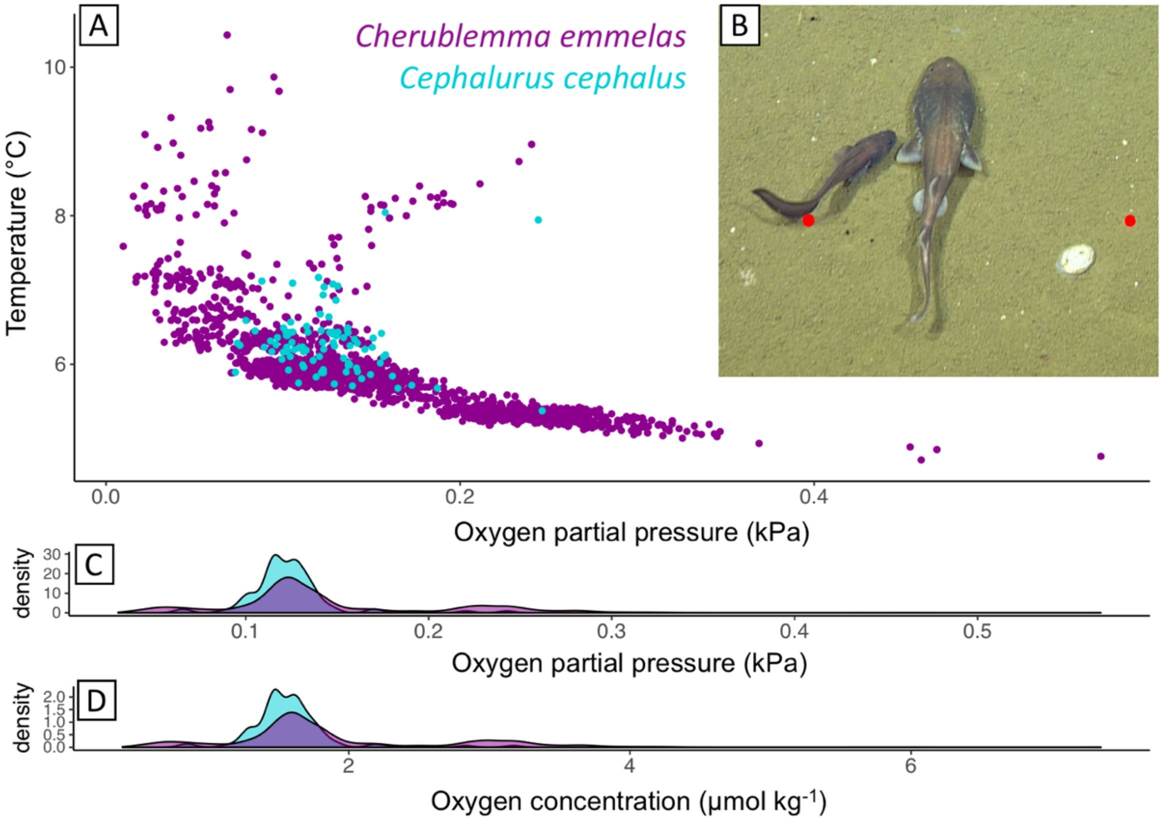

Figure 4.2. The cusk-eel, *Cherublemma emmelas*, and catshark, *Cephalurus cephalus*, display remarkable hypoxia tolerance in the Gulf of California. Oxygen and temperature niches (A) for the two ligooxyphiles (i.e. low-oxygen extremophiles) are shown by plotting each unique video observation of individuals of the two species, from the 60 hours of ROV seafloor video footage, in oxygen-temperature space (n = 2137 *C. emmelas* observations, purple points; n = 95 *C. cephalus* observations, turquoise points). Inset image (B) shows the two species (*C. emmelas* on left, *C. cephalus* on right) for relative size (red lasers are 29 cm apart). Marginal density of occurrence (representing probability of occurrence) for these two species are shown along oxygen axes, showing both oxygen partial pressure (kPa) (C) and oxygen concentration (µmol kg^{-1}) (D). Highest probability of occurrence occurs in areas with $pO_2 < 0.15$ kPa and $[O_2] < 2$ µmol kg^{-1}. Raw data with other oxygen units (ml l^{-1}, mg l^{-1}, mmHg, and matm) and code to reproduce this figure is available: 10.5281/zenodo.1256998.

CHAPTER 5

Characterizing deep-water oxygen variability in the Southern California Bight and seafloor community responses

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Abstract

When scientists study climate change, the focus is usually on changes to the mean conditions. However, animals live in temporally variable environments, and studies from shallow-water systems show that this natural variability influences organism exposure histories and vulnerability to climate change. One manifestation of climate change, decreasing ocean oxygen, has been recorded over the last 30 years in nearshore, upper-slope depths in the Southern California Bight (SCB), but how these changes compare to the magnitude of natural variability experienced by seafloor communities at short time-scales was unknown. Using an autonomous nanolander, high-frequency T, O_2, pHest, and salinity data and benthic community responses were collected at depths between 100-400 m off San Diego to determine: timescales of natural environmental variability, changes in variability with water depth, and community responses to variability. The diurnal oxygen range at all depths was found to exceed the annual long-term trend in oxygen loss. Depths of 200 and 400 m showed high oxygen variability, relative to the mean, which may help buffer communities at these depths to deoxygenation stress by exposing communities to periods of relatively high oxygen conditions across short time-scales (daily and weekly). Despite experiencing large natural O_2, T, and pH variability at short time-scales, communities do not respond at these shorter time-scales to changing conditions, however, day-night differences are apparent. Over 5-month, seasonal timescales, community responses do correlate with differences in environmental conditions. We find a transition from fish-dominated to invertebrate-dominated communities to be associated with lower oxygen conditions, suggesting this taxonomic change may be a useful ecological indicator of hypoxia. While this study focuses on the SCB, fewer resources and historical data are available for other regions of the world that are also experiencing

deoxygenation. Due to their small size and ease of use with small boats, nanolanders can serve as a powerful tool for studying environmental variability and seafloor community responses, which can improve our understanding of community vulnerability to climate driven environmental change.

Introduction

The role of natural environmental variability in influencing the ability of communities to tolerate climate change has recently been acknowledged by the scientific community. Communities and species living in stochastic environments are often more tolerant of extreme conditions than communities from environmentally constant areas (Bay and Palumbi 2014). In seasonally hypoxic fjords, temporal oxygen variability influences seafloor community beta diversity patterns, and can allow certain species to survive even when average oxygen conditions are below their critical oxygen thresholds (P_{crit}) (Chu et al. 2018). The anthropogenic signal of deoxygenation also takes a longer time to emerge in systems with higher natural oxygen variability (Long et al. 2016, Hensen et al. 2017). Variability itself of environmental parameters (T, O_2, pH) is therefore an important environmental factor to consider when studying the impacts of hydrographic gradients in the environment on communities.

This recognition has spurred an increase of studies in shallow water and intertidal areas to characterize the natural environmental variability at high temporal resolution (Frieder et al. 2012, Hofmann et al. 2011b, Levin et al. 2015). The high citation rate of these studies demonstrates the importance of this type of knowledge in better understanding the evolutionary selection of the present community and the existing environmental ranges of variability, which are both important factors to consider when predicting community responses to future climate-driven change.

While data on shallow-water environmental variability (< 100 m) has proven valuable, high-frequency deep-water oxygen measurements are rare and no moorings measured oxygen continuously below 100 m in the Southern California Bight (SCB). The California Cooperative Oceanic Fisheries Investigations (CalCOFI) long-term time series provides important quarterly measurements and shows decreases in oxygen conditions with time (Bograd et al. 2008, McClatchie et al. 2010). However, daily, weekly and even seasonal low oxygen extreme events (e.g. Send and Nam 2012) are not captured by the CalCOFI sampling frequency. Fish and invertebrates may be reacting to these short-term changes through physiological, behavioral, and community-level changes.

Environmental conditions in deeper water (> 100 m) are generally thought to be relatively stable, but this may not be true for coastal deep-water ecosystems in the SCB. Due to the physical oceanography and variable bathymetry of the SCB, nearshore deep-water areas on the shelf and slope may experience high variability due to localized upwelling events (Send and Nam 2012) and mixing from internal waves (Nam and Send 2011). The California Undercurrent transports warm, saline, low-oxygen subtropical water northward along the coast in the SCB and has a high-velocity core along the continental slope (Lynn and Simpson 1987). Strong seasonal variability of the California Undercurrent in terms of strength, depth, and direction (Lynn and Simpson 1987) likely contributes to deep-water oxygen variability along the continental margin between 100-400 m depth with biological consequences. The California Undercurrent has also strengthened over the past 25 years (Bograd et al. 2015).

Datasets on organismal and community responses to environmental variability are rare for deep-water ecosystems, however those that exist are informative and illustrate a dynamic deep-sea environment (Chu et al. 2018). Several recent studies from NEPTUNE (the North-East Pacific Time-Series Undersea Networked Experiments) in B.C. Canada show that even at 800-1000 m, fish behavior is linked to variations in environmental conditions across different temporal scales including day-night and internal tide temporalizations (Doya et al. 2014) and seasonal cycles (Juniper et al. 2013). Combined high-frequency quantitative sampling of environmental and biological data allows examination of which processes shape benthic communities (Matabos et al. 2014) and is ecologically meaningful because species behavior and activity can influence benthic-pelagic coupling through predator-prey interactions (Aguzzi et al. 2011).

Due to the narrow shelf, the variable bathymetry of the SCB, and the presence of submarine canyons, deep-water ecosystems occur close to shore and support many important fisheries species, including many species of slope rockfish, which may be vulnerable to deoxygenation (Keller et al. 2015, Keller et al. 2009, McClatchie et al. 2010). Habitat compression of demersal fish species due to the shoaling of low oxygen waters in the SCB is a concern because fish are more sensitive to hypoxia than most invertebrates (Vaquer-Sunyer and Duarte 2008), although different species on the NE Pacific margin have different tolerances (Chu and Tunnicliffe 2015, Keller et al. 2015). Therefore, we hypothesized that community dominance patterns would relate to oxygen conditions, with fish-dominated communities observed under higher oxygen conditions and invertebrate-dominated communities observed under lower oxygen conditions. Since upper slope rockfish are thought to be relatively hypoxia-intolerant (McClatchie et al. 2010), we also hypothesized that abundance and species richness of rockfish would positively vary with oxygen conditions.

Currently, tools for studying deep-water ecosystems include deep-submergence vehicles (HOVs, AUVs, and ROVs) and trawls. These approaches typically require significant resource investment, and the use of large ships with winch capabilities. Moorings and cabled observatories are also very useful, however, are usually fixed to specific sites. One of the goals of this research is to develop a lower-cost and spatially flexible approach for studying nearshore, deep-sea ecosystems that can be used to monitor deep-water oxygen variability and benthic community responses.

Unlike other components of this thesis, the focus of this chapter is on depths between 100-400 m, which are shallower than the oxygen minimum zone (OMZ). This depth zone is ecologically interesting because it encompasses the oxygen limiting zone (OLZ) ($O_2 < 60$ μmol kg^{-1} as defined in Gilly et al. 2013), a transition zone above the OMZ where dissolved oxygen levels become limiting enough to lead to the exclusion of certain hypoxia-intolerant species. This depth zone is also of interest because it has experienced some of the greatest loses in oxygen over the last 30 years (Bograd et al. 2008). Strong edge effects occur for benthic and demersal fish and invertebrates at upper and lower OMZ boundaries (Levin 2003, Gooday et al. 2010, Murty et al. 2009). Upper OMZ boundaries likely experience more temporal variability than lower boundaries because they are shallower, and benthic communities in the OLZ may be highly responsive to short-term and seasonal changes in oxygenation. We hypothesized that communities would show diurnal differences based on light attenuation with depth, and were interested in testing if diurnal community differences were more pronounced than community-level differences relating to oxygen conditions.

The goals of this chapter are to: increase sensor accessibility to nearshore deep-water ecosystems through the development and testing of an autonomous nanolander, to characterize the magnitude of deep-water oxygen variability at upper slope depths in the SCB and study seafloor community responses to natural oxygen variability, to compare how variability changes across depths and timescales (semidiurnal, diurnal, weekly, and seasonal), to identify the dominant timescale of variability for oxygen, to determine how frequently communities at different depths are exposed to hypoxia, and to compare the magnitude of natural variability to the longer-term oxygen loses observed (Bograd et al. 2008, Booth et al. 2014, Ren et al. 2018).

Methods

Landers have several advantages compared to submersibles, ROVs, trawls, moorings, and cabled observatories for deep-sea research. These include lower cost combined with spatial flexibility. Unlike moorings or cabled observatories, which are typically designed to remain in one spot, landers can easily be recovered and redeployed to new depths and locations (Priede and Bagley 2000, Jamieson 2016). Kevin Hardy, retired Scripps' Development Engineer, has a long history of developing landers for deep-sea applications, and built the landers used for the *DEEPSEA CHALLENGE* Expedition (Gallo et al. 2015), which were successfully deployed to the New Britain and Marina trenches. However, these landers were large and required a large ship with an A-frame and winch or crane to deploy. We were interested in developing a similar, but smaller system that would allow researchers access to deep-sea ecosystems without the need for large research ships – a tool that could be deployed by one or two people out of a small boat. Specifically, the scientific goal was to design a small, autonomous deep-sea lander that could be outfitted with sensors capable of continuously collecting environmental and community data for several weeks at a time within OLZ depths in the Southern California Bight.

With these goals in mind, the "nanolander" *Deep Ocean Vehicle (DOV) BEEBE*, was developed and built by Kevin Hardy (Global Ocean Design, San Diego, CA) (Fig. 5.1 A). The nanolander frame is made of marine-grade high-density polyethylene (brand name "Starboard") and reinforced with fiberglass pultruded channel and angle beams for structure, reducing in-water weight. Alloy 316 stainless steel fasteners hold the frame together. These structural components of the nanolander are pressure-tolerant, and may be used at any depth of the ocean. *DOV BEEBE* stands 5.25 ft tall (1.6 m) and is 1.17 ft (36 cm) wide and 1.17 ft (36 cm) deep (Fig. 5.1 B). Within the frame sit three main spheres that are 10 inches (~25 cm) in diameter. Styrene trawl float spheres were used for *DOV BEEBE*, which are rated to 1000 m, however borosilicate glass spheres may be used to 10,000 m. The main spheres are used both for buoyancy and instrument housing. When needed, additional smaller styrene spheres were used to provide an additional 5.5 lb of buoyancy, and a total of four additional small spheres can be added. When *DOV BEEBE* is deployed, the vertical distance from the base of the nanolander to the seafloor is ~18 inches (~51 cm). This distance is defined by the length of the anchor chain connecting the lander release system to the expendable iron anchor. The length of this anchor chain may be shortened or lengthened to suit the research goal.

All three main styrene spheres of *DOV BEEBE* are used to support electronics and instrumentation required for deployment, data collection, and recovery of the nanolander. The upper sphere is the command-control sphere, and houses an Edgetech BART (Burnwire-Acoustic Release-Transponder) board, which is the prime means of communication with the instrument. A transducer is bounded to the exterior of the command-control sphere, positioned to point upwards with a clear view to the surface. The Edgetech BART board has four pre-programmed commands: one which enables acoustic responses, one which disables acoustic responses, and two which initiate a burn command to provide voltage to one of the two burn wires. An overboard transducer and an Edgetech deckbox are used to communicate acoustically with the BART board in the command control sphere. The Deckbox also allows distance ranging on the nanolander when acoustic communication is enabled. The power supply for the BART board is housed in the command control sphere, as is a GPS tracker with a separate battery source.

The middle sphere functions as a "battery pod" which houses the batteries and battery management system (BMS) that support the two external LED lights. Rechargeable lithium-polymer batteries were used, and the battery pod was designed to allow the batteries to be recharged through an external cable and charger system, without having to open the sphere. For all but one deployment, a 30-ampere hour (Ah) battery stack was used to power the LED lights, which is composed of three 14.8v/10 Ah units. For the last deployment, the battery pod was upgraded to a 32 Ah battery, composed of two 14.8v/16 Ah batteries. In each case, each individual battery (10 or 16 Ah) had its own battery management system (BMS) with a low voltage cut-out (LVCO) to ensure that battery discharge never went below a critical threshold (12.0 v), which would damage the battery. The circuit engineered to power the LED lights consisted of five components: Battery > Battery Management System (BMS) > Relay > LED Driver > LED lights.

The relay and LED drivers were contained within the lower sphere, which houses all components of the camera system, and includes the viewport. The camera system uses a

Mobius Action Camera with a time-lapse assembly, which was modified for our research goals by Ronan Gray (SubAqua Imaging Systems, San Diego, CA) and William Hagey (Pisces Design, La Jolla, CA). The camera system has 14 different time-lapse options, including continuous video, time-lapse images at the following time-intervals (30 sec, 1 min, 2 min, 5 min, 10 min, 15 min, 30 min, and 60 min), and time lapse video at the following intervals (1 min video every 5 min, 5 min/30 min, 10 sec/10 min, 20 sec/20 min, 30 sec/30 min, and 60 sec/60 min). For the data deployments, we used a sampling interval of 20 seconds of video every 20 minutes.

The camera sphere is designed with a sealed magnetic switch which, when an external magnet is disengaged, triggers the camera system to begin sampling at the pre-determined interval. The camera system has a small internal LED light which turns on when the camera is recording, and a light sensor inside the camera sphere detects this light source, and triggers the external LED lights to power on. Each of the two LED lights is connected by connecting cable to the camera sphere, and the lights themselves are attached to the body of the nanolander, on either side of the middle sphere. The camera sphere is connected to the battery pod with an external connector cable, which provides the power source for the external LED lights. Each of the two LED lights are connected by cable to the camera sphere, and the lights themselves are secured to the body of the nanolander, on either side of the middle sphere.

All spheres were sealed using a Global Ocean Design Deck Purge Box. Prior to sealing the spheres, the sealing faces and O-ring of the matching hemispheres were carefully cleaned with rubbing alcohol and then a thin layer of silicon high vacuum grease was applied. The two hemispheres were then closed and vacuum sealed, and held together by a vacuum of

~12 psi. Three successive cycles of applying a vacuum were done to remove moisture from air inside of the sphere by using a desiccant cartridge.

Below the bottom camera sphere, *DOV BEEBE* has a mounted SBE 37-SMP-ODO instrument. The MicroCAT CT(D)-DO is a highly accurate sensor designed by Sea-Bird Scientific for moorings and other long-duration, fixed-site deployments. It includes a conductivity, temperature, pressure, and optical dissolved oxygen sensor, along with internal batteries, memory, an integral pump, and an RS-232 serial interface for communicating with the instrument and downloading data. The oxygen sensor is an individually calibrated, field-proven SBE 63 optical dissolved oxygen sensor. The MicroCAT is housed in a titanium housing, rated to 7000 m, but the pressure sensor is only rated to 2000 m. Initial sensor accuracy is +/- 3 μmol kg^{-1} for oxygen measurements, +/- 0.1% for pressure measurements, +/- 0.002°C for temperature measurements, and +/- 0.0003 S m^{-1} for conductivity measurements, and drift is minimal. The SBE MicroCAT was programmed to take samples every 5 minutes for the length of the whole deployment.

A drop-arm, used for bait deployment, is also mounted in front of *DOV BEEBE*, which is secured with a release during deployment. Initially a galvanic release was used which took 5-6 hours to release following deployment, but the presence of the drop-arm directly in front of the camera viewport affected the camera’s exposure levels, so subsequent deployments used several “Wint O Green” lifesavers as a release. The lifesavers provided enough structural support to secure the arm during descent through the water column, but dissolved and dropped the arm within a few minutes of landing on the bottom. The drop-arm served three functions: it helped stabilize the nanolander from turning and moving when exposed to current, it had a 6 inch (15.24 cm) cross-bar, which provided a visual sizing reference for observations made with the camera system, and it was used to attach bait to the nanolander for each deployment, which was within the camera's field of view. The bait used for each deployment was composed of an assortment of demersal fishes that are part of the Southern California Bight upper margin demersal fish community. These fishes were previously collected by otter trawls and frozen. Bait was secured within a mesh cantaloupe bag and secured to the drop-arm with Zip-Ties for each deployment. The content of bait used for each deployment is provided in Table 1, and for all deployments all bait had been eaten by the time the nanolander was recovered.

DOV BEEBE is positively buoyant in water, and is deployed to seafloor depths with the help of 40 lbs of sacrificial weights. Either four stacked 10-lb iron plates or two 20-lb shackles were used as weights for the deployments. With this added weight, *BEEBE*'s estimated descent rate was ~100 m per minute. The weights were attached by a sliding link onto a metal chain, and each side of the metal chain was then secured near the base of the nanolander to a burn wire. The two burn wires introduce a redundancy, which is a safety feature, because successful burn of either burn wire allows the metal link to slide off the chain and drop the weights, releasing the nanolander from the bottom. The burn wires are attached to a connector cable that connects to the upper command control sphere, which provides power for the burn. It takes ~6-8 minutes for the burn to complete and the burnwire loop to release, following which the nanolander ascends to the surface at a rate of ~60 m per minute. Once at the surface, *DOV BEEBE* floats ~1.5 feet (0.45 m) above the water and has a large flag, which additionally assists with visual detection of the nanolander (Fig. 5.1 E).

A total of ten deployments were conducted with the nanolander *DOV BEEBE* (Table 5.1). Three were testing deployments, that were purely used for testing nanolander performance (D1, D2, and D9). The remaining seven deployments were used for data collection and ranged from 15-35 days (Table 5.1). Both environmental and camera-based community data were collected during six of these seven deployments, and only environmental data are available from one of the deployments (D3) due to a technical problem with the camera system. Data from these seven deployments were analyzed.

Originally the goals of the study were to assess both high-frequency and seasonal variability in environmental conditions in an area known to be important rockfish habitat – the Del Mar Steeples Reef. We aimed for ~3-week-long deployments at ~100, 200, 300, and 400 m during both the fall/winter, a period of relaxed upwelling, and the spring/summer, a period of strong upwelling. However, we were only able to complete five of these eight planned data deployments due to unexpected delays to the development timeline of building and testing the lander, and due to recovery issues during the 10th deployment, after which *DOV BEEBE* ended up drifting south into Mexican waters. The completed deployments included all four depths in the fall, and the ~100 m deployment in the spring.

Upon recovery of the nanolander, time-series data from the MicroCAT were analyzed to assess how high-frequency, natural environmental variability (O_2, T, salinity) change with depth. Since partial pressure of oxygen is more biologically meaningful than oxygen concentration (Hofmann et al. 2011a), we calculated oxygen partial pressure from oxygen concentration using the R code provided as a supplement to Hofmann et al. (2011a), and then converted from matm to kPa. Oxygen partial pressure was subsequently used for the seafloor community analyses.

Oxygen and pH naturally co-vary along the continental margin driven by respiration, and while no pH or pCO_2 sensors were mounted on *DOV BEEBE*, pH was estimated based on the empirical equations derived for this region using CalCOFI data and carbonate system measurements (Alin et al. 2012), to look at pH variability as well. The following equation was used to estimate pH, using the coefficients for α_0-α_3 and the reference conditions for the calibration data set presented in (Alin et al. 2012):

$$pHest = \alpha_0 + \alpha_1(T-T_r) + \alpha_2(O_2 - O_{2,r}) + \alpha_3[(T-T_r)*(O_2 - O_{2,r})]$$

The mean and ranges of temperature, oxygen, and pHest were determined and compared across depths and deployments to characterize differences in environmental variability that seafloor communities are exposed to. The coefficient of variation (CV) (i.e. the ratio of the standard deviation to the mean) was calculated for T, O_2, and pHest for each deployment as a standardized measure of dispersion and compared across deployments and depths. The observed long-term secular changes as described by Bograd et al. (2008), were compared to the magnitude of natural oxygen variability observed during deployments.

Previous studies have found that changes in oxygen and pH in the Southern California Bight are associated with changes in the volume of advected Pacific Equatorial Water (PEW) in the California Undercurrent (Bograd et al. 2015, Nam et al. 2015). PEW is characterized by low oxygen, warm, and high salinity conditions. Spiciness, which is a state variable that is conserved along isopycnal surfaces (Flament 2002), can be used as a tracer for PEW (Nam et al. 2011, Nam et al. 2015). Therefore, we calculated spiciness using the “oce” R package (Kelley and Richards 2017) and examined how the correlation between spiciness and oxygen concentration and temperature and oxygen concentration varies across depths and deployments.

To identify the dominant timescale of variability for oxygen, a spectral analysis was conducted as in Frieder et al. (2012) on the oxygen concentration time-series for each deployment. To look at diurnal and semidiurnal patterns, one day was used as the unit of time, and the number of observations based on the sampling frequency, was 288. Spectral analyses were conducted on detrended time-series using a fast fourier transform. Results were displayed using a periodogram and the period of the dominant signal was reported and compared across deployments. The oxygen time-series for each deployment were also decomposed to look at the trend, daily, and random signals that contribute to the overall data patterns.

Video segments collected by the camera system were annotated to quantify how community responses vary with environmental conditions. A total of 4,293 20-sec video segments were collected and annotated in total for the six deployments where video was successfully collected (Table 5.2). For each 20-second video, both invertebrates and vertebrates were identified to lowest taxonomic level and quantified. All demersal fish species within the frame of view were quantified. For certain invertebrate species of interest for fisheries, for example crabs, *Cancer spp.*, and spot prawns, *Pandalus platyceros*, true counts were done. For all other invertebrates, counts were conducted when there were 10 or fewer individuals, and then presence was estimated and annotated as being in the tens, hundreds, or thousands. For community analyses, invertebrate counts categorized as “tens”, “hundreds”, and “thousands”, were assigned values of 50, 500, and 1000, respectively.

Since visibility was impaired during certain deployments due to high turbidity, each video clip was categorized by quality of visibility using the following categories: 1 (can see the bottom, good visibility), 2 (can only see the drop-arm, poor visibility), or 3 (drop-arm can no longer be seen, no visibility). Only samples with a visibility category of 1 were utilized in subsequent community analysis so that differences in community patterns were not due to differences in visibility across deployments.

Based on the timestamp for each video-clip and the sample time from the MicroCAT environmental samples, video samples were matched with the environmental conditions for each video segment. Since we were also interested in diurnal community responses due to day-night differences, we assigned all samples between 6:00 AM and 5:59 PM as “day” and all samples between 6:00 PM and 5:59 AM as “night”.

To look at changes in the benthic and demersal community with relation to environmental conditions, we performed the following analyses. Non-metric multidimensional scaling was used to assess community similarity across deployments. Since running an nMDS analysis for all samples was highly computer intensive, fifty samples (i.e. video clips) from each deployment were randomly selected using a random number generator as representative of each deployment. These were used to project community differences in ordination space. The R package “vegan” (Oksanen et al. 2017) was used for nMDS analysis and a Wisconsin double standardization was performed and counts were transformed using a square-root transformation. These standardizations are frequently used when working with datasets with high count values and have been found to improve nMDS results (Oksanen et al. 2017). Bray-Curtis dissimilarity was used as the input and community dissimilarities were mapped onto ordination space for the nMDS analysis.

Additionally, for each deployment, an nMDS analysis was performed to look at differences in communities in relation to time of day (“day” versus “night”), and in relation to environmental oxygen conditions. To group samples by oxygen conditions, we created three categories: “High”, “Intermediate”, and “Low”. These categories were determined based on the oxygen partial pressure time-series for the entire deployment: “High” samples were those that were above the third quartile of oxygen conditions, “Low” samples were those that were below the first quartile, and “Intermediate” samples were those that fell within the first and third quartile. Oxygen categories were determined separately for each deployment based on the deployment time series. Deployments D5 and D10 were grouped, since both were conducted at the same location, but during different seasons, therefore giving a larger range of oxygen conditions. For these deployment-specific analyses, the full dataset of samples was used, after the samples with poor visibility were removed. In addition to the community-level analyses, for certain species of interest, we also looked at species-level patterns in relation to oxygen conditions and time of day.

We also tested if dominance by fishes versus invertebrates in the benthic community was a community-level metric that related to the environmental oxygen conditions. For each sample, we determined if the community was fish or invertebrate dominated (based on if there were more fishes or more invertebrates observed in each 20-minute video sample). Samples were then categorized as “Fish Dominant”, “Equal”, or “Invertebrate Dominated” and we assessed if dominance pattern was correlated with oxygen conditions. We tested the hypothesis that invertebrate dominated communities would be present under lower oxygen conditions across all deployments, across season at 100 m, and during a single deployment at 200 m (D6).

Results

Nanolander performance

Overall, *DOV BEEBE* was found to be a very reliable platform for deployment, recovery, and data collection needs (Fig. 5.1). Acoustic communication was reliable during all deployments, and deployment and recovery protocols were straightforward once developed, which is encouraging from the perspective of training future users. Deployment and recovery were easy using small boats (Fig. 5.1 C and 5.1 D), and *DOV BEEBE* could be transported on a lab cart or in the back of a small car. The nanolander platform was robust and showed very few signs of wear following multiple deployments. There were no signs of leakage or vacuum loss with the spheres during deployments. Despite recovery issues during the 10th deployment, which led to a prolonged 16-day drift period at the surface during which *BEEBE* covered at least ~267 km as it floated south, all instrumentation was intact and still working upon recovery. Biofouling was not observed during any of the deployment periods, and was minimal and limited to juvenile barnacles following the surface drift period during deployment 10. Here we review some of the minor issues and areas for improvement.

For any long-term deep-sea deployments, memory and power capacity are two key issues to be grappled with. The nanolander *DOV BEEBE* has five separate components that require battery power: 1) the SeaBird MicroCAT-ODO sensor, 2) the Edgetech BART board, 3) the GPS unit, 4) the camera system, and 5) the LED lights. Seamless integration of these was required to utilize the full capabilities of the nanolander. The camera system had a 128 GB micro SD card, and memory and power were not issues for the camera system itself, which continued recording throughout the full lengths of the deployments. The battery pack for the camera system was fully recharged following every recovery and prior to redeployment. The video quality was high enough to allow species-level identifications and the light from the LEDs was sufficient to light the field of view. The SeaBird MicroCAT-

ODO also performed without any issues and had sufficient battery and memory capacity for all deployments.

The highest power requirement was for the two LED lights, which each run on 30V with a 1 Amp current when powered on. To supply the appropriate amount of power, one sphere was entirely used as a “battery pod” to house the batteries and battery management system (BMS). Based on the power draw of the LED lights and assuming full efficiency of all components in the circuit, ~8 hours of LED performance was expected. At the sampling frequency of 20 seconds every 20 minutes, this would have allowed for video samples to be collected over a period of 480 hrs or 20 days. The greatest limitation encountered during *DOV BEEBE*’s deployments was inefficiency within the design of the LED power supply system, which led to much poorer LED field performance than estimated based on the battery capacity. As opposed to 8 hours of LED performance time, field performance ranged from 2.2 to 6.6 hours (Table 5.2), which meant that the time-series of biological data collected was shortened and ranged from 5.5 to 16.5 days, respectively.

Following completion of the last field deployment, additional tests were done to understand why the power supplied to the LED lights was far below that approximated from the system parameters. The circuit engineered to power the LED lights consisted of five components: Battery > Battery Management System (BMS) > Relay > LED Driver > LED lights. A discharge test using a West Mountain Radio Computer Battery Analyzer III (CBA) of the 16 Ah lithium-polymer battery with the low-voltage cut-out (LVCO), yielded 15.86 Ahs, or 99.1% of the rated capacity, implying that the batteries and BMS were performing as expected. Testing the battery discharge through the LED driver, showed 95% efficiency, meaning that this element was also performing as expected. The LED driver is a necessary component of the lights system because it prevents damage to the LEDs due to thermal runaway, which occurs when the forward voltage of the LED changes with temperature.

The last element inspected was the relay, which is light-sensitive and functions to sync the timing between the camera and the LED lights. Inside the camera sphere, the camera system has a small light that turns on when the pre-programmed recording interval begins. This light is detected by the light-sensitive relay, which then conveys the signal to the LED driver and delivers power to the LED lights. The relay installed in *DOV BEEBE* draws power during the entire deployment, since it is constantly "on", effectively waiting for a light. When the relay was removed from the circuit, and all other components of the circuit were tested, performance increased to the expected ~8 hours, confirming that the continuous power draw of the relay was the problem. A new solid-state relay has since been tested as a replacement for the previously used relay. With the use of the solid-state relay, the LEDs showed 8 hours of performance time. These results suggest that future deployments will be able to collect ~20 days of biological time-series information, based on the sampling frequency used (20 sec every 20 min).

Most recoveries for *DOV BEEBE* were very straightforward and would consist of stopping over the deployment site, enabling communication with *DOV BEEBE* using the Deckbox and transducer, then ranging on *DOV BEEBE* to determine approximate distance from the instrument, and then sending a burn command to initiate voltage being provided to the burn wire to drop the weights. Depending on the depth, it would take 9-14 minutes from the time the burn command was first sent, to the time when *DOV BEEBE* would surface, and *DOV BEEBE*'s ascent was relatively rapid (~60 m/min) and vertical. Once at the surface, *DOV BEEBE*'s surface signature was easy to detect due to the bright colors of the spheres and the additional large flag (Fig. 5.1 E). *DOV BEEBE* floats vertically at the surface and not horizontally, due to the inherent stability in design of the nanolander with more buoyancy at the top, and more weight at the bottom (Fig. 5.1 E). When recovered in normal circumstances during the day, visual detection was sufficient and no GPS tracking was needed to find *DOV BEEBE*. In case of emergency, a GPS tracker was initially integrated within the command control sphere, but the battery limitations as well as the position of the unit presented problems for reliable use. Consequently, an active GPS unit was not in place for most deployments.

This ended up being problematic during the 10th deployment, when we experienced recovery issues. While it is still not completely clear what *DOV BEEBE* became caught on, the leading hypothesis is that following the successful burn of the first burn wire, and the initiation of *BEEBE*'s ascent, the bait bag on the drop arm became caught on a small piece of extra metal on the metal shackles that had been used as sacrificial weights for the deployment. This hypothesis is supported by the following lines of evidence. First, upon recovery of the nanolander, both burn wires were inspected and both had burned and released appropriately, suggesting that there were no issues with weight release. Second, inspection of the video footage upon recovery did not show any obvious features (e.g. rocky ledges, large kelp rafts) for *DOV BEEBE* to be caught on. Third, upon recovery, it was noted that the bait bag had a large tear on the underside, which is not something observed during previous deployments. A tear on the underside is consistent with the drop arm moving down as the nanolander begins ascending, which would result in the bait bag moving past the dropped weights. Lastly, inspection of images from the last deployment of the shackles used as sacrificial weights shows a small metal extension that the bait bag could have become caught on. For all deployments prior, four stacked metal plates were used as the sacrificial weight, and future deployments should continue utilizing these instead of shackles because they do not have any components that would allow the bait bag to get caught.

From the SBE MicroCAT, a small change in the depth (~0.3 m) can be observed which corresponds to the weights dropping and *DOV BEEBE* beginning to ascend before getting caught. About 10 hours following the initial attempted recovery, CTD data shows that *DOV BEEBE* was released from whatever it was caught on and surfaced. Unfortunately, this took place just after sundown and strong surface currents (~35 cm s^{-1}) were moving to the southwest. The Del Mar mooring, which was within line of sight to where *DOV BEEBE* was deployed, was displaced 40 m to the south and 10 m to the west due to the strong surface current conditions that day. Consequently, *DOV BEEBE* likely drifted out of Southern California waters and offshore into Mexican waters before the following morning, which may explain why it was not reported or pulled up by anyone in the heavily trafficked San Diego area.

DOV BEEBE then drifted for 16 days, before a tuna boat belonging to Baja Aqua Farms came across it on April 14, 2018 at 30°35'8.76"N, 116°47'35.40"W. This location was far offshore (~~50 miles offshore of Punta Colonet, Mexico), and 267 km south of its deployment site. Based on contact information provided on *DOV BEEBE*, the fishermen contacted us, and returned the instrument. Since *DOV BEEBE* did not have a functional GPS unit, no information was available about its location during the whole period it was lost. To prevent situations like this in the future, future deployments will include a functional GPS tracker. Currently, a new SPOT Trace GPS tracker is being tested on Phil Zerofski's nanolander, *DOV Munk*. The SPOT Trace uses motion-activated tracking and sends text and email messages at pre-determined time-intervals when new movement is detected, and would be mounted inside the upper command-control instrument sphere.

Environmental Variability

Natural variability of environmental parameters was assessed using time-series collected from seven deployments and compared across depths (100, 200, 300, and 400 m), and season (fall compared to spring). Means and ranges for temperature, oxygen, salinity, and pH for each deployment are provided in Table 5.3. Oxygen concentration (µmol kg^{-1}) time series for each deployment are provided in the Appendix Supp. 5.1. At ~100 m, conditions were never hypoxic (i.e., < 60 µmol kg^{-1}), although the mean oxygen concentration was significantly lower during the spring upwelling season deployment (D10, mean $O_2 = 103.95$ µmol kg^{-1}), compared to the fall deployment when upwelling is relaxed (D5, mean $O_2 = 132$ µmol kg^{-1}) (ANOVA, $p < 0.001$). pHest was also lower during the spring deployment (D10, mean pHest = 7.696) than during the fall deployment at ~100 m (D5, mean pHest = 7.759) (ANOVA, $p < 0.001$), and temperatures were on average 1.3°C colder, consistent with upwelling conditions (Table 5.3, Fig. 5.2).

At ~200 m, hypoxic conditions were encountered, however conditions were only hypoxic for relatively short portions of the deployment (~13% for D3, ~2% for D4, and never hypoxic for D6). Even though *DOV BEEBE* was deployed 14 m deeper during D6 than D3 and D4, average oxygen conditions were higher during D6 (Fig. 5.2, Table 5.3). This is likely due to a late component of the upwelling period being captured during D3 and D4. The decomposed trend for the time-series for both D3 and D4 shows oxygen increasing through time (Appendix Supp. 5.2), consistent with a relaxation of upwelling. These results suggest that at depths around 200 m, benthic organisms are seasonally exposed to hypoxic conditions during periods of strengthened upwelling, but these hypoxic conditions are not continuous. Despite the ~80 m difference in depth, temperature conditions at 98 m in the spring (D10) were like temperatures at 178 m during the late summer and early fall (D3, D4), although oxygen conditions and pHest were still higher at 98 m (D10) (Fig. 5.2).

At ~300 m (D7) and ~400 m (D8), mean temperatures were colder, and mean oxygen and pH conditions were lower (Table 5.3, Fig. 5.2). At both depths, conditions were hypoxic for the entire time-series, and at 400 m (D8) conditions were severely hypoxic (i.e. $O_2 < 22.5$ $\mu mol\ kg^{-1}$) for ~1% of the time-series (Table 5.3). Even at ~400 m seafloor communities can be exposed to OMZ conditions due to natural environmental variability. Both D7 and D8 were conducted during the fall/winter, when upwelling conditions are relaxed, therefore, our time-series likely captured the less extreme (higher oxygen, higher pH) conditions the benthic communities at these depths are exposed to throughout the year. This suggests that at ~300 m, communities are consistently exposed to hypoxic conditions, and that the upper boundary of the OMZ may be even shallower than 400 m during the peak upwelling season. Unfortunately, we were unable to conduct deployments during the spring upwelling period for these depths, so a seasonal comparison is not available.

While we expected that variability in oxygen concentration would decrease with depth, one of the interesting results was that the largest variance in oxygen conditions over these short time-scales was observed during D3 and D4 at ~200 m (Table 5.3). All three deployments from ~200 m show broad probability density distributions of environmental conditions (Fig. 5.2) and large ranges in oxygen and pHest for the deployment period (Table

5.3). The coefficient of variation (CV) for oxygen at 200 m was ~2 times higher than for the 100 m deployments (Table 5.3).

Compared to shallower depths, both D7 (~300 m) and D8 (~400 m), had much narrower probability density distributions of environmental conditions (Fig. 5.2), but the ranges in oxygen and pHest for D8 were only slightly smaller than for D7 (Table 5.3). It is also worth noting that while absolute variability in oxygen conditions may be lower at 300 and 400 m, it may be biologically relevant to consider the relative variability compared to the mean. For oxygen, the CV was greatest for D3 and D4 at ~200 m (13.72% and 12.92%, respectively), followed by D8 at ~400 m (10.20%), then D6 at ~200 m (9.82%), then D7 at ~300 m (7.02%), and finally D5 and D10 at ~100 m (5.07% and 5.10%, respectively) (Table 5.3). Thus, considering oxygen variability relative to the mean may be especially important for deeper communities. Interestingly, temperature did not exhibit the same pattern of variability, with the highest variance (CV) observed during D5 (~100 m) (Table 5.3). Variance in pHest (CV) was almost twice higher at shallower depths (< 200 m), than at ~300 or ~400 m (Table 5.3).

The oxygen concentration time-series for all deployments were also deconstructed (Appendix Supp. 5.2-5.4) and a spectral analysis was performed to look at dominant timescales and underlying patterns of oxygen variability. We found that for all deployments, the dominant frequency was close to the semidiurnal tidal period (~12.4 hrs) (Fig. 5.3), therefore the dominant signal of oxygen variability at each depth is due to sloshing by the tide. The deconstructed time-series also show a clear diurnal and semi-diurnal signal (Appendix Supp. 5.2-5.4). It is worth noting that the relative amplitude of the dominant signals in the periodograms decrease with depth, suggesting that the strength of the tidal signal, while still dominant at deeper depths, is not as strong (Fig. 5.3). The periodogram for D7 at ~300 m is also interesting in that it is much noisier than that for the other deployments, and has many more high-frequency and several additional low-frequency signals that emerge (Fig. 5.3). While we are unsure of why this might be, it is worth noting that D7 had the worst visibility of all the deployments and high turbidity was characteristic of much of the deployment. It is possible that the noisy periodogram for this deployment may be related to physical drivers (e.g. currents, internal bores, breaking internal tides) giving rise to the high turbidity observed at this depth.

Additionally, we looked at the correlation between dissolved oxygen concentration and both temperature and spiciness to better understand the mechanisms giving rise to different oxygen conditions (Fig. 5.4). In all cases, we found a significant positive correlation between temperature and oxygen for all deployments (LR, $p < 0.001$), however, the explanatory power of the regressions differed across depths (100, 200, 300, and 400 m) and the slopes of the regressions differed between locations (Scripps Reserve and Del Mar Steeples Reef). At depths deeper than 200 m, there was less variance around the linear trend. The highest amount of variance explained by the linear regression was found for D8 (~400 m, $R^2 = 0.90$), and the lowest amount for D6 (~200 m, $R^2 = 0.41$). In looking at the relationship between temperature and oxygen concentration, all deployments from Del Mar Steeples Reef (D5, D6, D7, D8, and D9) have a similar slope, while the two deployments which were done in the Scripps Reserve (D3 and D4) have a steeper slope (Fig. 5.4). The deployment site for D3 and D4 in the Scripps Reserve is in a narrow, deep tendril of the Scripps canyon system, which is surrounded by shallower bathymetry. In contrast, the Del Mar deployment sites are on a gradually sloping margin. It is possible that differences in the local bathymetry of these sites give rise to the different slopes observed in the correlation between temperature and oxygen for the deployment time-series.

We found that oxygen was significantly correlated with spiciness for all deployments as well (LR, $p < 0.001$), however, the slopes and explanatory power of this relationship differed across depths (100, 200, 300, and 400 m) and season (fall and spring) (Fig. 5.4). D5 and D10 were conducted at the same location at ~100 m depth but with D5 in the fall and D10 in the spring. Consequently, it was interesting to see a very different relationship between oxygen and spiciness for these two deployments (Fig. 5.4). For D5 (Fall), there was only a weak positive relationship between spiciness and oxygen, and while this relationship was statistically significant (LR, $p < 0.001$), explanatory power was low ($R^2 = 0.31$). In contrast, during D10 (Spring), dissolved oxygen was negatively correlated with spiciness, and the linear fit had high explanatory power ($R^2 = 0.81$).

In fact, the relationship between oxygen and spiciness for D10, was very similar to that observed for the three deployments (D3, D4, and D6) at ~200 m. These three deployments all had a negative relationship between spiciness and oxygen concentration, with high explanatory power for the linear fits ($R^2 = 0.98$, 0.92, and 0.61, respectively), and a similar slope to that for D10 (Fig. 5.4). A negative relationship between spiciness and dissolved oxygen is symptomatic of input of Pacific Equatorial Water, which is brought up by the California Undercurrent. Our results suggest that input of Pacific Equatorial Water is key to determining near-seafloor oxygen conditions at ~200 m in the Southern California Bight, and that during active upwelling in the spring, Pacific Equatorial Water upwells to 100 m, thus affecting oxygen conditions at this shallower depth.

Interestingly, at deeper depths (~300 and 400 m), the relationship between spiciness and oxygen is still significant (LR, $p < 0.001$), but the correlation is positive, with high explanatory power of the linear fit (D7 $R^2 = 0.61$, D8 $R^2 = 0.68$). The change in this relationship between the ~200-m and 300-m deployments suggests that there may be an important change in water masses across this depth zone. At ~300 m and deeper, added input of Pacific Equatorial Water increases the oxygen conditions, in contrast to the negative relationship at shallower depths. Since changes in the volume of Pacific Equatorial Water brought up by the California Undercurrent have been implicated in the decreases in oxygen observed in the Southern California Bight (Booth et al. 2014, Bograd et al. 2015), it is worthwhile to note that increased input of this water mass could have a nonlinear effect on oxygen conditions in this area: increasing oxygen conditions at deeper depths, while decreasing them at shallower depths.

Community differences and relationship to environmental conditions

Community data were collected during six deployments (Table 5.2), representing a total of 4,293 20-second videos that were annotated for organismal observations. One of the first unexpected observations made was that certain deployments had clear water conditions with excellent visibility for the entire deployment, whereas other deployments had high sediment loads in the water column and poor visibility.

For deployments D4, D5, D8 and D10, conditions were clear and visibility was unimpaired for the entire deployment. During D6 (~200 m) at Del Mar Steeples Reef, visibility conditions deteriorated throughout the deployment, with several samples having almost no visibility at the end of the deployment. For D6, 65% of samples had good visibility, 32% had impaired visibility, and 3% had severely impaired visibility. The following deployment, D7, which was also at Del Mar Steeples but deeper at ~300 m, had poor visibility throughout most of the deployment. For D7, less than 2% of samples had good visibility, 78% had impaired visibility (Fig. 5.5), and 20% had severely impaired visibility. Of note, the visibility conditions encountered for the samples categorized as severely impaired visibility for D6 and D7 were worse than the visibility observed during the test deployment (D1, Table 5.1) at ~5 m near the Marfac finger pier, in San Diego Bay. We were not expecting to find this high level of turbidity, and this suggests that some mechanism is responsible for especially high turbidity at this depth zone between 200-300 m on the margin. It is worth considering if these conditions persist throughout the year and what the ecological effects may be for the benthic and demersal communities of these turbid conditions.

For the subsequent community analyses, only samples categorized as having unimpaired visibility were retained. Differences in benthic and demersal communities were observed during the deployments and Figure 5.5 shows a representative image of each community. D5 and D10 were done in the same spot at Del Mar Steeples Reef, but under different seasonal conditions (fall versus spring). The bathymetry of this location differed from other deployment locations in that rocky ledges were evident surrounding the deployment site, and animals were observed actively swimming in and out of rocky crevices. The community at the Del Mar Steeples Reef was characterized by high numbers of rockfish (*Sebastes spp.)* (Fig. 5.5)*,* especially the halfbanded rockfish (*S. semicinctus*), but also included other rarer rockfish species such as the flag (*S. rubrivinctus*), Bocaccio (*S. paucispinis*), rosy (*S. rosaceus*), and greenstriped rockfish (*S. elongatus*). Other fish species included the pink surfperch, *Zalembius rosaceus*, combfish, *Zaniolepis spp.,* and the spotted cusk-eel, *Chilara taylori*. Invertebrates were not abundant, but included an unidentified gastropod, the tuna crab, *Pleuroncodes planipes*, a yellow coral, as well as others. Except for the singular yellow coral, all other invertebrates were mobile. Communities showed a high degree of similarity between the two deployments (Fig. 5.6).

One interesting observation was that there appeared to be fewer bait-attending fauna observed at D5 and D10 sites than at deeper deployments. While Pacific hagfish (*Eptatretus stouti*) did find the bait rapidly, fewer *E. stouti* overall were observed, and they left much of the bait uneaten. Other known bait-attending species, such as the pink urchin, (*Strongylocentrotus fragilis*), were not present during these deployments. While tuna crabs (*P. planipes*) were present, they did not feed on the bait, in contrast to deeper deployments. Instead, unidentified gastropods were observed feeding at the 100-m bait, mainly during the night hours.

Deployments D4 and D6 were both at ~200 m, although in two different locations (Table 5.1), and the communities observed were very different across these deployments (Fig. 5.5 and 5.6), despite the similar depth and similar environmental conditions (Table 5.3, Fig. 5.6). Despite the location of D6 being close to Del Mar Steeples Reef, the bottom was soft sediment with no evidence of rocky ledges or outcrops, and was similar to benthic conditions for D4. Eelpouts (*Lycodes spp.),* cusk-eels (*C. taylori*), lizardfish (*Synodus lucioceps*), and crabs (*Cancer spp.*) were commonly observed during D4, and more typical deep-water species such as Dover sole (*Microstomus pacificus*), chimaeras (*Hydrolagus colliei*), and dogface witch-eels (*Faciolella equatorialis*), were observed here (Fig. 5.5). In contrast, rockfish (*Sebastes spp*.), combfish (*Zaniolepis spp*.), Pacific sanddab (*Citharichthys sordidus*) were commonly observed during D6, but ultimately the community was dominated by tuna crabs (*P. planipes*) and pink urchins (*S. fragilis*) (Fig. 5.5). Tuna crabs and pink urchins rapidly moved in, attracted by the bait, and then remained at high densities throughout the course of the 3-week deployment during D6. In contrast, during D4, no pink urchins were observed, and while tuna crabs were observed during the deployment, there were never more than 100 present. In contrast, most samples from D6 had more than 100 tuna crabs present, and some had over 1000 tuna crabs present. Pink urchins were active and mobile during D6, and changed their orientation based on the current, always orienting down-current from the bait. Crabs (*Cancer spp.)* were also present during D6, but were not as abundant as during D4. Spot prawns (*Pandalus platyceros*) were common community members observed during both D4 and D6, and were seen in similar numbers, but were not observed during any other deployments.

Only one deployment each was conducted at the two deeper depths (~300 m and 400 m) and both deployments were near the Del Mar Steeples Reef, although seafloor conditions were soft sediment with no rocky outcrops observed. As previously noted, D7 (~300 m) had poor visibility for most of the deployment (Fig. 5.5). From the few samples that allowed a view of the bottom, it appeared that the community was dominated by tuna crabs (*P. planipes*) and pink urchins (*S. fragilis*), similar to D6, however, they were present in lower abundances than at D6. D7 and D6 show high community similarity due to high dominance of tuna crabs and urchins at these sites (Fig. 5.6). Fish were rarely observed and included Pacific hake (*Merluccius productus*), rockfish (*Sebastes spp.*), Pacific hagfish (*E. stoutii*), and hundred-fathom codling (*Physiculus rastrelliger*).

In contrast to D7, D8 (~400 m) had very good visibility with no turbidity observed throughout the deployment. D8 represented the deepest deployment and communities were dissimilar from all other deployments (Fig. 5.6). The community at D8 was dominated by pink urchins (*S. fragilis*), but these were present in lower abundances and less active than at D6. Tuna crabs (*P. planipes*) were also present, but at lower abundances than pink urchins, and at lower abundances than observed during D6 and D7. Pacific hagfish (*E. stoutii*), blacktip poacher (*Xeneretmus latifrons*), dogface witch eels (*F. equatorialis*), Dover sole (*M. pacificus*), and shortspine thornyhead (*Sebastolobus alascanus*) were the most common fishes observed. Except for *E. stoutii* and *F. equatorialis*, most fishes exhibited very little movement. This contrasted with much higher activity levels of fish observed during shallower deployments, during which most fish were swimming and active. Similarly, tuna crabs observed during D8 were also less active than those observed during D6 and D7.

Since upper slope rockfish are thought to be relatively hypoxia-intolerant (McClatchie et al. 2010), and since they were dominant community members during both D5 and D10 despite the large seasonal difference in environmental conditions, we were interested in whether rockfish abundance or species richness differed across deployments or oxygen conditions. We found that rockfish abundances were significantly higher during D10 in the spring than D5 in the fall (Fig. 5.7 A) (ANOVA, $p < 0.001$), which was the upwelling season, and there was no correlation observed between rockfish abundance and oxygen conditions (Fig. 5.7 B). In contrast, species richness was slightly higher during D5 but this difference was modest and barely significant (Fig. 5.7 C) (ANOVA, $p = 0.03$). No positive relationship was observed between oxygen partial pressure and rockfish species richness (Fig. 5.7 D). Our results suggest that rockfish community patterns do not appear to be influenced by oxygen variability, or the variability of environmental conditions that co-vary with oxygen (pHest, temperature).

We also looked at a community-level metric in relation to environmental oxygen conditions: whether communities were dominated by invertebrates or fishes. We hypothesized that higher-oxygen conditions would be characterized by fish dominance, compared to lower-oxygen conditions, which would be characterized by invertebrate dominance. When all deployments were pooled, there was a significant difference (Kruskal-Wallis, $p < 0.001$) in oxygen conditions between communities that were fish-dominated, and communities that were invertebrate-dominated, with communities that had an equal number of fish and invertebrates characterized by intermediate oxygen conditions (Fig. 5.8 A). Deployments D6 (200 m), D7 (300 m), and D8 (400 m) were characterized by invertebrate dominance for either all or most (>98%) samples. In contrast, D4 (200 m), D5 (100 m), and D10 (100 m) were characterized by mixed communities, with fish-dominated communities more characteristic for D5 and D10 (~100 m, Del Mar Steeples Reef), whereas for D4 (~200 m Scripps Reserve), 33% of samples were dominated by fish, 44% were invertebrate dominated and 23% had equal representation of fishes and invertebrates.

For the deployments that had a mix of invertebrate- and vertebrate-dominated communities (D4, D5, and D10), we tested to see if fish-dominated communities were also characterized by higher oxygen conditions than invertebrate-dominated communities throughout the deployment time-series. Pooling across all deployments introduces depth as a co-factor, whereas focusing on data collected from one deployment removes this co-variable. In contrast to the overall pattern observed, for D4 we did not see any significant difference (Kruskal-Wallis, $p = 0.90$) in oxygen conditions for fish-dominated or invertebrate-dominated communities, even though a range of oxygen conditions were experienced during this deployment (Fig. 5.8 B). However, pooling deployments D5 and D10, which were conducted during different seasons but at the same location and depth, showed a pattern more consistent with the overall pattern observed across all deployments (Fig. 5.8 C). At ~100 m near the Del Mar Steeples reef, there was a significant difference in oxygen conditions between invertebrate- and fish-dominated communities (Kruskal-Wallis, $p < 0.001$), with lower-oxygen conditions characteristic of invertebrate-dominated communities.

Our results suggest that benthic communities under lower-oxygen conditions exhibit more invertebrate dominance, whereas benthic communities in better-oxygenated areas are more fish dominated (Fig. 5.8). However, these transitions do not seem to happen in response to natural variability over the time-course of days to weeks (Fig. 5.8 B), but are consistent with seasonal timescales (Fig. 5.8 C). Since oxygen co-varies with temperature (Fig. 5.4) and pH, and is also related to watermass (Fig. 5.4), we cannot state that this effect is due singularly to the oxygen regime, but given that demersal fish are more hypoxia-sensitive than invertebrates overall (Vaquer-Sunyer and Duarte 2008), we hypothesize that oxygen is likely playing an important role.

While watching the video samples from each deployment, we noted certain instances of animal behavior and community patterns that appeared to be related to time of day. For example, during D4 and D6, we observed large schools of small pelagic fish that would be present by the bottom during daytime hours and which would often swarm and crash into the bottom in high densities in apparent response to the nanolander lights. These fish were only observed during daytime hours, and frequently several individuals would get stuck within the bait bag while swarming the bottom. Crabs (*Cancer spp*.) and tuna crabs (*P. planipes*) took advantage of this additional food source and were observed catching these small pelagic fish. Similarly, gastropods during D5 and D10 were observed in higher numbers at night, appearing to feed on the bait, than during the day. Cusk-eels, *C. taylori*, were also more frequently observed at night, as were chimaera (*H. colliei*).

In Figure 5.9, we present some examples of species that appeared to show a diurnal behavior based on abundance in video samples. Cusk eels (*Chilara taylori*), chimaeras (*Hydrolagus colliei*) and spot prawns (*Pandalus platyceros*) showed diurnal patterns with more frequent observations at night (Fig. 5.9). In contrast, rockfish (*Sebastes spp.*), crabs (*Cancer spp.*), and lizardfish (*Synodus lucioceps*) did not show differences in abundance between daytime and nighttime hours (Fig. 5.9) Even though count data do not show a diurnal trend for rockfish (Fig. 5.9), we did note that rockfish activity levels differed between day and night. At night, rockfish were usually observed resting on the bottom or within rocky outcrops, and not moving. In contrast, rockfish were swimming and active during most daytime observations, and appeared to be swimming up in the water column to feed in the early morning.

Since we observed diurnal differences for several species, we were interested in if diurnal differences were apparent for the community overall. We hypothesized that shallower communities would show stronger diurnal differences than deeper communities based on light attenuation with depth. We were also interested in assessing if diurnal differences were more pronounced than community-level differences relating to oxygen conditions. To look at the importance of day-night versus oxygen differences on community patterns, we pooled data from the two 100 m deployments (D5 and D10) at Del Mar Steeples Reef, and compared these patterns to those observed for the deeper deployments at Del Mar Steeples Reef: D6 at ~200 m and D8 at ~400 m. Communities were differentiated by whether samples were from high, low, or intermediate oxygen levels (Fig. 5.10 A, C, E) and whether samples were from the day or night (Fig. 5.10 B, D, F).

We found that, except for the shallowest deployment, community similarity did not appear to be related to the environmental oxygen conditions. Communities under high, intermediate, and low oxygen conditions showed a high degree of overlap (Fig. 5.10 C, D). At 100 m (Fig. 5.10 A), communities under low oxygen conditions (within the lowest quartile), did appear to be more dissimilar from communities found under intermediate and high oxygen conditions. Since samples were pooled between the spring and fall deployment, this may indicate that community level differences in relation to oxygen levels may be more pronounced across monthly timescales, than across weekly timescales. Community-level differences may also relate to other upwelling conditions, including changes in temperature, pH, or productivity which co-vary with oxygen.

In contrast to finding a relative lack of community differences in relation to differing oxygen conditions, we found that diurnal differences were observed, and that communities during the day and night differed at 100 m (Fig. 5.10 B) and at 200 m (Fig. 5.10 D). Consistent with our hypothesis, diurnal differences appeared greater at shallower depths (Fig. 5.10 B) but were no longer evident at deeper depths (~400 m) (Fig. 5.10 F). The results suggest that at short time-scales (i.e. weekly), diurnal patterns are more pronounced that patterns relating to oxygen conditions.

Discussion

Due to their compact design, small landers such as *DOV BEEBE* can provide easy access to nearshore, deep-sea ecosystems. We found that the lander performed well and reliably over the course of the deployments, and was a valuable tool for studying oxygen variability and benthic community responses along the upper margin of the Southern California Bight. By collecting high-frequency measurements on near-seafloor environmental conditions, we could compare how the natural variability in environment oxygen conditions experienced by benthic and demersal communities along the upper slope, compares to the magnitude of oxygen change experienced for this region over the last 30 years.

The California Current System is expected to experience the impacts of hypoxia and ocean acidification on benthic communities sooner than other regions (Alin et al. 2012) because upwelling brings deep, oxygen-poor, and CO_2-rich waters into nearshore ecosystems along the US West Coast (Feely et al. 2008). The SCB region may be particularly vulnerable to habitat compression because the depth of the 22.5 μmol kg^{-1} oxygen boundary (ie. upper OMZ boundary), considered severely hypoxic (Hofmann et al. 2011a), occurs at a shallower depth here (~450 m) than in northern California, Oregon, and Washington (Helly and Levin 2004, Moffitt et al. 2015) (Fig. 5.1). A notable exception is the inshore hypoxia that sets up seasonally on the Oregon shelf (Chan et al. 2008, Grantham et al. 2004). It remains to be seen how upwelling intensity will change with climate change; summertime winds that drive upwelling are projected to intensify at higher latitudes and weaken at lower latitudes (Rykaczewski et al. 2015).

Upper slope depths appear to be especially affected by global trends of decreasing ocean oxygen on the US West Coast. Off Monterey Bay in Central California, depths between 100-350 m have seen declines in oxygen of 1.92 μmol kg^{-1} year^{-1} between 1998-2013 (Ren et al. 2018). In the Southern California Bight, oxygen declines of 1-2 μmol kg^{-1} year^{-1} have been reported by several studies over a period of ~30 years (Bograd et al. 2008, McClatchie et al.

2010, Meinville and Johnson 2013), with the largest relative changes occurring at 300 m (Bograd et al. 2008). In nearshore, sub-mixed-layer waters (<100 m), even faster rates of oxygen decline (4.41 μmol kg^{-1} yr^{-1}) have been reported in the SCB from 1998-2011 (Booth et al. 2014). Two main mechanisms for these observed decreases in oxygen have been proposed. The first, and dominant mechanism at deeper depths (200-400 m), is that increasingly more Pacific Equatorial Water (PEW) is being advected northward in the California Undercurrent (CUC) and that the oxygen concentrations of this source water are decreasing (Meinvielle and Johnson 2013, Bograd et al. 2015, Ren et al. 2018). The second mechanism, is increased respiration, which is suspected to contribute more to the decreases in oxygen observed at shallower depths (< 150 m) (Booth et al. 2014, Bograd et al. 2015, Ren et al. 2018). To compare the magnitude of natural variability over short time scales from our data with the trend in oxygen decrease, we looked at the annual rates of decrease reported for the SCB nearshore region (Bograd et al. 2008), since all our deployments were nearshore.

From our data, we see that at 100 m, at daily time scales, semidiurnal and diurnal variability exposes benthic communities to ~4-7 μmol kg^{-1} differences in oxygen conditions (Appendix Supp. 5.2). Across, weekly time-scales, benthic communities experience a range of oxygen conditions of ~32 μmol kg^{-1} (D10, spring) – 46 μmol kg^{-1} (D5, fall) (Table 5.3); this range is approximately 30% of the mean oxygen conditions. Across seasonal timescales, benthic communities at 100 m are exposed to even greater variability. Between the fall (D5) and spring (D10), mean oxygen conditions decreased by 28 μmol kg^{-1} (Table 5.3), and the total range was 65 μmol kg^{-1}. During our deployments, we did not capture any extreme event-based decreases in oxygen that have been reported by other studies using data from the Del

Mar mooring (Nam et al. 2015), but when these are considered, overall variability over an annual timescale at ~100 m is likely even greater.

Therefore, at 100 m, the rate of oxygen decrease observed (1.25-1.5 μmol kg^{-1} $year^{-1}$ loss) (Bograd et al. 2008), is less than the diurnal variability in oxygen conditions naturally experienced by benthic communities. Since this change over time relates to the mean oxygen conditions, this would suggest that over the course of ~20 years, the oxygen conditions seen now at 100 m in the spring (upwelling season), would be seen in the future in the fall, while spring conditions would be even lower (~75 μmol kg^{-1} mean $[O_2]$), potentially exposing these communities to periodic hypoxic conditions. Currently, our data showed that communities at ~100 m were not exposed to periodic hypoxia (Table 5.3).

One of the surprising findings was that at 200 m temperature, oxygen, and pH exhibited high variability (Fig. 5.2), greater at times than the variability observed at 100 m. Communities at these depths experience 10-12 μmol kg^{-1} differences in oxygen at semidiurnal and diurnal time-scales (Appendix Supp. 5.3). Over weekly timescales, communities experience a range of oxygen conditions that are ~40-59% of the mean conditions (Table 5.2). These depths have experienced an oxygen decline of 1-1.25 μmol kg^{-1} $year^{-1}$ loss (Bograd et al. 2008), suggesting that if this same rate of oxygen decline continues, the mean oxygen conditions at these depths (which ranged from ~70-82 μmol kg^{-1} from our data) will be hypoxic in 10-20 year. Currently, communities are only rarely and periodically exposed to hypoxic conditions (Table 5.3). However, we do not have data for this depth during the spring, thus it's possible that communities during the spring are already exposed to hypoxic conditions more frequently.

If mean conditions do become hypoxic at 200 m, the high variability we observed in environmental conditions at this depth may be advantageous to benthic community members that may otherwise be hypoxia intolerant. Frieder et al. (2014) concluded that high-frequency pH variability was an underappreciated source of pH-stress alleviation for invertebrates that were sensitive to low pH conditions. In a hypoxic fjord, slender sole, *Lyopsetta exilis*, were also observed living under mean oxygen conditions that were lower than their critical oxygen threshold (P_{crit}), due to the presence of oxygen variability around the mean (Chu et al. 2018). Similarly, the high variability of environmental conditions at 200 m may help buffer some of the negative effects of changing mean environmental conditions for benthic communities at 200 m.

The greatest relative changes in oxygen in the SCB have been reported at 300 m and represent an absolute change of 0.5-0.75 μmol kg^{-1} $year^{-1}$ (Bograd et al. 2008). In contrast to the high environmental variability observed at 200 m, variability at 300 m was reduced and more similar to variability at 400 m (Fig. 5.2, Table 5.3). At daily timescales, a tidal signal still influenced oxygen conditions, which ranged ~2 μmol kg^{-1} (Appendix Supp. 5.4). At weekly time scales, the range of oxygen conditions was ~19 μmol kg^{-1}, or ~39% of mean conditions at this depth (49.38 μmol kg^{-1}). No seasonal comparison is available, and the one deployment was conducted during the fall, so the annual range will be greater. Conditions at 300 m were always hypoxic, so these depths likely do not provide suitable habitat for hypoxia intolerant species under current conditions.

We note that 300 m is an interesting depth which may be at an important boundary between two different water masses. The correlation between spiciness and oxygen concentration is negative at 200 m (indicative of high input of PEW), and then positive at 300

m. These different water masses can give rise to the formation of internal waves, that may be responsible for the noisy periodogram (Fig. 5.4), and the high turbidity observed during most of the deployment at 300 m (Fig. 5.5). However, these additional frequencies of variability do not seem to translate into a higher magnitude of variability of oxygen conditions. Poor visibility conditions have also been observed during two separate ROV dives at ~340 m off Point Loma (unpublished), suggesting high turbidity conditions may be the norm at these depths on the upper margin in the SCB, but additional deployments are needed to confirm this. Conditions observed during the deployment at ~300 m were frequently poorer than the visibility conditions at 5 m in the San Diego Bay, near the Marfac Finger pier, and it is worth considering how this poor-visibility environment may influence the benthic communities that are present at these upper slope depths.

At 400 m, absolute variability of oxygen conditions was only slightly lower than that at 300 m (Table 5.3), but since the mean conditions were ~20 μmol kg^{-1} lower at 400 m, the relative variability in oxygen conditions was higher at 400 m. At daily timescales, oxygen varied ~2 μmol kg^{-1} with the tides (Appendix Supp. 5.4), and at weekly timescales, we observed a range of 17 μmol kg^{-1}, which represented 59% of the mean. Therefore, the amount of oxygen variability relative to the mean at 400 m, was similar to that at 200 m, suggesting that variability in oxygen conditions may provide some reprieve to benthic communities at this depth from low mean oxygen conditions. At this depth, we recorded severely hypoxic conditions ($O_2 < 22.5$ μmol kg^{-1}) for ~1% of the deployment time (Table 5.3), suggesting that even though this community is above the depth frequently associated with the upper boundary of the OMZ (450 m), it is still periodically exposed to OMZ conditions. Oxygen decreases of 0.25-0.5 μmol kg^{-1} year^{-1} have been reported for depths of 400 m (Bograd et al. 2008), and if these trends continue, in 13-26 years, this depth zone may become the upper boundary of the OMZ.

While we have related our results to reported trends for the SCB for the last 30 years, it is important to acknowledge that oxygen in this region reflects multidecadal oxygen variability associated with the Pacific Decadal Oscillation (PDO). During the 1950s and 1960s, oxygen levels were also very low in the SCB, and McClatchie et al. (2010) note that at ~250 m, conditions were as low or lower than those observed recently. Therefore, benthic communities have been exposed to these low oxygen periods in the relatively recent past, but these conditions may become more extreme with climate change. It is unclear if the 1-2 μmol kg^{-1} $year^{-1}$ decreasing oxygen trend will continue over the next 20 years, but nanolanders are an additional tool that could be used to monitor future changes near the seafloor.

One of the unexpected results of this study was that we did not see any evidence of seafloor community-level responses to daily and weekly oxygen variability (Fig. 5.8 and 5.10), and especially at shallower depths (100-200 m), day-night differences were important sources of community-level variation (Fig. 5.9 and 5.10). Based on our results, communities seem to respond to changes in environmental conditions across monthly timescales, as seen for the community-level differences observed for the two deployments at ~100 m at Del Mar Steeples Reef (Fig. 5.6, 5.7, 5.8, and 5.10), but these differences may also relate to differences in food availability during the upwelling season. Communities also differ across depths, where mean environmental conditions differ (Fig. 5.7). Therefore, it is unlikely that community-level response to hypoxia can be observed using observation time-series over weekly timescales.

There are two conditions in which this may not be the case. First, the Del Mar mooring has recorded strong event-based changes in dissolved oxygen (Nam et al. 2015) in which case oxygen conditions rapidly increase or decrease over a short time-period (< 2 weeks). Rapid changes such as these that are outside of the typical regime of oxygen variability may lead to more immediate community responses. However, we did not capture any such events during our deployments. Secondly, community-level responses may be observed if the mean environmental conditions are close to a critical threshold for a species that is dominant in the community. However, tolerances to hypoxia are species-specific, with high intraspecies variability as well, so longer time-series may be needed to track a community-level change. Given that we did not see community-level responses at these shorter timescales, this suggests that future deployments may sample less frequently and therefore be able to sample over longer time periods. For example, reducing sampling to a 20 second video sample every hour or every two hours would increase the time-series length three or six times respectively with the same power capacity. Assuming a full eight hours of battery power for the LED lights with the improved relay, and a sampling rate of 20 seconds of video every 2 hours, we could collect a benthic time-series over 120 days with corresponding environmental data.

The lack of community-level response to diurnal and weekly oxygen variability seen in our data may not be surprising given that animals have several ways that they can respond to stressful conditions, which would not affect community-level abundance, diversity, or composition patterns. For example, fish can become less active during period of hypoxia to reduce metabolic demand (Richards 2009, 2010), or can decrease feeding behavior during low oxygen periods (Wu 2002, Nilsson 2010). Therefore, at daily and weekly timescales, benthic and demersal animals likely respond to changes in oxygen availability through behavioral and physiological responses. Our data did show that the transition from fish- to invertebrate-dominated communities though space or time may be a valuable community-level metric or indicator that could be used to track the effects of hypoxia on seafloor communities.

Ocean deoxygenation is a global problem, and many of the areas where large decreases in oxygen have been observed occur in developing countries, such as along the western and eastern coast of Africa (Schmidtko et al. 2017). Large oxygen losses have also been observed in the Arctic (Schmidtko et al. 2017), where the seafloor habitat is understudied. Continental shelves and margins provide many ecosystem services, including fisheries, and changes in oxygen conditions may impair the productivity of these environments. Small autonomous landers, such as *DOV BEEBE*, could expand the capabilities of developed and developing countries to monitor and study environmental changes along their coastlines since they can be deployed using small boats. One of the benefits of the nanolander design is that it is modular and easy to modify to fit the scope of research that is needed. For example, a sound trap and an additional RBR MicroCAT were added to *DOV BEEBE* for the last deployment, and the extra weight was easily offset by adding an additional small styrene flotation sphere for buoyancy. Other sensors and instruments could therefore easily be incorporated into the nanolander design based on research needs. For continental margins and seafloor habitats, a global array of nanolanders, similar in scope to the Argo program, could be envisioned which would greatly expand our understanding of climate change impacts on seafloor communities.

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Literature Cited

Aguzzi, J., Company, J.B., Costa, C., Menesatti, P., Garcia, J.A., Bahamon, N., Puig, P., Sarda, F. 2011. Activity rhythms in the deep-sea: a chronobiological approach. Front. Biosci. 16, 131–150.

Alin, S.R., Feely, R.A., Dickson, A.G., Hernandez-Ayon, J.M., Juranek, L.W., Ohman, M.D., Goericke, R. 2012. Robust empirical relationships for estimating the carbonate system in the southern California Current System and application to CalCOFI hydrographic cruise data (2005-2011). J. Geophys. Res. 117, C05033.

Bay, R.A., Palumbi, S.R. 2014. Multilocus adaptation associated with heat resistance in reef-building corals. Current Biology 24, 2952-2956.

Bograd, S.J., Castro, C.G., Lorenzo, E.D., Palacios, D.M., Bailey, H., Gilly, W., Chavez, F.P. 2008. Oxygen declines and the shoaling of the hypoxic boundary in the California Current. Geophys. Res. Lett. 35, L12607.

Bograd, S.J., Buil, M.P., Lorenzo, E.D., Castro, C.G., Schroeder, I.D., Goericke, R., Anderson, C.R., Benitez-Nelson, C., Whitney, F.A. 2015. Changes in source waters to the Southern California Bight. Deep-Sea Res II 112: 42-52.

Booth, J.A.T., Woodson, C.B., Sutula, M., Micheli, F., Weisberg, S.B., Bograd, S.J., Steele, A., Schoen, J., Crowder, L.B. 2014. Patterns and potential drivers of declining oxygen content along the southern California coast. Limnol. Oceanogr. 59(4), 1127-1138.

Chan, F., Barth, J.A., Lubchenco, J., Kirincich, A., Weeks, H., Peterson, W.T., Menge, B.A. 2008. Emergence of anoxia in the California Current large marine ecosystem. Science 319, 920.

Chu, J.W.F., Curkan, C., Tunnicliffe, V. 2018. Drivers of temporal beta diversity of a benthic community in a seasonally hypoxic fjord. R. Soc. Open sci. 5: 172284.

Chu, J.W.F., Tunnicliffe, V. 2015. Oxygen limitations on marine animal distributions and the collapse of epibenthic community structure during shoaling hypoxia. Global Change Biology. doi: 10.1111/gcb.12898

Doya, C., Aguzzi, J., Pardo, M., Matabos, M., Company, J.B., Costa, C., Mihaly, S., Canals, M. 2014. Diel behavioral rhythms in sablefish (*Anoplopoma fimbria*) and other benthic species, as recorded by the Deep- sea cabled observatories in Barkley canyon (NEPTUNE-Canada). Journal of Marine Systems 130, 69-78.

Feely, R.A., Sabine, C.L., Hernandez-Ayon, J.M., Ianson, D., Hales, B. 2008. Evidence for upwelling of corrosive “acidified” water onto the continental shelf. Science 320, 1490-1492.

Flament, P. 2002. A state variable for characterizing water masses and their diffusive stability: Spiciness, Prog. Oceanogr. 54: 493–501.

Frieder, C.A. 2013. Evaluating low oxygen and pH variation and its effects on invertebrate early life stages on upwelling margins. University of California, San Diego. 182 pgs.

Frieder, C.A., Gonzalez, J.P., Bockmon, E.E., Navarro M.O., Levin, L.A. 2014. Can variable pH and low oxygen moderate ocean acidification outcomes for mussel larvae? *Glob. Change Biol.* 20(3), 754-764.

Frieder, C.A., Nam, S.H., Martz, T.R., and Levin, L.A. 2012. High temporal and spatial variability of dissolved oxygen and pH in a nearshore California kelp forest. Biogeosciences 9, 3917-3930.

Gallo, N.D., Cameron, J., Hardy, K., Fryer, P., Bartlett, D.H., Levin, L.A. 2015. Submersible- and lander-observed community patterns in the Mariana and New Britain trenches: Influence of productivity and depth on epibenthic and scavenging communities. Deep-Sea Res. I 99, 119-133.

Gilly, W.F., Beman, J.M., Litvin, S.Y., Robison, B.H. 2013. Oceanographic and biological effects of shoaling of the oxygen minimum zone. Annu. Rev. Mar. Sci. 5, 393-420.

Gooday, A.J., Bett, B.J., Escobar, E., Ingole, B., Levin, L.A., Neira, C., Raman, A.V., Sellanes, J. 2010. Habitat heterogeneity and its influence on benthic biodiversity in oxygen minimum zones. Marine Ecology 31, 125-147.

Grantham, B.A., Chan, F., Nielsen, K.J., Fox, D.S., Barth, J.A., Huyer, A., Lubchenko, J., Menge, B.A. 2004. Upwelling-driven nearshore hypoxia signals ecosystem and oceanographic changes in the northeast Pacific. Nature 429, 749-754.

Helly, J.J., Levin, L.A. 2004. Global distribution of naturally occurring marine hypoxia on continental margins. Deep-Sea Res. I 51, 1159-1168.

Henson, S.A., Beaulieu, C., Ilyina, T., John, J.G., Long, M., Séférian, R., Tjiputra, J., Sarmiento, J.L. 2017. Rapid emergence of climate change in environmental drivers of marine ecosystems. *Nat. Commun.* 8:14682

Hofmann, A.F., Peltzer, E.T., Walz, P.M., Brewer, P.G. 2011a. Hypoxia by degrees: establishing definitions for a changing ocean. Deep-Sea Res. I 58, 1212–26.

Hofmann, G.E., Smith, J.E., Johnson, K.S., Send, U., Levin, L.A., Micheli, F., Paytan, A., Price, N.N., Peterson, B., Takeshita, Y., Matson, P.G., Crook, E.D., Kroeker, K.J., Gambi, M.C., Rivest, E.B., Frieder, C.A., Yu, P.C., Martz, T.R. 2011b. High-frequency dynamics of ocean pH: A multi-ecosystem comparison. PLoS ONE 6(12), e28983.

Jamieson, A.J. 2016. Landers: Baited cameras and traps. In Biological Sampling in the Deep Sea. Ed. Malcolm R. Clark, Mireille Consalvey, and Ashley A. Rowden. John Wiley & Sons, Ltd.

Juniper, S.K., Matabos, M., Mihaly, S., Ajayamohan, R.S., Gervais, F., Bui, A.O.V. 2013. A year in Barkley Canyon: A time-series observatory study of mid-slope benthos and habitat dynamics using the NEPTUNE Canada network. Deep-Sea Res. II 92, 114-123.

Keller, A.A., Ciannelli, L., Wakefield, W.W., Simon, V., Barth, J.A., Pierce, S.D. 2015. Occurrence of demersal fishes in relation to near-bottom oxygen levels within the California Current large marine ecosystem. Fish. Oceanogr. 24(2), 162-176.

Keller, A.A., Simon, V., Chan, F., Wakefield, W.W., Clarke, M.E., Barth, J.A., Kamikawa, D., Fruh, E.L. 2009. Demersal and invertebrate biomass in relation to an offshore hypoxic zone along the US West Coast. Fisheries Oceanography 19(1), 76-87.

Kelley, D., Richards, C. 2017. oce: Analysis of Oceanographic Data. R package version 0.9-22. https://CRAN.R-project.org/package=oce

Levin, L.A. 2003. Oxygen minimum zone benthos: Adaptation and community response to hypoxia. Oceanography and Marine Biology: an Annual Review 41, 1-45.

Levin, L.A., Lieu, K.-K., Emeis, K.-C., Breitburg, D.L., Cloern, J., Deutsch, C., Giani, M., Goffart, A., Hofmann, E.E., Lachkar, Z.., Limburg, K., Liu, S.-M., Montes, E., Naqvi, W., Ragueneau, O., Rabouille, C., Sarkar, S.K., Swaney, D.P., Wassman, P., Wishner, K.F. 2015. Comparative biogeochemistry-ecosystem-human interactions on dynamic continental margins. Journal of Marine Systems 141, 3-17.

Long, M.C., Deutsch, C., Ito, T. 2016. Finding forced trends in oceanic oxygen. *Glob. Biogeochem. Cycles* 30, 381–397.

Lynn, R.J., Simpson, J.J. 1987. The California Current System: The seasonal variability of its physical characteristics. Journal of Geophysical Research 92(C12), 12,947-12,966.

Matabos, M., Bui, A.O.V., Mihaly, S., Aguzzi, J., Juniper, S.K., Ajayamohan, R.S. 2014. High-frequency study of epibenthic megafaunal community dynamics in Barkley Canyon: A multi-disciplinary approach using the NEPTUNE Canada network. Journal of Marine Systems 130, 56-68.

McClatchie, S., Goericke, R., Cosgrove, R., Auad, G., Vetter, R. 2010. Oxygen in the Southern California Bight: Multidecadal trends and implications for demersal fisheries. Geophysical Research Letters 37: L19602.

Meinvielle, M., Johnson, G.C. 2013. Decadal water-property trends in the California Undercurrent with implications for ocean acidification. J. Geophys. Res. Oceans 118: 6687-6703.

Moffitt, S.E., Moffitt, R.A., Sauthoff, W., Davis, C.V., Hewett, K., Hill, T.M. 2015. Paleoceanographic insights on recent oxygen minimum zone expansion: lessons for modern oceanography. PLoS ONE 10(1), e0115246.

Murty, S.J., Bett, B.J., Gooday, A.J. 2009. Megafaunal responses to strong oxygen gradients on the Pakistan margin of the Arabian Sea. Deep-Sea Res. II 56, 472-487.

Nam, S.H., Send, U. 2011. Direct evidence of deep water intrusions onto the continental shelf via surging internal tides. J. Geophys. Res., 116, C05004.

Nam, S., Takeshita, Y., Frieder, C.A., Martz, T., Ballard, J. 2015. Seasonal advection of Pacific Equatorial Water alters oxygen and pH in the Southern California Bight. J. Geophys. Res. Oceans 120: doi:10.1002/ 2015JC010859

Nilsson, G.E. 2010. Respiratory physiology of vertebrates: Life with and without oxygen. Cambridge University Press, New York, 334 pgs.

Oksanen, J., Blanchet F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H, Szoecs E., Wagner, H. 2017. vegan: Community Ecology Package. R package version 2.4-4. https://CRAN.R-project.org/package=vegan

Priede, I.G., Bagley, P.M. 2000. In situ studies on deep-sea demersal fishes using autonomous unmanned lander platforms. Oceanography and Marine Biology: an Annual Review 38, 357-392.

Ren, A.S., Chai, F., Xue, H., Anderson, D.M., Chavez, F.P. 2018. A sixteen-year decline in dissolved oxygen in the Central California Current. Scientific Reports 8: 7290.

Richards, J., 2009. Metabolic and molecular responses of fish to hypoxia. Fish Physiol. 27, 443–485.

Richards, J., 2010. Metabolic rate suppression as a mechanism for surviving environmental challenge in fish. Prog. Mol. Subcell. Biol. 49, 113–139.

Rykaczewski, R.R., Dunne, J.P., Sydeman, W.J., Garcia-Reyes, M., Black, B.A., Bograd, S.J. 2015. Poleward displacement of coastal upwelling-favorable winds in the ocean's eastern boundary currents through the 21st century. *Geophys. Res. Lett.* 42, 6424–31.

Schmidtko, S., Stramma, L., Visbeck, M. 2017. Decline in global oceanic oxygen content during the past five decades. Nature 542: 335-339.

Send, U., Nam, S. 2012. Relaxation from upwelling: the effect on dissolved oxygen on the continental shelf. J. Geophys. Res., 117, C04024.

Vaquer-Sunyer, R., Duarte, C.M. 2008. Thresholds of hypoxia for marine biodiversity. Proc. Natl. Acad. Sci. USA 105, 15452–57.

Wu, R.S.S., 2002. Hypoxia: from molecular responses to ecosystem responses. Mar. Pollut. Bull. 45, 35–45.

Tables

Table 5.1. Information for all ten deployments conducted with *DOV BEEBE* including deployment dates, length, location, depth, instrumentation, data use, and notes from the deployments. Deployments D3, D4, D5, D6, D7, D8, and D10 were used for data collection.

Deployment	Dates	Deployment time	Location	Depth	Sensors	Data Analyzed	Deployment Notes
D1	Apr 19-27, 2017	~8 days	Marfac Finger Pier	5 m	SBE 37-SMP-ODO, Camera system	N/A	DOV BEEBE deployed off the Marfac finger pier to test acoustic communication, burn wires, camera system and lights, and SeaBird MicroCAT. Drop-arm restrained with a galvanic release (~6 hours before arm dropped) and baited with chicken.
D2	Jun 23-26, 2017	~3 days	NOAA SWFSC rockfish tank	~2 m	Camera system	N/A	DOV BEEBE deployed in the NOAA SWFSC rockfish tank to test nanolander performance, camera visibility, new low-voltage cut-out for the battery management system, and and rockfish responses to LED lights and nanolander. Deployment shows that camera visibility is good with adequate focus both up-close and far away, with some minor graininess. Low-voltage cut-out worked well. Rockfish did not exhibit any apparent avoidance or attraction behavior to the lights or nanolander.
D3	Aug 17-Sep 1, 2017	~15 days	Scripps Coastal Reserve (32.87108° N, 117.26459° W)	179 m	SBE 37-SMP-ODO, Camera system*	Environmental data	First field deployment of DOV BEEBE in the Scripps Coastal Reserve. Goals were to: 1) test DOV BEEBE capability during a full-length deployment and check that all systems were intact and functioning, 2) to test deployment and recovery methodology off of a Scripps small boat, 3) check camera angle, and 4) start looking at environmental variability and community responses. Drop arm was baited with a bag of frozen Rex soles in a cantalope bag, and secured with a galvanic timed release. Deployed using SIO18. Lights didn't work because an internal cable had blocked the light sensor that triggers the LED lights. We changed the sensitivity of the light sensor.
D4	Sep 7-Sep 25, 2017	~19 days	Scripps Coastal Reserve (32.87108° N, 117.26457° W)	178 m	SBE 37-SMP-ODO, Camera system	Environmental and community data	Redeployment of DOV BEEBE in the Scripps Coastal Reserve. Goals were to: 1) test DOV BEEBE capability during a full-length deployment and make sure that all systems were intact and functioning, 2) continue perfecting deployment and recovery methodology, 3) to check camera angle, and 4) to collect data on environmental variability and community responses. Drop-arm was baited with a bag of frozen slender soles and hake and secured with a galvanic timed release. Deployed using SIO18 to same location as D3.
D5	Sep 29-Nov 3, 2017	~35 days	Del Mar Steeples Reef (32.93765° N, 117.31675° W)	99 m	SBE 37-SMP-ODO, Camera system	Environmental and community data	First deployment of DOV BEEBE to rocky reef site off of Del Mar, representing the first of the 4 planned fall/winter deployments. Goals of the deployment were to collect data on environmental variability and community responses at a rocky reef area with rockfish, and to continue perfecting deployment and recovery methodology. Drop arm was baited with frozen slender sole and hake and secured with 3 "Wint O Green" Lifesavers, which took <20 minutes to dissolve and for the drop-arm to drop. Deployed using John P. Scripps boat. Acoustic communication worked well, and it took 10 minutes to recover BEEBE. Despite being deployed for 1 month, there was very little corrosion or biofouling on the nanolander (small amount of rust on some of the screws).
D6	Nov 9-29, 2017	~20 days	Del Mar Steeples Reef (32.93762° N, 117.3254° W)	192 m	SBE 37-SMP-ODO, Camera system	Environmental and community data	This was the second deployment at Del Mar Steeples reef, moving into deeper depths (~200 m). This represented the second of the 4 planned fall/winter deployments. Drop-arm was baited with a cantalope bag of slender sole, hake, and hundred fathom codlings, and secured with 3 "Wint O Green" Lifesavers, which took <20 minutes to dissolve. Used SIO18 for deployment.
D7	Dec 12, 2017 - Jan 5, 2018	~24 days	Del Mar Steeples Reef (32.93633°N, 117.33422°W)	295 m	SBE 37-SMP-ODO, Camera system, Sound Trap	Environmental and community data	This was the third deployment at Del Mar Steeples reef, continuing into deeper water. This represented the third of the 4 planned fall/winter deployments. Drop-arm was baited with a cantalope bag of frozen rex soles, eelpouts, hake and one rockfish, and secured with 3 "Wint O Green" Lifesavers, which took <20 minutes to dissolve. Acoustic communication worked well and it took 15 minutes to recover BEEBE. BEEBE came up with a lot of fine sediment.
D8	Jan 23-Feb 8, 2018	~16 days	Del Mar Steeples Reef (32.93105°N, 117.34875°W)	399 m	SBE 37-SMP-ODO, Camera system	Environmental and community data	This was the fourth deployment at Del Mar Steeples reef, continuing into deeper water. This represented the fourth and last of the 4 planned fall/winter deployments. Drop-arm was baited with a cantalope bag of 6 rex soles and secured with 4 "Wint O Green" Lifesavers, which took <20 minutes to dissolve. Took about 15 minutes to recover BEEBE, and no sediment was present.
D9	Mar 1-5, 2018	~4 days	La Jolla Cove at Lilly's site	30 m	SBE 37-SMP-ODO, Camera system	N/A	Short deployment to Lilly's site to test nanolander performance and get some photographs and video of BEEBE underwater
D10	Mar 8-Mar 29, 2018	~21 days	Del Mar Steeples Reef (32.93765°N, 117.31675°W)	98 m	SBE 37-SMP-ODO, Camera system, Sound Trap, RBR CTD with ODO and PAR	Environmental and community data	This was the first of the 4 planned spring/summer deployments at Del Mar Steeples Reef and represented the shallowest of the 4 planned. The location was the same as D5. The goal of this deployment was to compare an upwelling to a non-upwelling period. New components of this deployment included a new light, new 32 AmpH battery pod, RBR CTD with ODO and PAR sensors, and Jack Butler's Sound Trap. Drop-arm was baited with a cantalope bag of 2 rex soles, 3 hake, and one hundred fathom codling and secured with 3 "Wint O Green" Lifesavers, which took <20 minutes to dissolve. We added an additional orange sphere (additional 5.5 lb buoyancy), to offset new sensor weight. Recovery on this deployment was problematic. Communication was excellent, but BEEBE got stuck on something on the bottom. BEEBE surfaced at night and began a long drift to the south, drifting for 16 days before it was picked up by Baja Aqua Farms off Colonet Bay, Mexico. Finally recovered BEEBE from Baja Aqua Farms on April 27, 2018.

Table 5.2. Camera and light performance for each data deployment, with total number of 20-second video samples available for the community analysis indicated. Table shows the number of samples recorded on the camera overall, as well as the amount of time the LED lights functioned for each deployment time. Number of samples recorded by the camera were a function of deployment length and not camera capacity, which was never exceeded during these deployments. LED lights exhibited a behavior where they would first fail and then flicker on and off for a certain number of additional 20-second video segments, before failing completely. This length of time is also indicated in the table.

	D4	**D5**	**D6**	**D7**	**D8**	**D10**
Depth (m)	178	99	192	295	399	98
Number of video clips recorded	1320	2523	1448	1744	1178	1575
Amount of time for total videos recorded (h)	7.33	14.02	8.04	9.69	6.54	8.47
Number of videos before LED lights first failed	1009	859	1013	407	594	397
Amount of time before lights first failed (h)	5.61	4.77	5.63	2.26	3.30	2.21
Amount of time between first and final light failure (h)	1.02	1.42	0.06	0.21	0.11	0.02
Number of 20-sec video samples for analysis	1009	876	1012	406	594	396
Number of video samples with good visibility	1009	876	656	6	594	396

Table 5.3. Mean environmental conditions for each deployment. Table shows the deployment dates, sampling interval, time series length, mean depth, temperature, oxygen, pHest, and salinity conditions, as well as the ranges and coefficient of variation (CV) for temperature, oxygen, and pHest for each deployment. The percentage of deployment time that conditions were hypoxic ($[O_2] < 60$ µmol kg^{-1}) or severely hypoxic ($[O_2] < 22.5$ µmol kg^{-1}) is also indicated.

	D3	**D4**	**D5**	**D6**	**D7**	**D8**	**D10**
Dates	Aug 17-Sep 1, 2017	Sep 7-Sep 25, 2017	Sep 29-Nov 3, 2017	Nov 9-29, 2017	Dec 12, 2017 - Jan 5, 2018	Jan 23-Feb 8, 2018	Mar 8-Mar 29, 2018
MicroCAT Interval	1 sample every 5 minutes	1 sample every 5 minutes	1 sample every 5 minutes	1 sample every 5 minutes	1 sample every 5 minutes	1 sample every 5 minutes	1 sample every 5 minutes
No. Samples	4,303	5,212	10,061	5,757	6,912	4,663	6,123
Timeseries Length (hr)	358.50	434.25	838.33	479.67	575.92	388.50	510.20
Depth (m)	179.10	177.90	98.81	191.60	295.50	399.40	98.10
Mean Temp (°C)	10.07	9.88	11.10	9.51	8.39	7.42	9.80
Temp Range (°C)	9.72-10.43	9.45-10.44	10.35-12.26	8.94-10.21	7.99-8.77	6.97-7.89	9.39-10.30
CV Temp (%)	1.35	1.69	2.89	2.11	1.88	2.02	1.70
Mean [O2] (umol/kg)	70.75	77.61	132.00	82.10	49.38	28.97	103.95
[O2] range (umol/kg)	48.82-103.87	49.41-108.26	110.40-156.50	63.33-102.96	39.89-59.36	21.19-38.41	91.22-123.01
CV [O2] (%)	13.72	12.92	5.07	9.82	7.02	10.20	5.72
Mean O2 Sat (%)	25.60	27.97	48.67	29.35	17.25	9.91	37.36
O2 Sat Range (%)	17.55-37.79	17.66-39.37	40.11-58.50	22.52-37.27	13.81-20.89	7.18-13.26	32.54-44.55
pO2 (kPa)	5.50	6.01	10.33	6.32	3.77	2.20	7.94
pO2 Range (kPa)	3.77-8.11	3.79-8.45	8.52-12.41	4.85-8.02	3.02-4.56	1.59-2.94	6.92-9.47
Conditions hypoxic	12.64%	1.88%	0%	0%	100%	100%	0%
Conditions severely hypoxic	0%	0%	0%	0%	0%	1.12%	0%
Mean pHest	7.646	7.655	7.759	7.658	7.594	7.553	7.696
pHest Range	7.607-7.704	7.605-7.711	7.713-7.814	7.625-7.699	7.575-7.613	7.538-7.572	7.671-7.732
CV pHest (%)	0.22	0.23	0.20	0.19	0.09	0.08	0.15
Mean Salinity (psu)	33.85	33.87	33.43	33.89	34.05	34.09	33.74

Figures

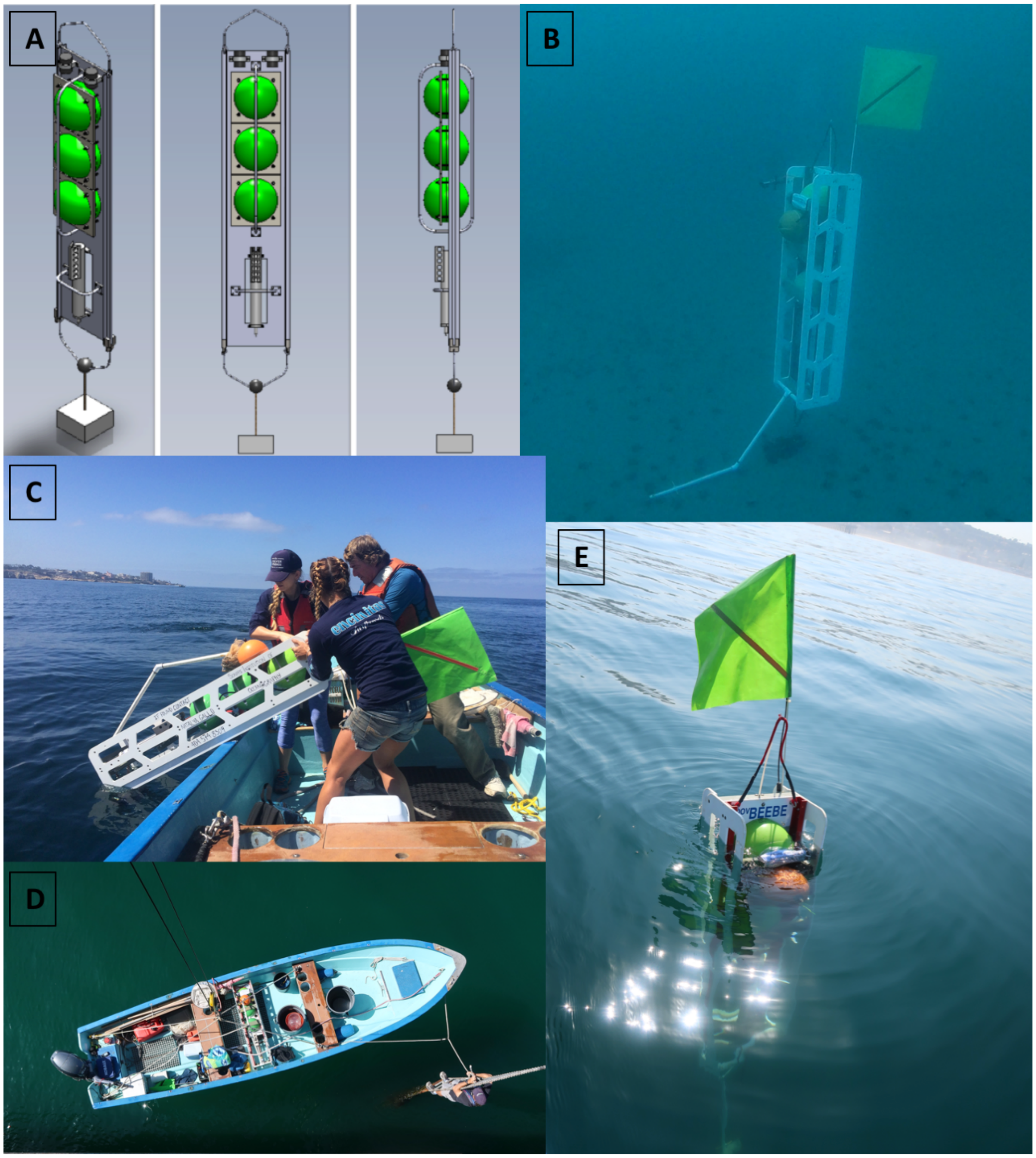


Figure 5.1. *DOV BEEBE* is an autonomous lander capable of operating to 1000 m depth. It is outfitted with a Seabird MicroCAT-ODO environmental sensor for collecting high-frequency measurements of near-seafloor temperature, oxygen, salinity, and pressure, and a camera and light system for collecting videos of seafloor communities. The early design for *DOV BEEBE* is shown in A, and *DOV BEEBE* is shown deployed at 30 m depth in B. *BEEBE* can easily be deployed by several people (C) from a small boat (D), and, without weights, is positively buoyant at the surface and has an easily visible surface signature (E). *DOV BEEBE* was designed and built by Kevin Hardy (Global Ocean Design).

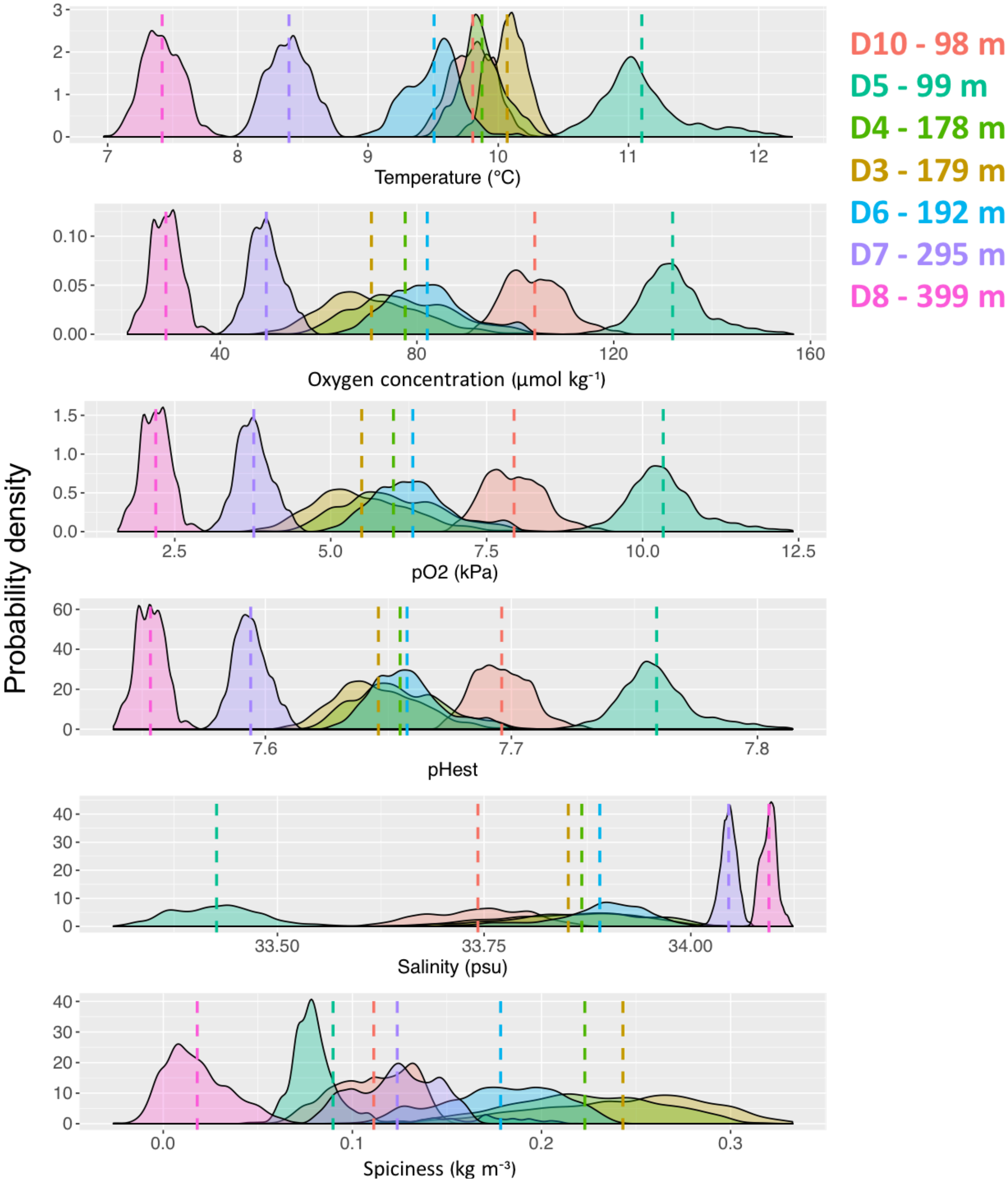


Figure 5.2. Mean and variance of near-seafloor temperature, oxygen concentration, oxygen partial pressure, pHest, salinity, and spiciness. The probability density of data collected for each deployment is shown, with the color of the data distributions corresponding to each deployment (as indicated in the legend along with the deployment depth). The mean is indicated with a dotted line in the same color and exact values are in Table 5.3.

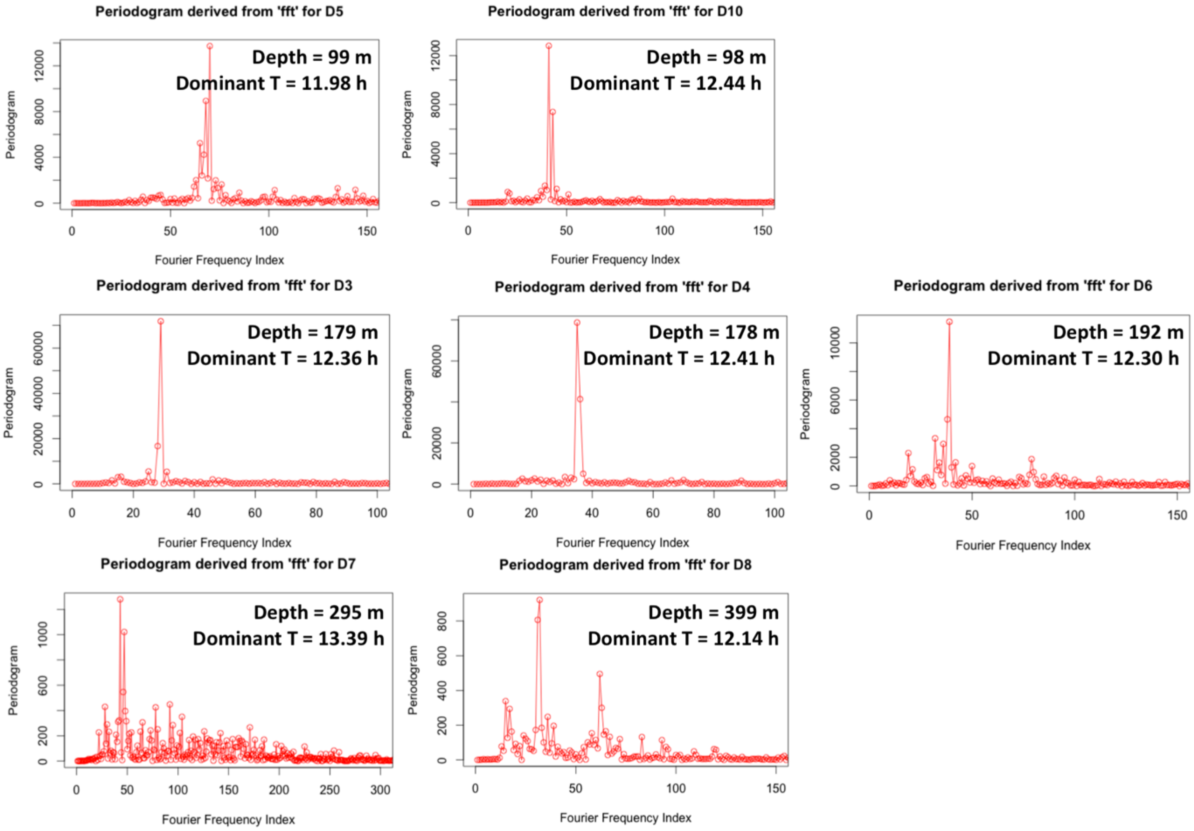


Figure 5.3. Periodograms are shown for each of the seven deployments. Periodograms are organized by deployment and deployment depth from shallowest (top) to deepest (bottom), and deployment depths are indicated. The dominant period identified is indicated, which corresponds to the highest peak on the periodogram. Note the differences in y-axis scale, across the periodograms: shallower deployments have a larger amplitude signal than deeper deployments. The oxygen time series for each deployment were also decomposed to look at the trend, daily, and random signals that contribute to the overall data patterns (Supp. 5.2-4).

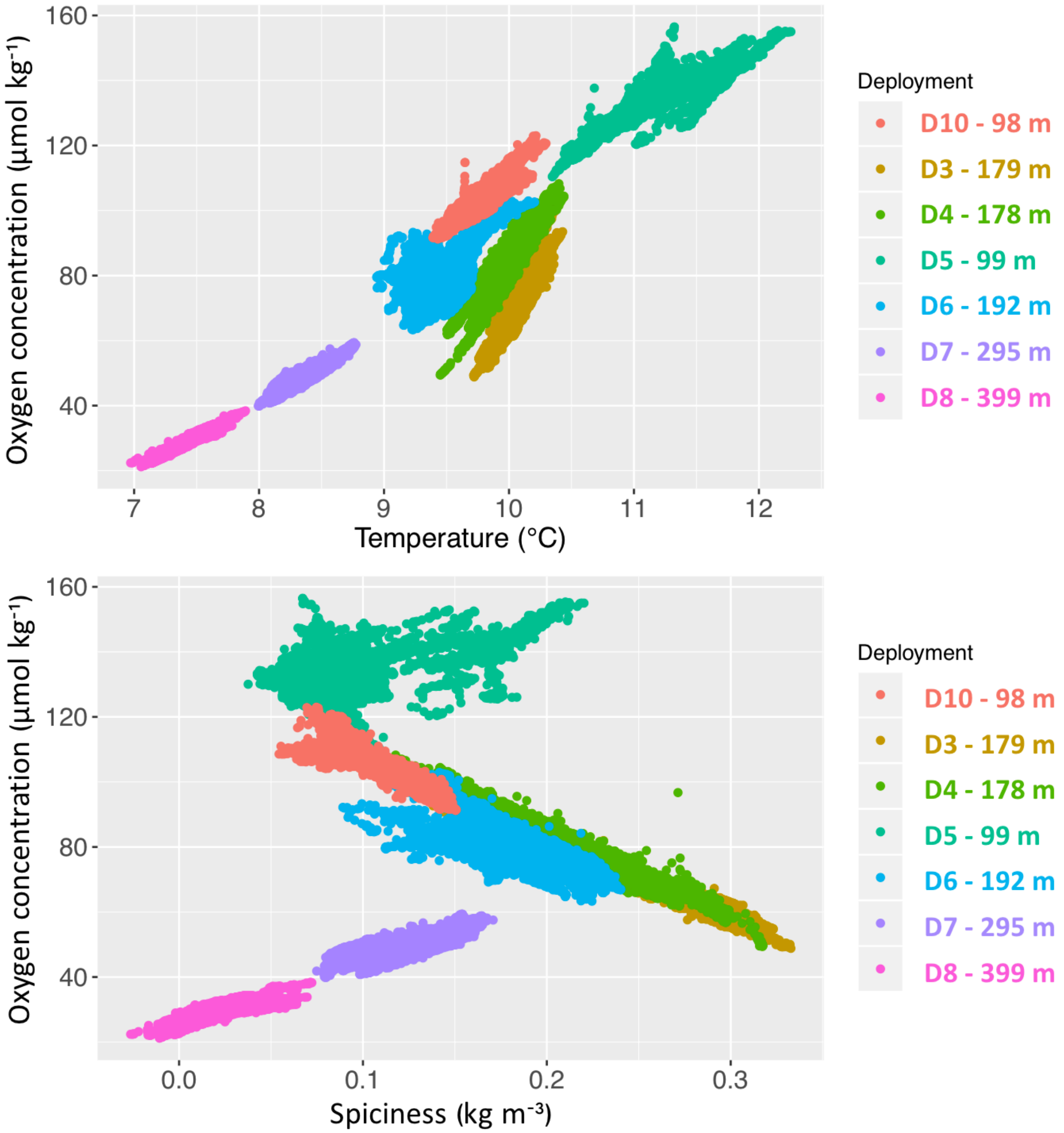


Figure 5.4. Near-bottom dissolved oxygen concentration shown as a function of temperature and spiciness. The color of data points corresponds to each deployment (as indicated in the legend along with the deployment depth).

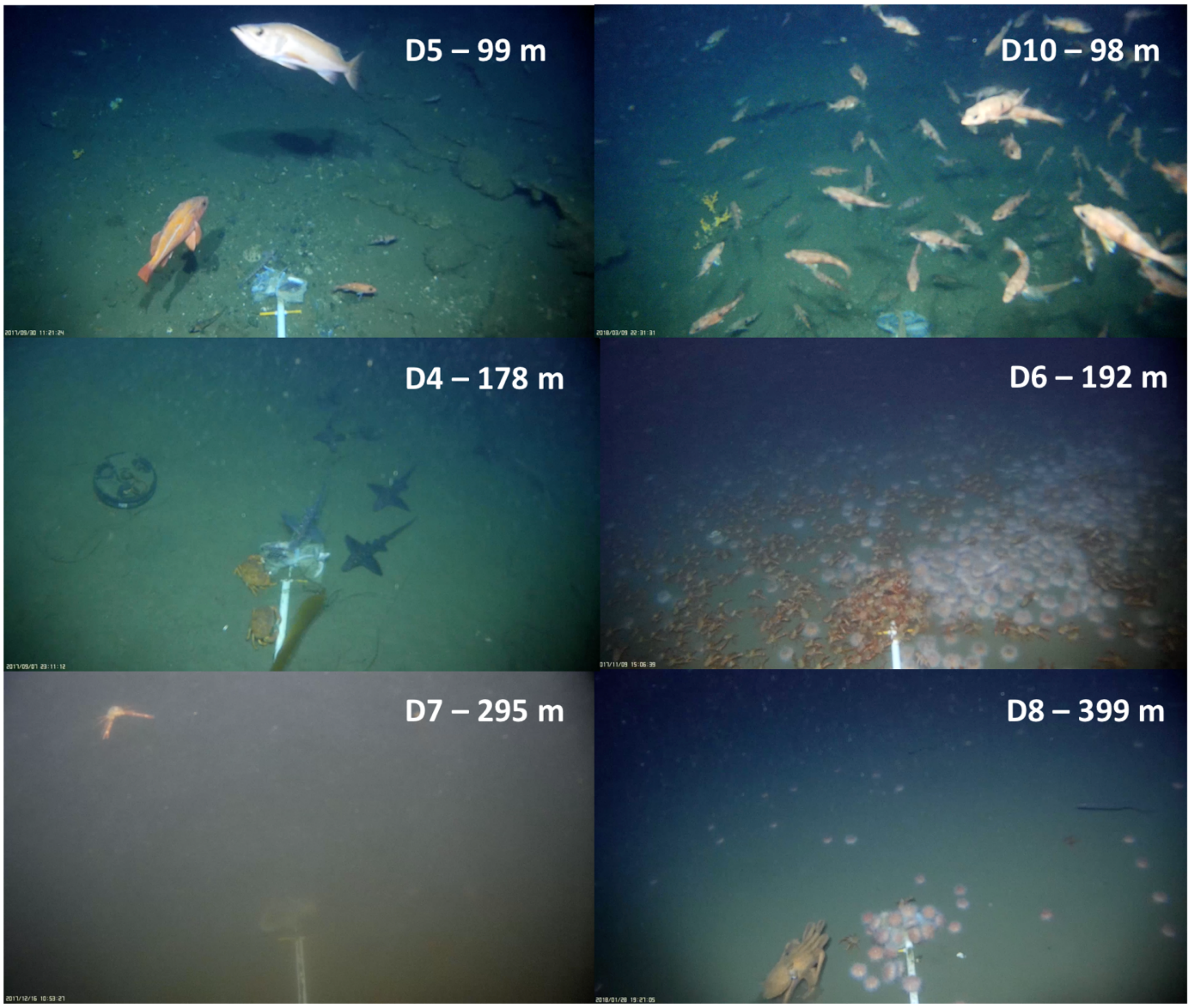


Figure 5.5. Representative images are shown from each of the six video deployments. For each deployment, 20-second videos were recorded every 20 minutes, and a framegrab is shown here. Images are ordered by deployment depth from shallowest (top, ~100 m) to deepest (bottom right, ~400 m). Poor visibility conditions were encountered for most of D7, and this image is representative of average conditions for the deployment. Images show examples of fauna that were observed during each deployment.

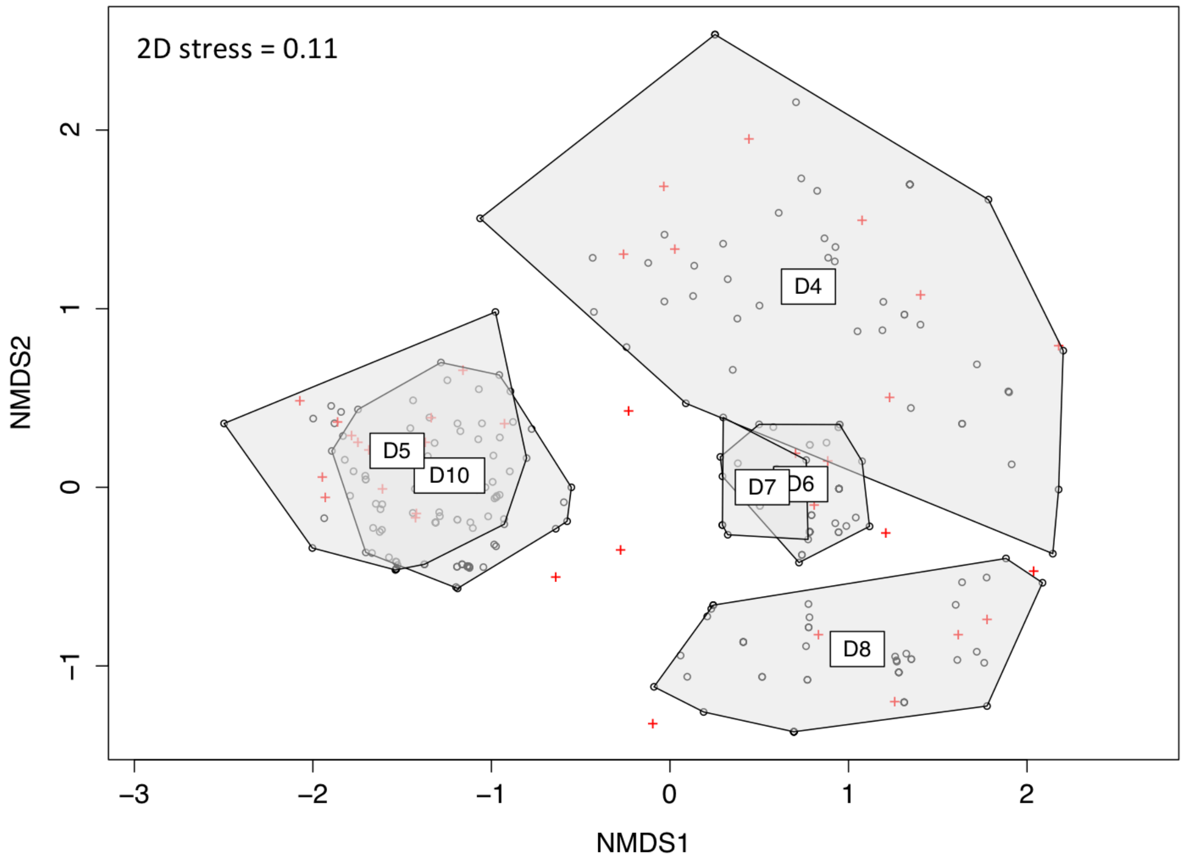


Figure 5.6. Non-metric multidimensional scaling plot based on a Bray-Curtis similarity matrix of square-root transformed count data of benthic and demersal organisms from a randomly-selected subset of samples (n = 50) from each deployment. All samples were used for D7, since fewer than 50 samples with good visibility were available. Circles show samples, and distance between circles indicates the similarity of communities (i.e. closer = more similar). Communities from D5 and D10, both from ~100 m at Del Mar Steeples have a high degree of community similarity, but are dissimilar from all other deployments. Deployment depths from shallowest to deepest are: D10 (98 m), D5 (99 m), D4 (178 m), D6 (192 m), D7 (295 m), and D8 (399 m).

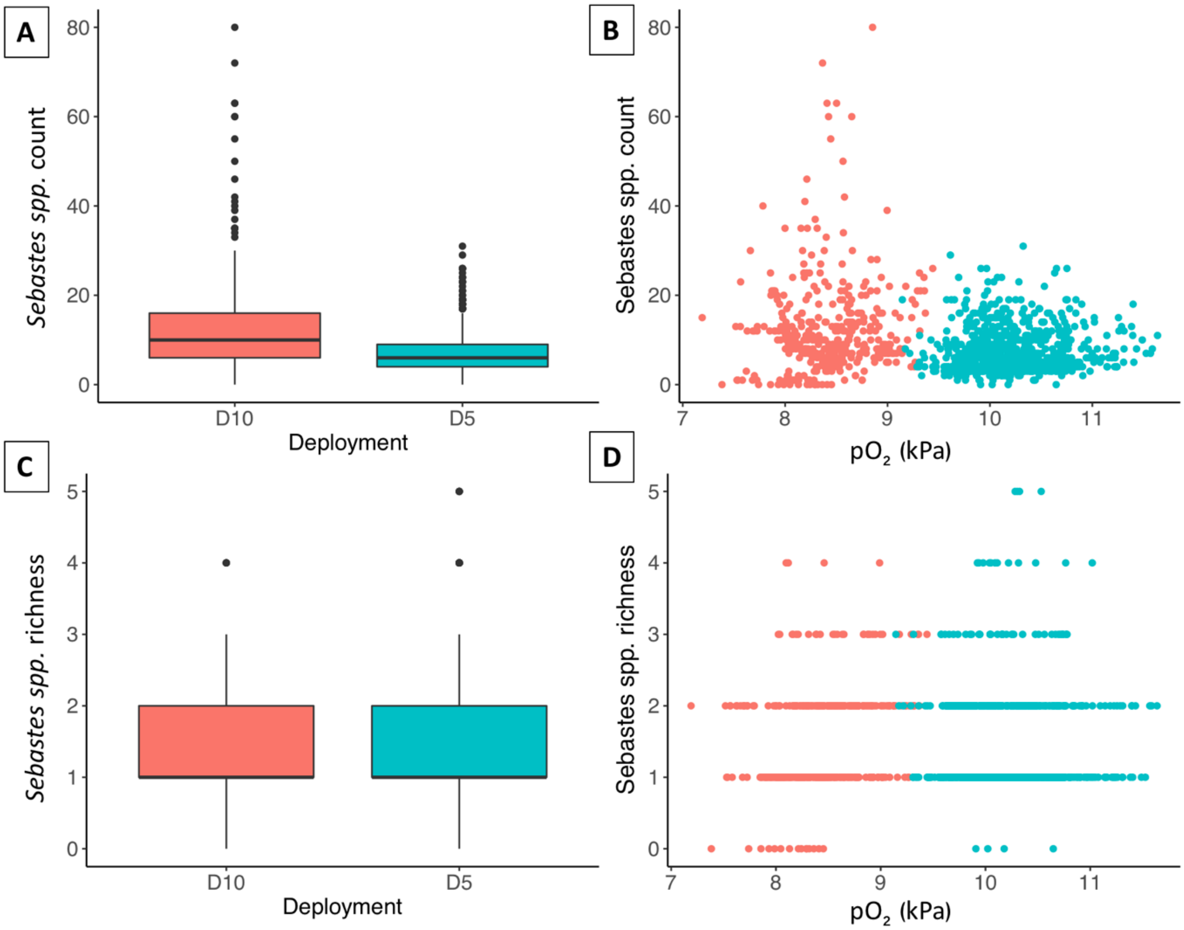


Figure 5.7. Abundances (A, B) and species richness (C, D) of rockfish (*Sebastes spp.*) were compared across deployment and oxygen conditions for the two deployments done at ~100 m at the Del Mar Steeples Reef. Data from the spring deployment (D10) are shown in red and data from the fall deployment (D5) are shown in blue.

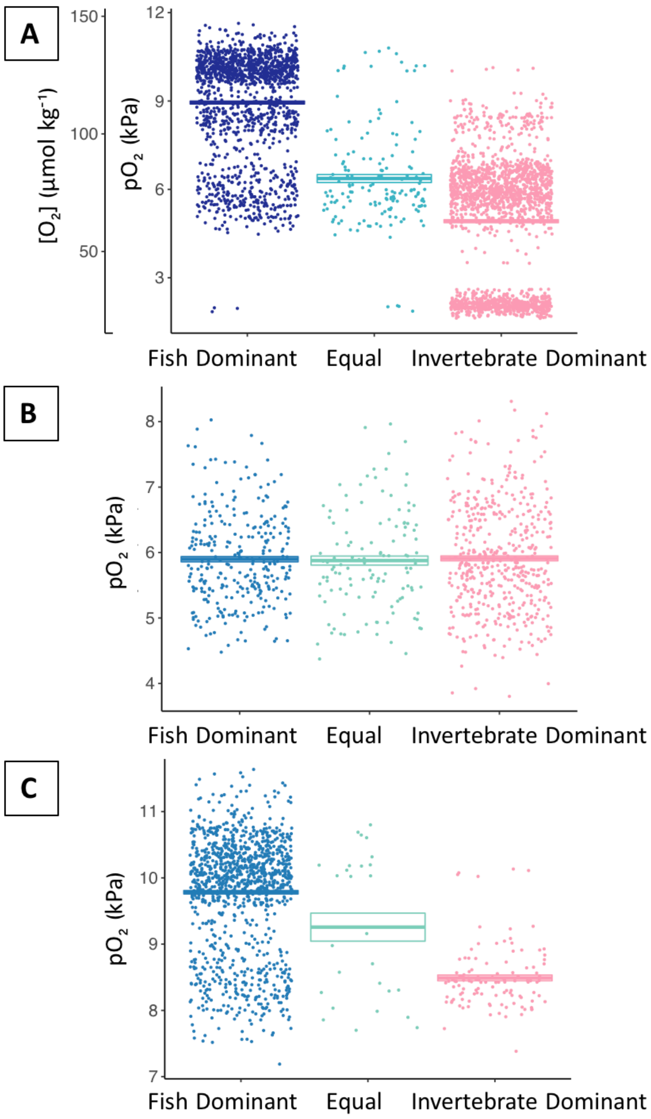


Figure 5.8. Fish-dominated communities occur at higher oxygen levels than invertebrate-dominated communities when looking across depths and seasonal timescales, but these differences are not seen over weekly timescales. Points represent 20-second video samples, and the mean +/- standard error oxygen conditions (kPa) for communities that were dominated by fish (blue), invertebrates (pink), or had an equal number of fish to invertebrates (green). When pooling data across all deployments (A), fish-dominated communities are found under oxygen conditions that are significantly higher (K-W, $p < 0.001$) than invertebrate-dominated communities. Panel B shows community differences within one deployment (D4, 178 m), and there was no significant difference in oxygen conditions between fish- or invertebrate-dominated communities (K-W, $p = 0.90$). Panel C shows community differences across two deployments at ~100 m (D5 - fall and D10 - spring), and here fish-dominated communities are characterized by higher oxygen conditions (K-W, $p < 0.001$).

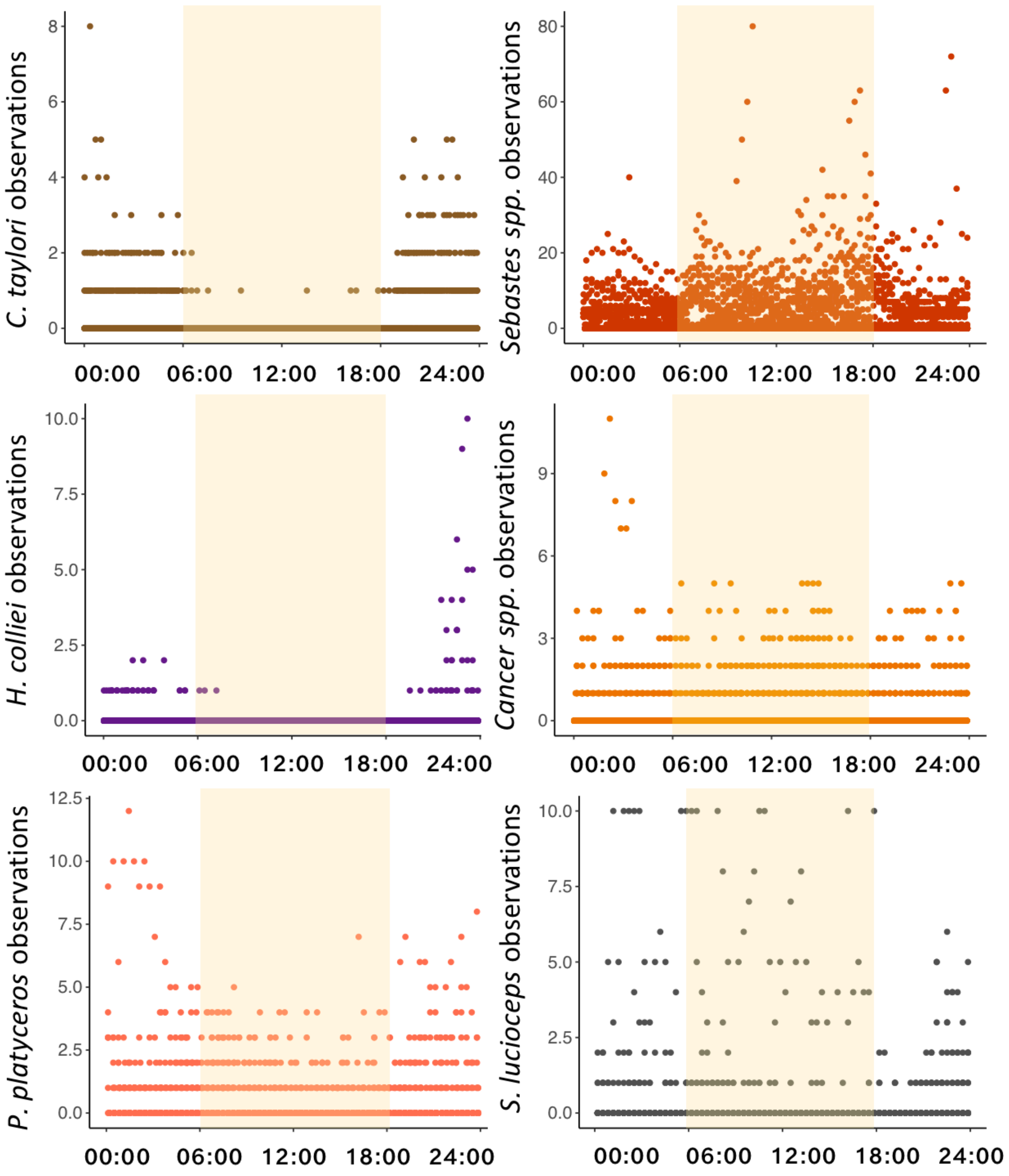


Figure 5.9. Diurnal behaviors based on count data from the video samples. Hours between 6:00 AM and 5:59 PM were considered "day" and are shown with a transparent yellow box. Points represent counts of each animal observed during 20-second video segments at different times of the day, pooled across the length of the whole deployment. Only data from deployments where these species were observed were used.

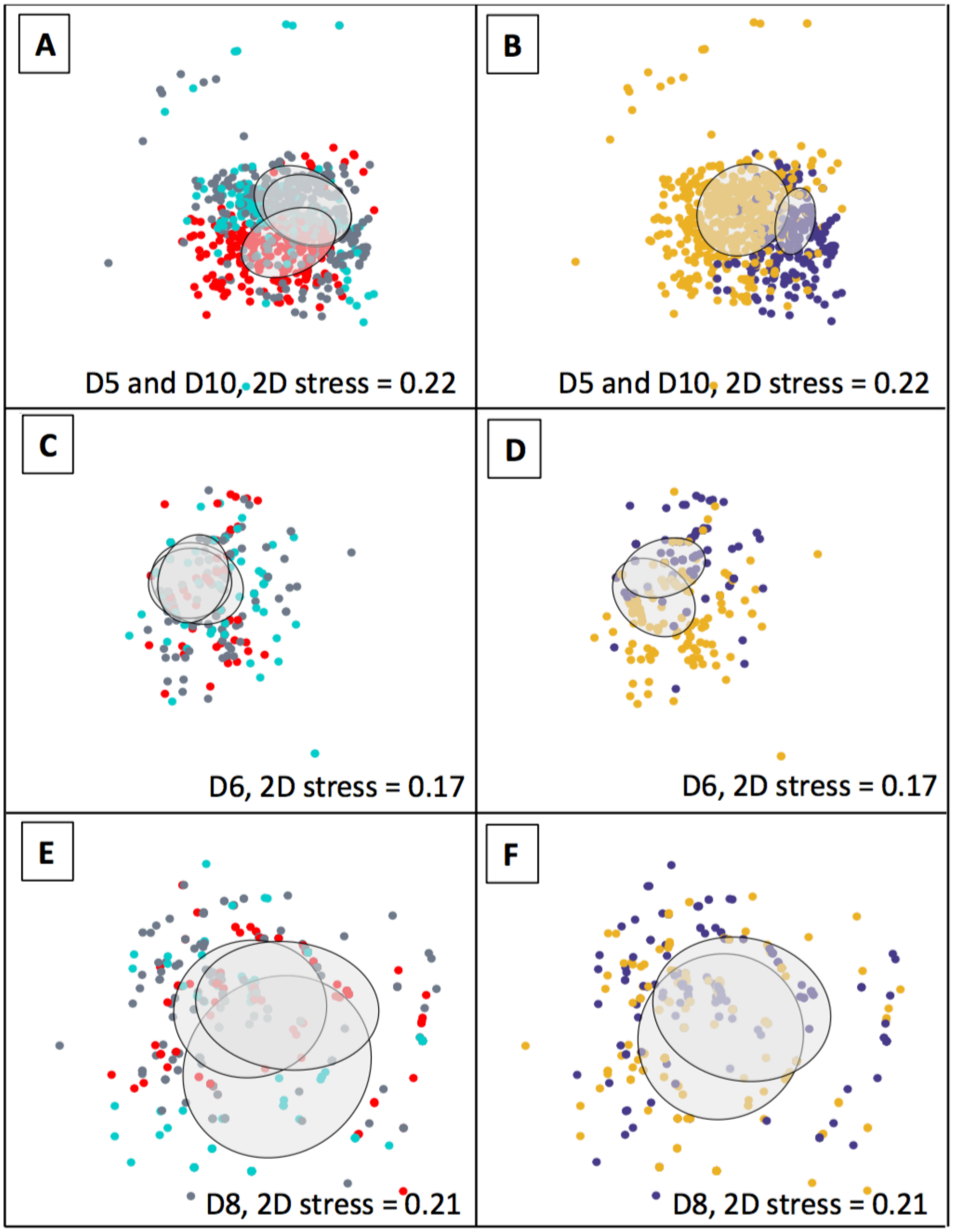
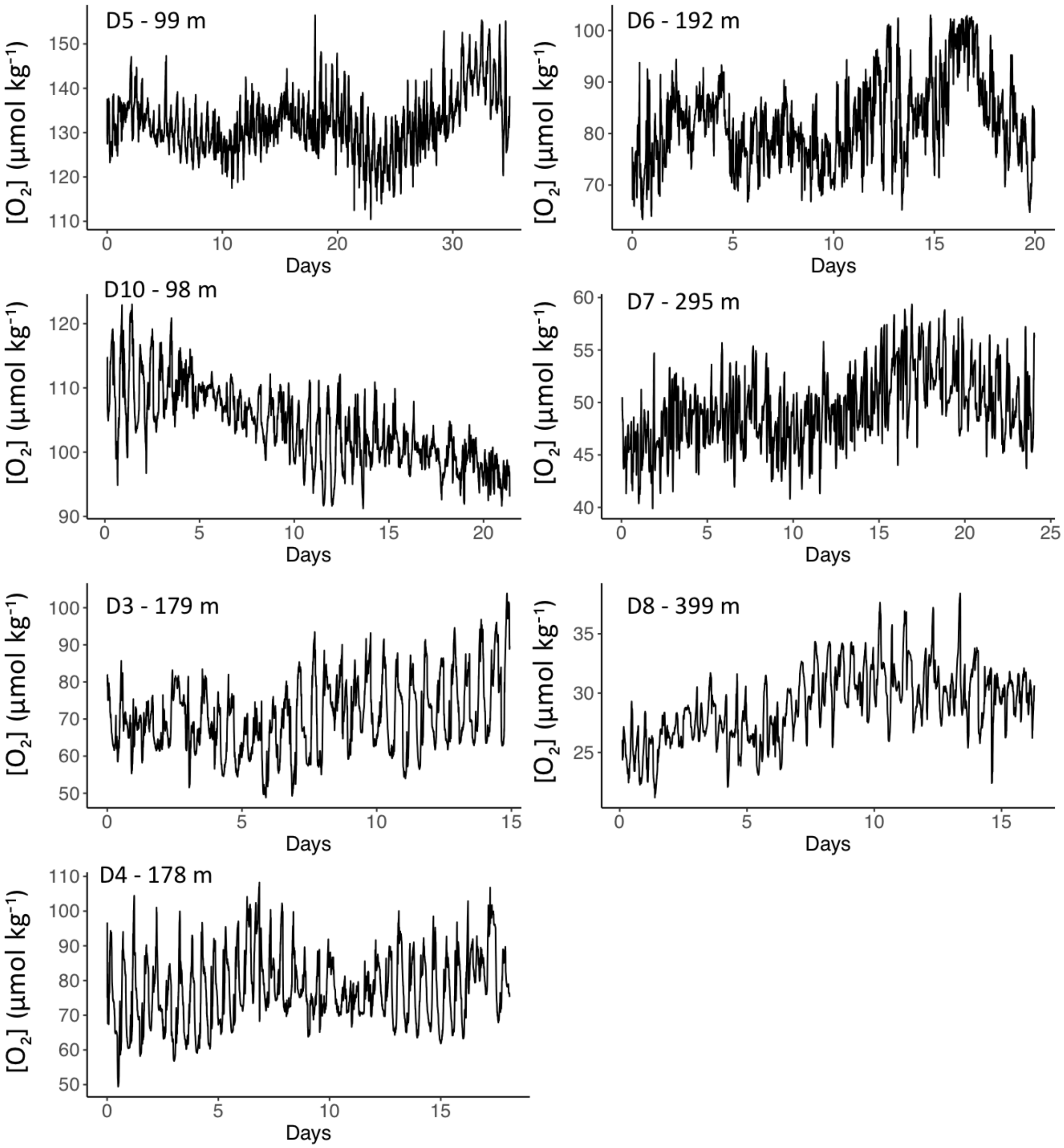
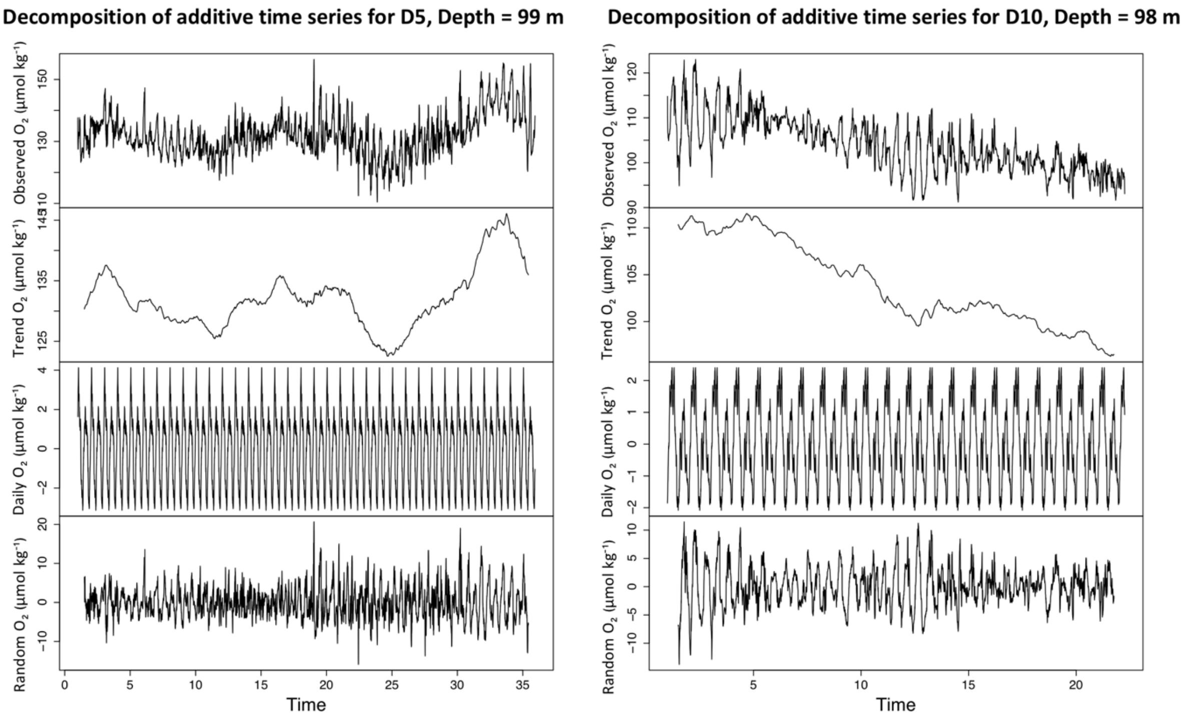


Figure 5.10. Non-metric multidimensional scaling plot of Bray-Curtis similarity matrix based on square-root transformed community data from deployments D5 and D10 at ~100 m (pooled) (A, B), from deployment D6 at ~200 m (C, D), and from deployment D8 at ~400 m (E, F). All deployments were done near the Del Mar Steeples Reef. Each point represents community composition for a 20-second video clip and colors indicate grouping by either oxygen conditions (A, C, E) or day versus night (B, D, F). Red points represent low oxygen conditions (1st quartile), gray points represent intermediate oxygen conditions (2nd and 3rd quartile), and turquoise points represent high oxygen conditions (4th quartile). Yellow points represent samples during the day (6:00 AM – 5:59 PM) and purple points represent samples during the night (6:00 PM – 5:59 AM). Ellipses represent grouping by category and show 50% confidence limits.

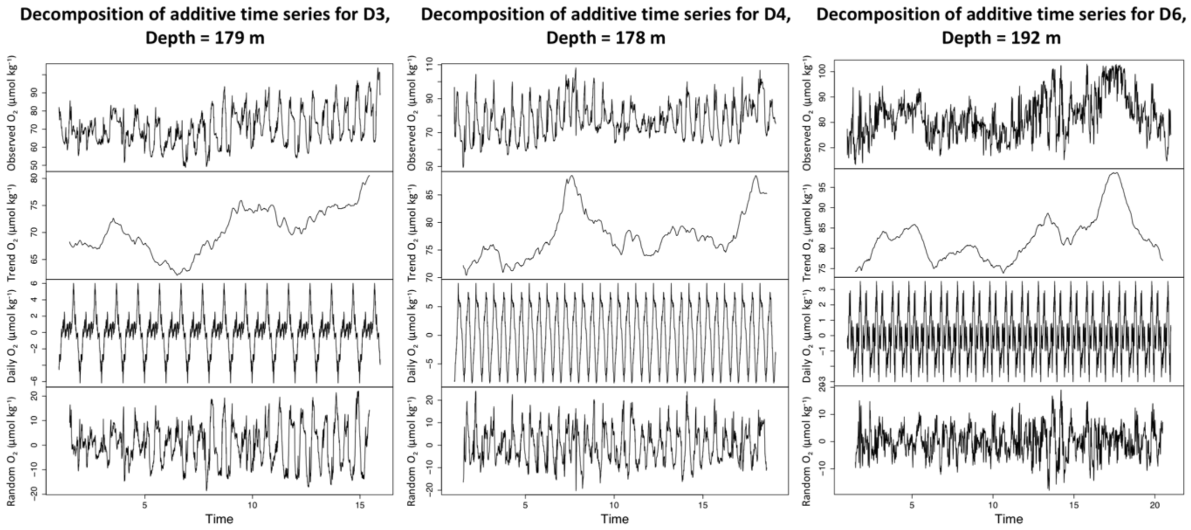
Chapter 5 Appendix



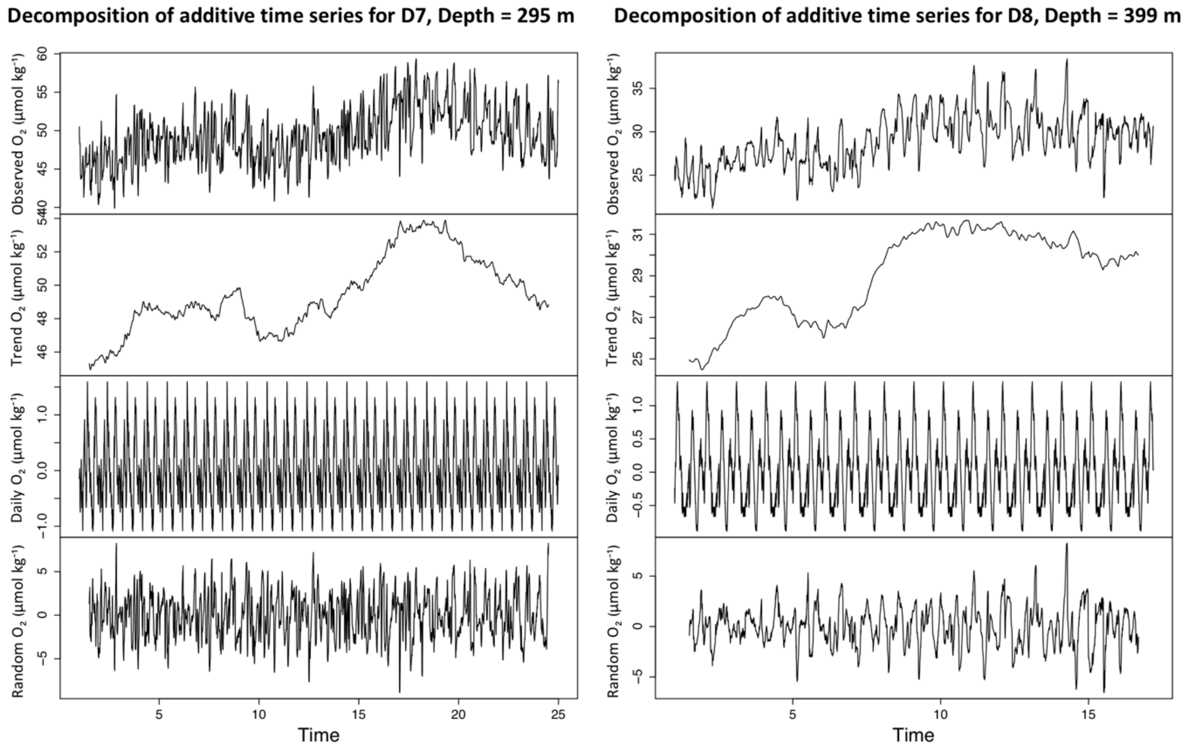
Supplementary Figure 5.1. Time series of dissolved oxygen concentration with deployment time (in days) for all seven deployments (Table 5.3).



Supplementary Figure 5.2. Decomposed time series of dissolved oxygen concentration for the two shallowest deployments at ~100 m on Del Mar Steeples Reef (D5 and D10) showing the actual observations, followed by the deconstructed trend, daily variability, and random variance. Dates for deployments were: September 29-November 3, 2017 (D5) and March 8-March 29, 2018 (D10).



Supplementary Figure 5.3. Decomposed time series of dissolved oxygen concentration for the three deployments at ~200 m (D3, D4, and D6) showing the actual observations, followed by the deconstructed trend, daily variability, and random variance. Dates for deployments were: August 17-September 1, 2017 (D3), September 7-September 25, 2017 (D4), and November 9-November 29, 2017 (D6).



Supplementary Figure 5.4. Decomposed time series of dissolved oxygen concentration for the two deepest deployments (D7 and D8), showing the actual observations, followed by the deconstructed trend, daily variability, and random variance. Dates for deployments were: December 12, 2017-January 5, 2018 (D7) and January 23-February 8, 2018 (D8).

CHAPTER 6

Implications of the oxygen minimum zone for the trophic ecology of demersal fish communities in the Southern California Bight

Natalya D. Gallo, Rasmus Swalethorp, Ray Lee, Lisa A. Levin

Abstract

Diel vertically migrating (DVM) organisms provide important food subsidies to deep-sea demersal fish communities on continental margins. On continental margins with OMZs, bentho-pelagic coupling may be reduced by the presence of low-oxygen waters that compress the daytime depth of the DVM community. We make use of the severely hypoxic conditions that occur along the continental margin in the Southern California Bight (SCB) to test this hypothesis and study how the trophic ecology of the demersal fish community changes spatially from a normoxic to a severely hypoxic habitat. Consistent with the hypothesis, we find that a shift in dominant feeding mode from bentho-pelagic to benthic occurs at the upper boundary of the oxygen minimum zone (OMZ) ($O_2 < 22.5$ μmol kg^{-1}), and is associated with a shift in demersal fish community composition. Fishes living within the OMZ, are predominantly benthic feeders and have enriched $\delta^{15}N$ signatures, suggesting they are feeding at a higher trophic level, than species living outside of the OMZ. A demersal fish community is still present within the core of the OMZ, where oxygen conditions can be as low as 7-8 μmol kg^{-1}, but the trophic niche of this fish community differs from that of fish communities in better-oxygenated areas. The OMZ core community has the lowest species richness and a smaller trophic niche breadth, compared to demersal fish communities outside of the OMZ, and at the upper and lower OMZ boundaries. Only ~20% of the seafloor in the SCB is at depths shallower than the upper boundary of the OMZ, therefore most demersal fish communities in the SCB must rely on benthic resources, which is a less efficient trophic pathway. While several studies have focused on the physiological tolerances of demersal fishes to hypoxic conditions, our results suggest that changes in pelagic food availability, related to the presence of low oxygen conditions, may contribute to determining the ranges of

demersal fish species, such a rockfish, on the US West Coast. Expansion of the OMZ with climate change may therefore have important understudied trophic impacts for ecologically important species.

Introduction

As oceans warm due to anthropogenic climate change, the global ocean oxygen inventory decreases in a process known as ocean deoxygenation, which is driven by changes in gas solubility, ocean ventilation, and biological consumption (Keeling et al. 2010, Levin 2018). Ocean deoxygenation ranks among the most important changes occurring in marine ecosystems (Breitburg et al. 2018). Climate models predict a 3-6% decrease in the ocean oxygen content during the 21st century in response to surface warming (Bopp et al. 2013). However, long-term ocean observations show that deoxygenation is occurring even faster than predicted by climate models (Oschlies et al. 2018). Since 1960, the global ocean oxygen content has decreased by more than 2% (Schmidtko et al. 2017). Ocean deoxygenation does not proceed uniformly across the ocean (Long et al. 2016), and certain regions like the Southern California Bight (Bograd et al. 2008) have experienced greater oxygen losses than the global mean. Organisms exhibit a range of tolerances to low levels of dissolved oxygen, with fish and crustaceans considered to be most sensitive to hypoxia (Vaquer-Sunyer and Duarte 2008). Oxygen limitation acts at multiple levels of biological organization. Diet is one of the most direct ways that an animal interacts with and responds to its environment. Since diet is a higher order functional process, it may be more sensitive to environmental changes than lower order processes (Pörtner et al. 2005, Pörtner et al. 2010). It is currently unknown how deoxygenation may impact trophic relationships.

The effects of changing oxygen conditions on trophic relationships has been less explored to date than shifts in species distributions related to changing oxygen conditions (Stramma et al. 2011, Sato et al. 2017). The few studies that have looked at the relationship between trophic ecology and environmental oxygen conditions suggest that low oxygen conditions can impact food web structure. Analysis of food webs during the early Cenozoic warm period (50 Ma) revealed that a warmer and less oxygenated ocean supported longer food chains and was unable to support a high abundance of top predators (Norris et al. 2013). In modern coastal zones, low oxygen conditions result in less upward trophic transfer, and energy flow becomes dominated by microbial pathways, leading to losses of benthic biomass (Diaz and Rosenberg 2008). Predator-prey relationship can also be altered under hypoxic conditions, thus changing the relative importance of different trophic pathways (Pihl 1994, Breitburg et al. 1997), and increasing the importance of benthic prey (Phil et al. 1992). Oxygen availability may also affect the types of feeding modes present within the benthic community, with fewer carnivorous taxa and simpler food webs seen under severely hypoxic conditions (Sperling et al. 2013). These studies suggest that oxygen limitation in marine ecosystems can impact food web structure; it is unknown if similar food web changes may be expected as the oceans lose oxygen with climate change.

Oxygen minimum zones (OMZs) ($[O_2] < 22.5$ μmol kg^{-1}) typically occur at depths between 100-1500 m along eastern boundary currents and are naturally low in oxygen due to the combined processes of high oxygen consumption at depth and limited ventilation (Wyrtki 1962). These low oxygen waters impact the pelagic community (Gilly et al. 2013), as well as the seafloor community in areas where OMZ waters intersect the continental margins (Levin 2003). Globally, OMZs make up over 1 million km^2 of permanently hypoxic continental shelf and bathyal sea floor (Helly and Levin 2004). Because of the steep gradients in oxygen present in OMZs, these systems can be used as natural laboratories to study the ecological consequences of oxygen-limiting environments and to gain insight into the effects of ocean deoxygenation on marine communities.

Demersal fishes, meaning fish species that are associated with the seafloor, are ecologically important as predators, support commercially-important fisheries, exhibit a loss of diversity under OMZ conditions, and exhibit a range of tolerances to hypoxic conditions (Gallo and Levin 2016). However, studies on the trophic ecology of demersal fish communities on continental margins with OMZs are rare, so it is unknown how the presence of low oxygen conditions affects their trophic ecology, and how the vertical and horizontal expansion of OMZs with climate change (Stramma et al. 2008) may influence trophic interactions and fisheries productivity.

Demersal fish living on the continental margin have two categories of food resources they can utilize: 1) benthic or epibenthic prey items, reliant on the detrital benthic pathway, or 2) pelagic prey items, reliant on an allochthonous pelagic pathway, that are made available through advection, migration, or sinking (Bjelland et al. 2000, Drazen et al. 2008, Drazen and Sutton 2017). Gut content and stable isotope analysis are valuable tools in illuminating key trophic relationships and exploring species' trophic niches (Stewart et al. 2017, Newsome et al. 2007). While gut contents provide a snapshot of the diet of the fish just prior to the time of capture, carbon (C) and nitrogen (N) stable isotope ratios in tissue provide a time-integrated reflection of consumer diets. $\delta^{13}C$ reflects the original carbon fixation process and can be used to distinguish the source pools of primary productivity (Boecklen et al. 2011, Layman et al. 2011). $\delta^{15}N$ is useful for determining trophic position because animals preferentially retain the heavier nitrogen in their diets, thereby becoming enriched in $\delta^{15}N$ relative to their prey, with each additional trophic level representing a +3 per mil enrichment (Boecklen et al. 2011, Layman et al. 2011). Stable isotopes can also distinguish between pelagic and benthic-supported food webs, since benthic food webs are typically more enriched in nitrogen and carbon isotopes (Trueman et al. 2014, Boyle et al. 2012, Boyle 2010).

While it is easy to assume that fish that are associated with the bottom should predominantly feed on benthic or epibenthic prey items, many studies suggest that the opposite is true. Studies from around the world show that pelagic resources are very important for supporting demersal fish communities living on continental margins. Migrating mesopelagic organisms, especially pelagic crustaceans (i.e. euphausiids) and mesopelagic fishes (i.e. myctophids and bathylagids), are important prey items for demersal fish communities in the Norwegian Sea (Bjelland et al. 2000), eastern and southern Tasmanian margin (Blaber and Bulman 1987, Bulman et al. 2002), on the northwest Atlantic Canadian margin (Houston and Haedrich 1986), on the US Mid-Atlantic margin (Sedberry and Musick 1978), and the northeast Atlantic UK-Irish margin (Mauchline and Gordon 1985, Trueman et al. 2014). This pattern of pelagic production supporting upper continental slope demersal fish communities is so common that it has been proposed that demersal fish feeding on pelagic prey at upper continental slope depths is probably the general rule (Houston and Haedrich 1986). The reason for this is that demersal fish that feed directly on pelagic organisms utilize a more efficient trophic pathway, and effectively skip at least one trophic level, compared to predominantly benthic feeders (Houston and Haedrich 1986). Assuming an average trophic efficiency of 10-20% (Lindeman 1942, Jennings et al. 2002), a much higher biomass of pelagic-feeding than benthic-feeding demersal fish can be supported in an ecosystem.

The diel vertical migration (DVM) undertaken by midwater organisms, to deeper depths during the day and up to shallower depths at night, results in the transfer of a significant amount of carbon and nutrients from the surface to the deep ocean (Davison et al. 2013, Klevjer et al. 2016). This diel vertical migration can be seen with echo sounders and acoustic Doppler current profilers, as acoustic backscatter from dense layers of midwater organisms, called deep-scattering layers (DSL). However, several studies have reported that the daytime depth of the DVM community is related to the subsurface oxygen concentrations: where subsurface oxygen conditions are low, the daytime depth of the DVM community is compressed into shallower waters (Bianchi et al. 2013, Netburn and Koslow 2015, Klevjer et al. 2016). Consequently, areas with OMZs are characterized by DVM communities with shallower daytime depth distributions (Bianchi et al. 2013), including in the Southern California Bight (Netburn and Koslow 2015). The mechanistic explanation for this relationship has recently been proposed to relate to variations in light penetration and not oxygen tolerances (Aksnes et al. 2017). However, given that light attenuation and dissolved oxygen are strongly correlated below 100 m (Aksnes et al. 2017), it is ecologically relevant to consider the oxygen gradients. Given the clear evidence of the importance of migrating mesopelagic fish and crustaceans for supporting demersal fish communities on continental margins in many parts of the world, this raises the question of the trophic consequences for demersal fish of the shallower DVM community in areas with OMZs.

The objective of this chapter is to understand how oxygen gradients along the continental margin affect the community structure and feeding ecology of the demersal fish community in the Southern California Bight (SCB). In the SCB, an OMZ extends from ~450-1250 m and productive surface waters are underlain by severely hypoxic conditions, affecting both pelagic and benthic communities (Nam et al. 2015, Netburn and Koslow 2015, Gallo and Levin 2016). Due to the long-term time-series collected by the CalCOFI program, there is also a high-quality 50+ year record of how subsurface oxygen conditions have changed in this region, showing that the area has experienced greater recent oxygen declines in recent years than the global mean (Ren et al. 2018, Bograd et al. 2008, Bograd et al. 2015). The goal of this study is to understand the functional consequences of low oxygen zones for demersal fish trophic ecology and to inform our understanding of how the continental margin food web may change as OMZs expand and their upper boundaries shoal. To do so, we test whether fish within the OMZ exhibit distinct feeding patterns, manifested as trophic level, degree of pelagic feeding, and trophic diversity, compared to fish communities living under higher oxygen conditions.

Methods

To assess how demersal fish community structure and trophic ecology change across oxygen gradients, the demersal fish community was sampled using otter trawls. Thirty-eight trawls were conducted in the Southern California Bight from 2012-2015. Twenty-one trawls were conducted as part of the NOAA Northwest Fisheries Science Center's West Coast Groundfish Bottom Trawl Survey (Keller et al. 2017). For these trawls, near-bottom environmental conditions were determined using CTD-O_2 sensors (Sea-Bird Scientific, Bellevue, WA, USA) that were deployed on the trawl nets. Mean depth, temperature, salinity and dissolved oxygen concentrations are reported for each trawl (Table 6.1). An Aberdeen-type trawl with a 3.8 cm mesh liner was used for the NOAA trawls. Seventeen additional otter trawls were conducted during student cruises through the Scripps Institution of

Oceanography, UCSD on the R/V *Robert Gordon Sproul*, R/V *New Horizon*, and the R/V *Melville*, using a deep-water trawl with a 4.2-cm mesh liner. For these trawls, environmental conditions were determined using CTD-O_2 casts (Sea-Bird Scientific, Bellevue, WA, USA) that were conducted immediately before the trawls were deployed, and corresponding environmental conditions are reported for the mean depth of the trawl. For each trawl, the GPS coordinates and bottom depth of the trawl start and end were recorded. All trawls were conducted along isobaths, to minimize sampling across depth zones within a single trawl. Trawl depths ranged from 96-1261 m, temperatures ranged from 3.49-11.35°C, oxygen concentrations were between 7.38-135.40 μmol kg^{-1}, and salinities were 33.71-34.48 psu (Table 6.1).

For each trawl, all demersal fish species were sorted and identified to the species level. Percent community composition for each species in each trawl was then determined to look at how community composition changes across oxygen gradients. Species richness was determined for each trawl by counting the number of demersal fish species present in each trawl (Table 6.2). For the SIO cruises, all demersal fish were counted and the density of the demersal fish community was determined by dividing the total number of fish by the calculated surface area trawled and is reported as number of fish m^{-2} (Table 6.2). For the NOAA cruises, a different methodology was used that is standard for the groundfish trawl survey. Instead of counts and densities, demersal fish community abundance is determined and reported as catch per unit effort (CPUE) in kg ha^{-1} (Table 6.2). Consequently, the NOAA data may over-represent larger species, while the SIO data may over-represent smaller, numerically abundant species.

The trophic sampling protocol aimed to extract three individuals of each demersal fish species from each trawl. These fish were frozen immediately, and then stored in the lab at -20°C until further analysis. For this study, cartilaginous fishes were not sampled for trophic analysis, however, are retained within the community analyses. Thirty-eight species or species groupings, representing 18 fish families were included within the trophic analysis (Table 6.3). Most often single species were identified, except for the following generic groups: *Nezumia spp.* includes *N. stelgidolepis* and *N. liolepis*, *Lycodes spp.* includes *L. pacifica* and *L. cortezianus, Zaniolepis spp.* includes *Z. frenata* and *Z. latipinnis*, and *Sebastes spp.* includes several rockfish specimens we were unable to identify to species level with high confidence. In the lab, mass (g) and standard length (cm) were determined, and sagittal otoliths, dorsal white muscle, and gut content were sampled from each fish. Sagittal otoliths were not analyzed for this study.

Stomach and intestines were initially removed during the dissection and stored in 95% ethanol at -20°C until gut content analysis was performed. During the gut content analysis, stomachs were separated from the intestine, blotted to remove excess moisture and weighed. Stomachs were then cut open and stomach contents were removed and reweighed. Each stomach was ranked as empty (1), not empty (2), or very full (3), and a ratio of stomach content mass to total stomach mass was determined. Gut contents were identified to lowest taxonomic level possible, and intestine contents were also inspected and identified when possible. The presence of sediment in the stomach contents or intestine was also noted. The stomach and intestine contents were determined to be mainly benthic or pelagic in origin for each individual. Gut contents were inspected for 666 individual fish.

A benthic or pelagic feeding mode was assigned *a priori* to all demersal fish species captured in the otter trawls. This designation was made based on previously published diet information, and confirmed with the gut contents observed from the collected specimens. “Benthic” feeders were defined as those feeding on organisms predominantly associated with the seafloor, representing an epi- or hyper-benthic diet, and included diet items such as bivalves, polychaetes, ophiuroids, benthic decapod shrimp, and tanaids. “Pelagic” feeders were defined as feeding on organisms predominantly associated with the water column, representing a pelagic or bentho-pelagic diet, and included diet items such as euphausiids, myctophids, and squid. These categorizations are similar to those used by Trueman et al. (2014). Based on the categorization of each species as a benthic or pelagic feeder (Table 6.3), the percent community composition of pelagic or benthic feeders in the demersal fish community for each trawl was then determined (Table 6.2).

Carbon and nitrogen stable isotope analysis were carried out on 702 individuals. Stable isotope samples were prepared using the following protocol, following Levin and Currin (2012). Briefly, ~4 mg dorsal white muscle samples were subsampled and placed into weighed tin capsules and dried at 60°C for 48 hours, then reweighed. Target dry weight was 0.5-0.75 mg. Samples were then acidified using phosphoric acid, were dried for an additional 48 hours at 60°C and then crimped. Samples were sent to Washington State University and run on an isotope ratio mass spectrometer (IRMS). As in Levin et al. (2013), samples were run on a Costech elemental analyzer interfaced with a continuous-flow Micromass Isoprime isotope ratio mass spectrometer. Isotope ratios are expressed as $\delta^{13}C$ or $\delta^{15}N$ in units of per mil (‰). Standards were PeeDee Belemnite for ^{13}C and nitrogen gas for ^{15}N (atmospheric).

Table 6.3 shows the number of individuals processed for gut content analysis (GCA) and stable isotope analysis (SIA) for each demersal fish species. Cartilaginous fishes (sharks, rays, and chimeras) were not sampled for SIA, because chondrichthyan fishes retain higher urea concentrations and synthesize trimethylamine N-oxide (TMAO), which complicates C:N-based lipid correction (Hussey et al. 2012, Carlisle et al. 2016, Shipley et al. 2017) and makes combining stable isotope data for bony and cartilaginous fish problematic. When chondrichthyans were present, they only made up a small proportion of the demersal fish community. Where available, published dietary information for cartilaginous species was referenced.

Since lipids are isotopically depleted in carbon, an arithmetic mass-balance correction method tested for deep-sea fish (Hoffman and Sutton 2010) was applied to lipid-rich samples whose C:N ratios were > 3.8. Sixty-six samples had a C:N ratio > 3.8, and were lipid corrected using the following equation:

$$\delta^{13}C_{corrected} = \delta^{13}C_{bulk} + (-6.39 \text{ x } (3.76 - C{:}N_{bulk}))/(C{:}N_{bulk})$$

The $C{:}N_{protein}$ (3.76 ± 0.07) and delta $\delta^{13}C_{lipid}$ (-6.39 ± 1.21 ‰) were used as provided in Hoffman and Sutton (2010). Hoffman and Sutton (2010) caution against applying a lipid correction for samples where the C:N ratio is > 8. Only 12 samples (3 SAB, 7 BHAG, 1 EB, and 1 LST) were identified with this high C:N ratio, and three of these samples were later identified as outliers and removed. The high C:N ratios obtained for hagfish in this study have also been reported from other studies (Zintzen et al. 2013), and may be an artifact of hagfish physiology, as opposed to true high lipid content (Kelleher et al. 2001, Drazen et al. 2011).

Following lipid correction, all stable isotope data (702 samples) was inspected for biologically unreasonable outliers to ensure that the data for each species or species group was representative. The outlierKD function in R was used to identify outliers for the $\delta^{13}C$ and $\delta^{15}N$ signatures of each of the 38 species categories. OutlierKD uses the Tukey's method to identify outliers which are above or below 1.5*IQR (interquartile range). Each identified outlier was inspected, and a total of 42 samples were removed as outliers (~6% of the total dataset). Samples were removed as outliers if both the $\delta^{13}C$ and $\delta^{15}N$ values were identified as outliers or if the $\delta^{15}N$ signature was unreasonably low ($\delta^{15}N < 8$). Subsequent analysis for the stable isotope data used this reduced dataset of 660 samples (Appendix Supp. 6.1).

Layman metrics (Layman et al. 2007) were used as measures of trophic niche for the demersal fish community. Layman metrics for nearest neighbor distance and standard deviation of nearest neighbor distance (a measure of community trophic species packing), nitrogen and carbon ranges (measures of trophic level diversity and food diversity exploited by the community, respectively), and mean distance to centroid (another measure of species packing) (Layman et al. 2007), were used to look at metrics for the entire demersal fish community within different oxygen regimes.

To estimate trophic level from the stable isotope data, particulate organic matter (POM) was collected using Niskin bottle samples from CTD casts conducted prior to trawls and was collected for both water column and bottom water samples. Water was vacuum-filtered through pre-combusted GF/F filters to collect POM, and POM samples were scraped into tin boats, dried, and run on the IRMS at Washington State University. The average $\delta^{15}N$ signature for the POM was determined, and based on this, trophic levels for this food web were calculated as in Chikaraishi et al. (2009):

$$TL_{bulk} = ((\delta^{15}N_{consumer} - \delta^{15}N_{producer})/3.4) + 1$$

Compound-specific stable isotope analysis (CS-SIA) provides a more precise method of determining the trophic level species are feeding at, due to amino-acid (AA) specific differences in fractionation of N isotopes. While this technique is more costly and time consuming than bulk stable isotope analysis, it can provide valuable insight to interpret trends observed with bulk isotopic data. We were interested in testing if the community and intraspecies patterns we observed using the bulk isotopic data, were consistent with results from CS-SIA, and selected five species as representatives to look at: the rubynose brotula (*Cataetyx rubrirostris*), the hundred fathom codling (*Physiculus rastrelliger*), shortspine thornyhead (*Sebastolobus alascanus*), longspine thornyhead (*Sebastolobus altivelis*), and California slickhead (*Alepocephalus tenebrosus*). Since only a smaller sample number could be run for CS-SIA, these samples were selected at random from those samples that had a bulk $\delta^{15}N$ signature within the 1st and 3rd quartile for all samples for that species and habitat category.

To prepare the CS-SIA samples, a small piece of dorsal white muscle tissue was removed and frozen at -80°C, freeze-dried overnight, and then weighed for dry mass. Samples were then hydrolyzed by adding 6M HCl to each sample and placing samples in an oven at 90°C for 24 hours. Samples were then dried on a centrifugal evaporator at 60°C, then redissolved in 0.5 mL 0.1M HCl, and filtered on a 0.2 um PTFE filter to remove particulates. Samples were redried and redissolved in 100 uL of 0.1% trifluoroacetic acid in MilliQ and injected on a semi-preparative scale column (Primesep A, 10 × 250 mm, 100 Å pore size, 5 µm particle size, SiELC Technologies Ltd.) connected to an Agilent 1200 series High Pressure Liquid Chromatography system equipped with degasser (G1322A), quaternary pump (G1311A) and autosampler (G1367B). Following AA separation on the column a fixed 1:5

flow splitter directed the flow into an Evaporative Light Scattering Detector (385-ELSD, G4261A) and an analytical fraction collector (G1364C), respectively. Purified amino acid samples were then dried on a centrifugal evaporator at 60°C, redissolved in 0.1% HCl in MilliQ, transferred into tin capsules (Costech, 3 x 5 mm) and dried overnight in a desiccator under vacuum. For each species phenylalanine (Phe) and glycine (Gly) as source amino acids, and glutamic acid (Glu) as the trophic amino acid was sent to the Isotope Lab at the University of California Santa Cruz N isotope analysis. Briefly, we used a Carlo Erba CHNS-O Elemental Analyzer (EA1108) connected via a Thermo Finnigan Gasbench II to a Thermo Finnigan Delta Plus XP isotope ratio mass spectrometer. Additional information can be found in Broek and McCarthy (2014). This instrument has been modified to analyze small sample sizes (1-5 μg N) and the isotopic data was corrected for instrumental drift and sample size. The precision of the IRMS was ±0.2 ‰ and the AA purification methodology had no effect on precision (R. Swalethorp unpublished).

Demersal fish community data from otter trawls was used to compare community metrics (composition, density or CPUE, and diversity), across oxygen gradients, while stable isotope analysis and gut contents analysis was used to assess how the trophic position and trophic niche specialization of the demersal fish community changes along hydrographic gradients along the margin. Several oxygen exposure categories were used to assess how demersal fish community metrics and trophic ecology change across the different oxygen exposure regimes encountered along the margin. These were outside of the OMZ ($O_2 \geq 22.5$ $\mu mol\ kg^{-1}$) (n=18), outer OMZ ($22.5\ \mu mol\ kg^{-1} < O_2 \leq 10\ \mu mol\ kg^{-1}$) (n=14), and within the OMZ core ($O_2 < 10\ \mu mol\ kg^{-1}$) (n=6). It should be noted that all non-OMZ fish communities came from depths shallower than the OMZ. Below 1250 m, oxygen levels also increase, but our study did not extend into these deeper areas.

Results

The community composition and trophic ecology of 38 demersal fish trawls in the Southern California Bight, was compared across different depths and oxygen conditions (Fig. 6.1). The influence of different environmental variables on demersal fish community composition, biomass, and diversity has been well studied for the US West Coast (Allen 2008, Miller and Schiff 2011, Miller and Schiff 2012, Keller et al. 2012, 2013, 2015, 2017), so the results of this study are presented as a point of comparison that largely agree with the trends described by other studies for the Southern California Bight and US West Coast.

At depths shallower than the upper OMZ boundary (~100-450 m), the dominant species were the slender sole (*Lyopsetta exilis*), Pacific sanddab (*Citharichthys sordidus*), and the rockfish, *Sebastes diploproa*, *S. helvomaculatus*, and *S. semicinctus* (Fig. 6.2 A). Within the OMZ, thornyheads (*Sebastolobus alascanus* and *S. altivelis*), hagfish (*E. deani*), grenadiers (*Nezumia liolepis* and *N. stelgidolepis*), and several eelpout species made up most of the community (Fig. 6.2 B). Within the OMZ core, the community composition was largely dominated by two species: the longspine thornyhead (*S. altivelis*) and the Dover sole (*Microstomus pacificus*) (Fig. 6.2 C). Demersal fish communities from the OMZ core differed from those outside of the OMZ (Fig. 6.2 D). Certain fish communities from within the OMZ showed high similarity to those outside of the OMZ, representing a transitional fish community at the OMZ upper boundary (Fig. 6.2 D). Clear differences in community composition were evident when sorting otter trawl samples, with trawls from depths shallower than the OMZ dominated by slender soles and rockfish (Fig. 6.2 E), and depths within the OMZ and OMZ core dominated by thornyheads (Fig. 6.2 F). The species with the broadest depth distribution (196-1261 m) was the Dover sole, *Microstomus pacificus*, which was present in most trawls.

Changes in community composition, were accompanied by changes in demersal fish density and diversity. We found no significant linear relationship between demersal fish density and dissolved oxygen, or demersal fish catch per unit effort (CPUE) and dissolved oxygen (LR, $p > 0.05$) (Fig. 6.3). Species richness exhibited a sharp non-linear decrease below a certain oxygen threshold (Fig. 6.3), which is consistent with the pattern observed on other upwelling margins (Gallo and Levin 2016). We found no significant difference in species richness when comparing samples from outside of the OMZ to those taken within the OMZ upper or lower boundary, but did find that species richness within the OMZ core ($O_2 <$ 10 μmol kg^{-1}) was significantly lower (Tukey's HSD, $p < 0.05$).

While trends in demersal fish community composition, density, and diversity have been well studied on the US Pacific margin (Allen 2008, Miller and Schiff 2011, Keller et al. 2012, 2013, 2015, 2017), relationships between the trophic ecology of the demersal fish community and the presence of the OMZ have not. One of the first questions we were interested in was if the isotopic signature of the fish community living within the OMZ differed from that of fish communities living outside of the OMZ. Chemosynthetic production has been found to play an important role as an additional trophic pathway for benthic infauna in OMZs (Levin 2003), in addition to photosynthetically-derived carbon, so we hypothesized that fish living within the OMZ, and especially within the core of the OMZ could have isotopic carbon signatures that were lighter, indicative of secondary consumption of chemosynthetic production. However, we did not find any evidence of this. There was no significant difference (ANOVA, $p = 0.866$) in mean $\delta^{13}C$ isotopic signatures in fish living outside of the OMZ ($\delta^{13}C = -18.09$ ‰), compared to within the outer OMZ ($\delta^{13}C = -18.11$ ‰), or within the OMZ core ($\delta^{13}C = -18.06$ ‰) (Fig. 6.4). Therefore, the base of the food web does not appear to change for the demersal fish community across the OMZ gradient.

We were also interested in whether the isotopic nitrogen signature of the demersal fish community differs within the OMZ, suggesting that fish are feeding at a different trophic level than outside of the OMZ. Based on one of the findings by Norris et al. (2013) – that less oxygenated oceans during the Cenozoic period supported longer food chains – we hypothesized that modern OMZ demersal fish communities may also rely on a longer food chain, and therefore have an enriched isotopic nitrogen signature than fish communities living under better oxygenated conditions on the margin. Our isotopic results support this hypothesis. The mean $\delta^{15}N$ signature of the demersal fish community is significantly higher within the outer OMZ ($\delta^{15}N = 16.82$ ‰), compared to outside of the OMZ ($\delta^{15}N = 15.83$ ‰), and this enrichment is even more pronounced within the OMZ core ($\delta^{15}N = 17.80$ ‰) (Tukey's HSD, $p < 0.001$) (Fig. 6.4).

To look at this relationship more closely, we regressed the $\delta^{15}N$ signatures of sampled fish with the environmental oxygen conditions they were captured in and found that the observed enrichment in $\delta^{15}N$ appears to be strongly correlated with oxygen conditions (Fig. 6.4). Especially for habitats within the OMZ where oxygen decreases from 20 to 10 μmol kg^{-1}, a strong enrichment in $\delta^{15}N$ of ~2 ‰ is observed (Fig. 6.4). These results suggest that across this oxygen gradient, food chain length is related to how severe the hypoxic conditions are.

Next, we were interested in understanding what may be responsible for the observed enrichment in $\delta^{15}N$ observed within the demersal fish community living in the OMZ. A change in the mean $\delta^{15}N$ signature of the demersal fish community could be due to a change in demersal fish species composition, or it could be due to intra-species diet changes for species present both inside and outside of the OMZ.

Since there is a clear change in demersal fish community composition with increasing depth, moving from above into the OMZ (Fig. 6.2), we compared the mean isotopic signatures of demersal fish species living only within the OMZ, only above the OMZ, or those, like the Dover sole, those spanning the margin. We found that, consistent with the overall community patterns, species that only lived within the OMZ had more enriched average $\delta^{15}N$ signatures than those that were never caught in the OMZ (Fig. 6.5). When estimating the trophic level for the different demersal fish species, species that were only present within the OMZ had an estimated trophic level of ~4, whereas most species that only lived above the OMZ had an estimated trophic level closer to ~3.4 (Fig. 6.5). Unexpectedly, the rubynose brotula, *Cataetyx rubrirostris*, a small fish only about 9 cm in total length, that appears to be an OMZ specialist, had the highest mean $\delta^{15}N$ signature (mean $\delta^{15}N = 18.58$ ‰).

Species that had a broader depth distribution and were captured both inside and above the OMZ had more intermediate $\delta^{15}N$ signatures (Fig. 6.5) to those that were either only OMZ or non-OMZ dwelling. To see if intra-species shifts were also contributing to the overall pattern of $\delta^{15}N$ enrichment within the OMZ, we looked at species that spanned multiple oxygen exposure regimes. Many demersal fish species undergo an ontogenetic migration, moving into deeper waters as they get older, so while the species may span a broad range of depths, individuals of a given age are not thought to be regularly moving across depth zones and feeding in different areas. For this reason, we assume that individuals that are captured outside of or within the OMZ, are feeding within the localized habitat where they were captured and not moving regularly into deeper or shallower areas to feed. We found that demersal fish species whose distribution spans environments with different oxygen exposures, such as Dover sole (*M. pacificus*), slender sole (*L. exilis*), and shortspine thornyhead (*S. alascanus*), tend to have an enriched δ^{15}N signature in the lower oxygen habitat of their range (Fig. 6.6). This was found for individuals for species that were captured both inside and above the OMZ (Fig. 6.6 A), and those that were captured within the OMZ core compared to the outer boundaries of the OMZ (Fig. 6.6 B). However not all species showed the same trend; a smaller number of species including sablefish (*Anoplopoma fimbria*), black eelpout (*Lycodes diapterus*), and the longspine thornyhead (*S. altivelis*) showed a less enriched signature under more hypoxic conditions (Fig. 6.6), in contrast to the general community-level patterns observed.

We further investigated whether these intraspecies shifts in δ^{15}N across oxygen zones were due to changes in N sources at the base of the food chain or an elongation of the food chain. This was done by evaluating the δ^{15}N of two source (Phenylanine, Glycine) and one trophic (Glutamic acid) AA in three select species: Shortspine thornyhead (*Sebastolobus alascanus*), longspine thornyhead (*S. altivelis*) and California slickhead (*Alepocephalus tenebrosus*), that inhabited the OMZ core, the upper and lower OMZ and above the OMZ (only *S. alascanus*). While we found no AA specific δ^{15}N differences between oxygen zones for *S. altivelis; S. alascanus* and *A. tenebrosus* demonstrated substantial but opposite differences (Table 6.4). Changes in trophic relative to source AAs pointed towards *S. altivelis* having a significantly longer food chain and *A. tenebrosus* having a significantly shorter food chain within the OMZ core (Tukey's HSD $p < 0.02$). The elevated bulk $\delta^{15}N$ levels observed in *A. tenebrosus* at lower oxygen concentrations (Fig. 6.6 B) may be driven by changes in N sources as indicated by the source AA Gly (Tukey's HSD $p < 0.01$). Glycine is particularly sensitive to bacterial reworking (McCarthy et al., 2007, Calleja et al., 2013) and elevated Glycine isotopic levels could point towards a greater reliance on degraded organic matter in the food chain. Although less comprehensive than the bulk data the CS-SIA results points towards several ecological mechanisms driving the observed $\delta^{15}N$ enrichment.

The surprisingly high bulk $\delta^{15}N$ levels observed in rubynose brotula (*Cataetyx rubrirostris*, Fig. 6.5), an exclusive OMZ core dweller, could not be explained or substantiated by the CS-SIA results and did not differ from those of the hundred fathom mora (*Physiculus rastrelliger*) a species with much lower bulk isotopic levels (Fig. 6.5, Table 6.4). Metabolic differences regulating N isotopic fractionation in AAs not analyzed in the present study could exist in e.g., *C. rubrirostris*.

Our results showed that both changes in species composition and intraspecific shifts were contributing to the overall community pattern of enriched $\delta^{15}N$ signatures within the OMZ, representing a more complex food chain under severely hypoxic conditions. Next, we were interested in understanding the mechanism that may explain this pattern. Since other studies have found that heavier $\delta^{15}N$ signatures may indicate a diet more reliant on benthic resources (Boyle et al. 2012), we grouped each species in our dataset as a benthic or pelagic feeder based on analyzed gut contents and previously published diet information (Table 6.3). Using the community composition data for each otter trawl, we tested whether the proportion of pelagic- versus benthic-feeding fishes changes moving deeper down the margin, into the

OMZ. We found that at shallower depths, under well-oxygenated conditions, pelagic-feeding fish dominated the fish community (~70 %) (Fig. 6.7). In contrast, benthic-feeding fishes dominated the fish community at deeper depths within the OMZ (~90 %) (Fig. 6.7). Interestingly, the shift in dominant feeding mode from pelagic to benthic coincided with the upper boundary of the OMZ (~450 m) (Fig. 6.7), suggesting that the decrease in oxygen may be responsible for the shift from pelagic-feeding to benthic-feeding in the demersal fish community under severely hypoxic conditions.

Similar to previous studies (Boyle et al. 2012), the isotopic carbon and nitrogen signatures of demersal fish species categorized as benthic feeders, based on diet information, were more enriched than those characterized as pelagic feeders, and this difference was statistically significant for both $\delta^{13}C$ (Fig. 6.8 A) and $\delta^{15}N$ (Fig. 6.8 B) (ANOVA, $p < 0.001$). Species that were *a priori* categorized as benthic feeders had more enriched $\delta^{15}N$ signatures on average than those categorized as pelagic feeders, and appeared to be feeding at a higher trophic level (Fig. 6.8 C). Some exceptions stand out, for example the Pacific grenadier, *Coryphaenoides acrolepis*, and several rockfish, *Sebastes semicinctus*, *S. helvomaculatus*, and *Sebastes spp.* had unexpectedly high $\delta^{15}N$ signatures, given that diet studies point to a mainly pelagic diet. This may suggest they are also utilizing benthic resources and feeding at a higher trophic level in the Southern California Bight. While we were unable to *a priori* categorize *Plectobranchus evides* (PRI) as either a pelagic or benthic feeder based on limited diet data, its relatively enriched trophic signature (mean $\delta^{15}N = 16.62$ ‰) compared to other species found in its shallow, normoxic habitat, suggests that it is likely a benthic feeder.

Given the observed shift to benthic feeders observed in the OMZ (Fig. 6.7) and the enriched $\delta^{15}N$ signatures of benthic feeders (Fig. 6.8), we next looked to see if the overall enrichment in $\delta^{15}N$ observed for the demersal fish community (Fig. 6.4) may be explained by a transition to benthic feeding under severely hypoxic conditions. To look at this, we estimated the average isotopic $\delta^{15}N$ signature for the demersal fish community for each otter trawl, by weighing isotope data by trawl composition, thus representing a weighted average by abundance. We then compared how the estimated isotopic $\delta^{15}N$ signature of the demersal fish community as a whole changed across the depth range sampled, and how this correlated with the observed shift from dominance by pelagic-feeders to dominance by benthic-feeders. We found that between ~300-700 m, the calculated $\delta^{15}N$ signature of the demersal fish community becomes enriched, and deeper than this there is little change to the isotopic signature (Fig. 6.9). This pattern coincides very closely with an increase in benthic-feeding fishes making up most the demersal fish community (Fig. 6.9). This transition appears to occur at depths that coincide with the upper OMZ boundary (~450 m), as conditions become severely hypoxic. One of the interesting considerations is that this relationship is not symmetrical, and we do not see a shift to more pelagic feeders or a return to a less enriched $\delta^{15}N$ community signature at depths below the core of the OMZ, where oxygen conditions begin to increase. This points to the likelihood that something important is happening at the depth range that coincides with the upper OMZ boundary, leading to a shift from pelagic feeding to benthic feeding by the demersal fish community.

Additionally, the trophic diversity of the demersal fish community was compared between OMZ and non-OMZ communities. One of the common characteristics of OMZ communities is a decrease in demersal fish species richness within the OMZ (Fig. 6.3) (Gallo and Levin 2016). To test if the trophic niche of the demersal fish community also shrinks as species richness decreases, Layman metrics (Layman et al. 2007) were used to compare the trophic niche of the demersal fish community within the OMZ, compared to above the OMZ, and at a finer level, within the upper boundary, core, and lower boundary of the OMZ. Contrary to the initial hypothesis, we found that trophic niche metrics were relatively similar for non-OMZ and OMZ fish communities. The total hull area, a measure of the niche breadth of the community, was only slightly greater (TA = 6.42) for the non-OMZ community compared to the OMZ fish community (TA = 6.11) (Fig. 6.10), although the mean distance to centroid and nearest neighbor distance, which are two measures of community trophic species packing, were lower for the non-OMZ community (CD = 0.89, NND = 0.32) compared to the OMZ community (CD = 1.24, NND = 0.43), suggesting that there is more overlap of individual species' trophic niches within the non-OMZ community. We also found that the non-OMZ community has slightly larger carbon (2.33) and nitrogen (5.13) ranges compared to the OMZ community (2.18 and 4.74, respectively), suggesting that the non-OMZ community did have slightly higher trophic level diversity and food diversity exploited by the community than the OMZ community.

While we only saw minor differences when comparing the non-OMZ to the OMZ community, differences in trophic niche became more apparent when taking a closer look at the trophic niches within the OMZ. Demersal fish species richness is lowest within the OMZ core ($[O_2] < 10$ µmol kg^{-1}), where oxygen levels are lowest, and here we find that the trophic niche of the demersal fish community does differ, consistent with our hypothesis. For the demersal fish community living in the OMZ core, the total hull area was only 2.05, meaning the trophic niche breadth was only 1/3 of that of the non-OMZ community. The carbon and nitrogen ranges were also smaller (1.37 and 2.55, respectively), suggesting less trophic level diversity and less prey diversity.

The similarity in trophic breadth found between the non-OMZ and overall OMZ community appears to be due to the larger trophic niche of the upper OMZ community. This community had a relatively large niche breadth (TA = 5.50), relatively large carbon and nitrogen ranges (2.18 and 5.53, respectively), and measures of species packing that were more similar to that of the OMZ fish community overall (CD = 1.25, NND = 0.56). Below the OMZ core, the trophic niche breadth of the demersal fish community was larger than that found for the OMZ core community, but still smaller than that found for the OMZ upper boundary (TA = 3.55). Interestingly, the lower OMZ fish community had the smallest carbon range (1.75), suggesting a more uniform base to the food chain, but still had a relatively large nitrogen range (4.07), suggesting trophic level diversity more similar to that found for the upper OMZ boundary demersal fish community.

A closer look at demersal fish communities within the OMZ (Fig. 6.10) suggests that ecological responses do not follow the oxygen threshold that is used by some to define an OMZ (e.g. $[O_2] < 22.5\ \mu\text{mol kg}^{-1}$), but occur at more extreme O_2 concentrations within the OMZ core ($[O_2] < 10\ \mu\text{mol kg}^{-1}$). Within the OMZ core, there is a decrease in the breadth of the trophic niche of the demersal fish community, compared to fish communities in better oxygenated habitats both inside and outside of the OMZ.

Discussion

Our results suggest that important trophic changes accompany shifts in the demersal fish communities living outside versus within the OMZ in the Southern California Bight, and therefore that hypoxic environments have functional impacts on demersal fish community trophic ecology. These changes include a reduction in the trophic niche breadth of the demersal fish community, a lengthening of the food chain supporting the demersal fish community, and a shift from pelagic to benthic feeding for fish within the OMZ.

The pronounced shift from a pelagic-supported to a benthic-supported demersal fish community at the upper boundary of the OMZ (Fig. 6.7) has important implications for benthic production and carbon storage on our margin. The results of this study contrast strongly with a similar study conducted on the UK-Irish continental slope, where the trophic ecology of the demersal fish community was examined across depth zones (500-1800 m) (Trueman et al. 2014) (Fig. 6.11). In the Northeast Atlantic, the biomass of benthic-feeding fishes decreased steadily from 500-1800 m, while the biomass of pelagic feeding fishes increased and peaked at 1800 m, where 80% of the total biomass was composed of pelagic-feeding fishes (Trueman et al. 2014). In contrast to the SCB, the Northeast Atlantic has a well oxygenated water column and the daytime depth of the DVM community extends below 1000 m, thus providing an important mechanism for bentho-pelagic coupling mediated through the pelagic-feeding demersal fish community. Over 50% of the demersal fish community biomass at depths between 500-1800 m in the Northeast Atlantic is supported by biological rather than detrital nutrient flux processes, resulting in an estimated additional 1 million tons of CO_2 captured through demersal fish trophic interactions (Trueman et al. 2014).

While the depth range of our study is shallower (100-1250 m) than the Trueman et al. (2014) study (500-1800 m), the results still provide an important comparison opportunity. In the SCB, instead of an increase in pelagic feeding with depth, the opposite occurs and below 500 m the demersal fish community is dominated by benthic feeders (Fig. 6.7). This suggests that the deep-sea demersal fish community in the SCB (below ~450 m) is not providing the same carbon transport ecosystem service as in the Northeast Atlantic, which we hypothesize to be related to the presence of the OMZ.

In the Northeast Atlantic, the transition to more pelagic feeding is also accompanied by an overall increase in demersal fish biomass (Trueman et al. 2014). We were interested if a similar positive relationship was observed for the Southern California Bight between percentage of pelagic feeders in the fish community and demersal fish density or biomass. We found no significant relationship between either CPUE or density and percentage of pelagic feeders in the demersal fish community (Fig. 6.12). Since there was a fair amount of variance in the data, it would be interesting for future studies with higher sample numbers to test this relationship.

Two mechanisms may be at play in reducing bentho-pelagic coupling at depths with low oxygen. The first – prey availability – may be directly impacted by the presence of low-oxygen water, leading to a shallower daytime depth occupied by the DVM community. This is consistent with several studies that find a compressed DVM in areas with OMZs (Netburn and Koslow 2015, Bianchi et al. 2013). Off Oregon, many migrating midwater fish and crustaceans reside at depths between 300-500 m during the day (Pearcy et al. 1977), and off northern Baja California, where hypoxic conditions are found even shallower, the daytime depth of offshore scattering layers is between 150 to 325 m (Isaacs and Schwartzlose 1965). This contrasts with the daytime depth of the DVM community which extends below 1000 m in the NE Atlantic (Trueman et al. 2014). Apart from differences in the availability of DVM prey, another mechanism may involve the actual ability of fish to actively swim off the bottom and feed on the DVM community. Active swimming is a more energetically expensive activity than resting on the bottom, and metabolic depression is a known adaptation to hypoxia in fishes (Nilsson 2010), so under more hypoxic conditions, fish may be physiologically less able to undertake this activity. Even swimming off the bottom 10 to 20 m may be too great for fish that are experiencing hypoxic physiological limitation. We are unable to distinguish between the two mechanisms, but suspect that both contribute to the decrease in bentho-pelagic coupling on the margin.

The importance of physical advection and vertical migration for transferring energy to seafloor communities has been recognized for some time (Genin et al. 1988). Isaacs and Schwartzlose (1965) estimated that the drift of zooplankton into areas that intercept the seafloor provided a food supply equivalent to as much as a steady-state phytoplankton productivity of carbon of 8 g $m^{-2}d^{-1}$, or approximately 40 times that of a highly productive region on the California coast. However, at depths below the upper boundary of the OMZ on eastern boundary current continental margins, detrital flux pathways may be more important mechanisms of carbon transport than biologically-mediated, active carbon transport mechanisms. At shallower depths, biologically-mediated transport is still key: “fish mediated export” by midwater diel vertical migrators has been approximated to be equal to the passive transport of particles at 400 m for the US West Coast (Davison et al. 2013), and high density communities of pelagic-feeding demersal fish, such as slender sole (*L. exilis*), are observed in our dataset at depths between 300-400 m. For the upper slope demersal fish community, other studies have also found that slender soles have the highest density (mean density = 16.18 1000 m^{-2}) compared to other demersal fish species, and rank first in the index of community importance (ICI) (Miller and Schiff 2011).

“Subsidies”, or the fluxes of organisms from productive to less productive habitats, strongly influence the structure and dynamics of recipient food webs in a wide range of environments (Polis, Anderson, and Holt 1997). Migrating pelagic organisms provide an important animal-mediated nutrient subsidy that supports the demersal fish communities on continental margins, but we suggest that this nutrient subsidy is disrupted, or compressed into shallower depths, in areas with OMZs. It is worth considering the implications this might have for fisheries production. Demersal organisms which feed directly on components of the downward flux skip at least one trophic level (Houston and Haedrich 1986). As a result, food can reach "pelagic" feeders via a shorter, more efficient pathway than available to demersal organisms which feed solely on benthic organisms. The trophic transfer efficiency associated with marine communities is estimated around 10-20% (Jennings et al. 2002, Blanchard et al. 2009). Thus, if the demersal fish living in the OMZ core are feeding one trophic level higher, that community can only support 10-20% of the biomass. This means that even if certain fisheries species can physiologically tolerate OMZ conditions such as sablefish, Dover sole, and short and longspine thornyheads (Fig. 6.2) (Gallo and Levin 2016), these fisheries will be less efficient and require more primary production to support fisheries production. It should be noted that a lower metabolic rate, which is a common adaptation of hypoxia-tolerant fish (Nilsson 2010), may affect trophic transfer efficiency and food requirements. At 800 m, the shortspine thornyhead only needs to eat once every 89 days, while the longspine thornyhead, which has an even lower metabolic rate, only needs to eat once every 136 days (Vetter and Lynn 1997). Interestingly, in our gut content analysis we did not find evidence of a notable decrease in feeding even within the OMZ-core community, where 30% of specimens analyzed had very full stomachs, 44% had partially-full stomachs, and 25% had empty stomachs. In comparison, for demersal fish sampled from areas above the OMZ, 26% had very full stomachs, 49% had partially full stomachs, and 25% had empty stomachs.

Subsidies from productive pelagic habitats to less-productive benthic habitats appear to be especially important for supporting rockfish populations, which are important recreational and commercial fisheries species for the US West Coast. Several studies have noted the importance of migrating mesopelagic fauna in supporting areas with high densities of rockfish (Isaacs and Schwartzlose 1965, Pereyra et al. 1969, Genin et al. 1988). The ecological significance of pelagic migrators being carried into areas over shallow topography and providing food resources for fisheries species was recognized as early as the 1960s (Isaacs and Schwartzlose 1965). In the Southern California Bight, migrating euphausiids, especially *Euphausia pacifica*, are a dominant prey item in the stomachs of rockfish living on shallow banks (100-300 m) (Genin et al. 1988). Similarly, off Oregon and Washington, *Sebastes flavidus*, feeds primarily on migrating mesopelagic fauna, primarily euphausiids or myctophids, with high-densities aggregations of rockfish reported in areas where vertically migrating fauna intercept the seafloor (Pereyra et al. 1969). Previous studies have discussed the potential impact of deoxygenation on rockfish communities with relation to their physiological tolerances (McClatchie et al. 2010), but our results suggest that trophic impacts should also be considered since most rockfish rely on the migrating pelagic community as their primary food source. An expansion of low oxygen waters with climate change may result in a reduction of pelagic prey availability that may be vital for supporting rockfish populations.

Based on the bathymetry of the Southern California Bight, more than 50% of the seafloor falls within the depth range between 450-1250 m, and is estimated to be exposed to OMZ conditions (Fig. 6.13). Only ~20% of the seafloor habitat occurs at depths shallower than the upper boundary of the OMZ (450 m). In these areas, the DVM community likely provides an important food subsidy that supports demersal fish communities on the upper margin. However, ~80% of the seafloor habitat of the Southern California Bight is at depths deeper than the OMZ upper boundary, where our results suggest that bentho-pelagic coupling is greatly reduced. In these areas, demersal fish communities are effectively limited to utilizing benthic resources, which is a less efficient trophic pathway. Therefore, the presence of the OMZ appears to have a large influence on the trophic ecology of demersal fish communities in the Southern California Bight.

One unexpected pattern we observed during this research is that there appears to be an intriguing relationship between feeding mode and species richness. While pelagic-feeders typically represent the numerically dominant species in demersal fish communities, there usually tends to be a higher species richness of benthic feeding species present in the community. For example, Bulman et al. (2001) found that of the 70 demersal fish species examined, 37 relied primarily on benthic prey, but that pelagic feeding dominated in 18 of the 28 commercial or numerically abundant species examined, and that 9 of the 12 quota species examined were primarily pelagic feeders. Houston and Haedrich (1986) also describe a similar trend in that there were more species of benthic feeders than pelagic feeders in the demersal fish community, but that the pelagic feeders were numerically more abundant (70.9% compared to 20.5%). On the US Mid-Atlantic continental margin, the two ecologically dominant species both primarily consumed pelagic prey items, though there were many benthic-feeding species present (Sedberry and Musick 1978). Similarly, there were many more benthic-feeding (n = 23) than pelagic-feeding fish species (n = 7) in the study by Trueman et al. (2014), even though more than 45% of the total trawled demersal fish biomass between 1000-1800 m was composed of 3 pelagic-feeding demersal fish species, and the biomass of pelagic feeders increased with depth. In this study, we also observed this pattern: at 300-400 m, the slender sole, *Lyopsetta exilis*, is numerically dominant and feeds on pelagic prey, but many other rarer benthic-feeding species are also present.

Therefore, there appears to be a general rule that when there is an opportunity to utilize pelagic resources by preying on the DVM community, this trophic pathway will support several, numerically dominant species, while within the same community, benthic resources will support a higher diversity of demersal fish species that are numerically rarer. Fisheries species tend to be those that are numerically dominant and have high biomass, and therefore demersal fisheries species are those more likely to be reliant on pelagic production and bentho-pelagic coupling. Trueman et al. (2014) notes that most commercially targeted deepwater fisheries operate at depths of highest demersal fish production, where the main commercial and bycatch species are pelagic feeders. Therefore, the reduction in bentho-pelagic coupling within the OMZ, likely affects fisheries production on the US West Coast margin. Shoaling of the OMZ with climate change may further reduce fish production by shallowing the daytime depth of the DVM community and reducing the area of seafloor where demersal fish species can utilize pelagic food resources.

Future Work

While much of this chapter focuses on community-level changes, there is ample opportunity to look more closely at intraspecific trends for species that have broad depth distributions, including species such as the Dover sole, *M. pacificus*, and the short and longspine thornyheads (*S. alascanus* and *S. altivelis*). For these species, it would be interesting to test if their trophic niche changes under different oxygen conditions using

Bayesian ellipses (Jackson et al. 2011). Additionally, it would be interesting to compare differences in trophic diversity based on metrics such as Levin's standardized niche and Pianka's index, calculated from the results of the gut content analysis.

Apart from the US West Coast, continental margins off the West Coast of Central and South America, Western Africa, and countries bordering the Indian Ocean also have oceanographic conditions in which midwater severely hypoxic water masses impinge on seafloor habitat. These areas also have adapted demersal fish communities capable of tolerating severely hypoxic conditions (Gallo and Levin 2016), and some of these species are commercially important as fisheries. It would be valuable to test our hypothesis about OMZs disrupting bentho-pelagic coupling and affecting the trophic ecology of the demersal fish community in these other comparative systems, to see if this pattern is consistent on other margins. Intensification of hypoxia due to climate-driven deoxygenation may alter the coupling and energy transfer across different marine habitats (from the pelagic zone to the seafloor), and the subsequent productivity of these different habitats. For example, off India, an intensification of shelf hypoxia was associated with a decrease in demersal fish landings, while pelagic fish landings remained relatively constant (Naqvi et al. 2006). Our results suggest that more work is needed on the trophic impacts of ocean deoxygenation, and that the expansion of low oxygen zones may alter species distributions not only through limits to physiological tolerance, but also through changes to important trophic pathways.

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Literature Cited

Aksnes, D.L., Rostad, A., Kaartvedt, S., Martinez, U., Duarte, C.M., Irigoien, X. 2017. Light penetration structures the deep acoustic scattering layers in the global ocean. Science Advances 3, e1602468.

Allen, M.J. 1982. Functional structure of soft-bottom fish communities of the southern California shelf. Ph.D. Thesis. University of California, San Diego, 577 p.

Allen, M.J. 2008. Bathymetic responses in functional structure of southern California demersal fish communities to Pacific Decadal Oscillation regimes and an El Nino. pp. 211-228 in: Weisberg, S.B. and Miller, K. (eds), Southern California Coastal Water

Research Project 2008 Annual Report. Southern California Coastal Water Research Project. Costa Mesa, CA.

Allen, L.G., Pondella, D.J., Horn, M.H. 2006. The ecology of marine fishes: California and adjacent waters. University of California Press, Berkeley, 660 p.

Bianchi, D., Galbraith, E.D., Carozza, D.A., Mislan, K.A.S., Stock, C.A. 2013. Intensification of open-ocean oxygen depletion by vertically migrating animals. Nature Geoscience 6, 545-548.

Bjelland, O., Bergstad, O.A., Skjaeraasen, J.E., Meland, K. 2000. Trophic ecology of deep-water fishes associated with the continental slope of the Eastern Norwegian Sea. Sarsia 85(2), 101-117.

Blaber, S.J.M., Bulman, C.M. 1987. Diets of fishes of the upper continental slope of eastern Tasmania: content, calorific values, dietary overlap and trophic relationships. Marine Biology 95, 345-356.

Blanchard, J.L., Jennings, S., Law, R., Castle, M.D., McCloghrie, P., Rochet, M.-J., Benoit, E. 2009. How does abundance scale with body size in size-structured food webs? J. Anim. Ecol. 78, 270 – 280.

Boecklen, W.J., Yarnes, C.T., Cook, B.A., James, A.C. 2011. On the use of stable isotopes in trophic ecology. Annu. Rev. Ecol. Evol. Syst. 42, 411-440.

Bograd, S.J., Castro, C.G., Lorenzo, E.D., Palacios, D.M., Bailey, H., Gilly, W., Chavez, F.P. 2008. Oxygen declines and the shoaling of the hypoxic boundary in the California Current. Geophys. Res. Lett. 35, L12607.

Bograd, S.J., Buil, M.P., Lorenzo, E.D., Castro, C.G., Schroeder, I.D., Goericke, R., Anderson, C.R., Benitez-Nelson, C., Whitney, F.A. 2015. Changes in source waters to the Southern California Bight. Deep-Sea Res II 112, 42-52.

Bopp, L., Resplandy, L., Orr, J.C., Doney, S.C., Dunne, J.P., Gehlen, M., Halloran, P., Heinze, C., Ilyina, T., Séférian, R., Tjiputra, J., Vichi, M. 2013. Multiple stressors of ocean ecosystems in the 21st century: projections with CMIP5 models. Biogeosciences 10, 6225-6245.

Boyle, M.D. 2010. Trophic interactions of *Bathyraja trachura* and sympatric fishes. Capstone Projects and Theses. Paper 65. California State University, Monterey Bay.

Boyle, M.D., Ebert, D.A., Cailliet, G.M. 2012. Stable-isotope analysis of deep-sea benthic-fish assemblage: evidence of an enriched benthic food web. J. Fish Biol. 80, 1485-1507.

Breitburg, D., Levin, L.A., Oschlies, A., Grégoire, M., Chavez, F.P., Conley, D.J., Garçon, V., Gilbert, D., Gutiérrez, D., Isensee, K., Jacinto, G.S., Limburg, K.E., Montes, I., Navqi, S.W.A., Pitcher, G.C., Rabalais, N.N., Roman, M.R., Rose, K.A., Seibel, B.A., Telszewski, M., Yasuhara, M., Zhang, J. 2018. Declining oxygen in the global ocean and coastal waters. Science 359(6371), eaam7240.

Breitburg, D.L., Loher, T., Pacey, C.A., Gerstein, A. 1997. Varying effects of low dissolved oxygen on trophic interactions in an estuarine food web. Ecol. Monogr. 67, 489–507.

Broek, T.A.B., McCarthy, M.D. 2014. A new approach to δ^{15}N compound-specific amino acid trophic position measurements: preparative high pressure liquid chromatography technique for purifying underivative amino acids for stable isotope analysis. Limnol. Oceanogr. Methods 12, 840-852.

Bulman, C., Althaus, F., He, X., Bax, N.J., Williams, A. 2001. Diets and trophic guilds of demersal fishes of the south-eastern Australian shelf. Mar. Freshwater Res. 52, 537-48.

Bulman, C.M., He, X., Koslow, J.A. 2002. Trophic ecology of the mid-slope demersal fish community off southern Tasmania, Australia. Mar. Freshwater Res. 53, 59-72.

Calleja, M.L., Batista, F., Peacock, M., Kudela, R., McCarthy, M.D. 2013. Changes in compound specific δ15N amino acid signatures and d/l ratios in marine dissolved organic matter induced by heterotrophic bacterial reworking. Marine Chemistry 149, 32-44.

Carlisle, A.B., Litvin, S.Y., Madigan, D.J., Lyons, K., Bigman, J.S., Ibarra, M., Bizzarro, J.J. 2016. Interactive effects of urea and lipid content confound stable isotope analysis in elasmobranch fishes. Can. J. Fish. Aquat. Sci. 999, 1–10.

Chess, J.R., Smith, S.E., Fisher, P.C. 1988. Trophic relationships of the shortbelly rockfish, *Sebastes jordani*, off central California. CalCOFI Rep. 29, 129–136.

Chikaraishi, Y., Ogawa, N.O., Kashiyama, Y., Takano, Y., Suga, H., Tomitani, A., Miyashita, H., Kitazato, H., Ohkouchi, N. 2009. Determination of aquatic food-web structure based on compound-specific nitrogen isotopic composition of amino acids. Limnol. Oceanogr. Methods 7, 740-750.

Cohen, D.M., Inada, T., Iwamoto, T., Scialabba, N. 1990. FAO species catalogue. Vol. 10. Gadiform fishes of the world (Order Gadiformes). An annotated and illustrated catalogue of cods, hakes, grenadiers and other gadiform fishes known to date. FAO Fish. Synop. 125(10). Rome: FAO. 442 p.

Davison, P.C., Checkley, D.M., Koslow, J.A., Barlow, J. 2013. Carbon export mediated by mesopelagic fishes in the northeast Pacific Ocean. Prog. Oceanogr. 116, 14-30.

Diaz, R.J., Rosenberg, R. 2008. Spreading dead zones and consequences for marine ecosystems. Science 321, 926–29.

Drazen, J.C., Buckley, T.W., Hoff, G.R. 2001. The feeding habits of slope dwelling macrourid fishes in the eastern North Pacific. Deep-Sea Res. I 48(3), 909-935.

Drazen, J.C., Popp, B.N., Choy, C.A., Clemente, T., De Forest, L.G., Smith, K.L. Jr. 2008. Bypassing the abyssal benthic food web: macrourid diet in the eastern North Pacific inferred from stomach content and stable isotopes analyses. *Limnol. Oceanogr.* 53, 2644–54

Drazen, J.C., and Sutton, T.T. 2017. Dining in the deep: the feeding ecology of deep-sea fishes. Annu. Rev. Mar. Sci. 9, 337-366.

Drazen, J.C., Yeh, J., Friedman, J., Condon, N. 2011. Metabolism and enzyme activities of hagfish from shallow and deep water of the Pacific Ocean. Comp. Biochem. Physiol. A Mol. Integr. Physiol. 159, 182−187.

Ebert, D.A. 2003. Sharks, rays, and chimaeras of California. Berkeley, University of California Press, 285 p.

Gallo, N.D., Levin, L.A. 2016. Fish ecology and evolution in the world's oxygen minimum zones and implications of ocean deoxygenation. Adv. Mar. Biol. 1-82.

Genin, A., Haury, L., Greenblatt, P. 1988. Interactions of migrating zooplankton with shallow topography: predation by rockfishes and intensification of patchiness. Deep-Sea Res. I 35(2), 151-175.

Gilly, W.F., Beman, J.M., Litvin, S.Y., Robison, B.H. 2013. Oceanographic and biological effects of shoaling of the oxygen minimum zone. Annu. Rev. Mar. Sci. 5, 393-420.

Helly, J.J., Levin, L.A. 2004. Global distribution of naturally occurring marine hypoxia on continental margins. Deep-Sea Res. I 51, 1159-1168.

Hoffman, J.C., Sutton, T.T. 2010. Lipid correction for carbon stable isotope analysis of deep-sea fishes. Deep-Sea Res I 57, 956-964.

Houston, K.A., Haedrich, R.L. 1986. Food habits and intestinal parasites of deep demersal fishes from the upper continental slope east of Newfoundland, northwest Atlantic Ocean. Marine Biology 92, 563-574.

Hussey, N.E., MacNeil, M.A., Olin, J.A., McMeans, B.C., Kinney, M.J., Chapman, D.D., Fisk, A.T. 2012. Stable isotopes and elasmobranchs: tissue types, methods, applications and assumptions. J. Fish Biol. 80, 1449–1484.

Isaacs, J.D., Schwartzlose, R.A. 1965. Migrant sound scatterers: Interaction with the sea floor. Science 150(3705), 1810-1813.

Jackson, A.L., Inger, R., Parnell, A.C., Bearhop, S. 2011. Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses in R. J. Animal Ecol. 80, 595-602.

Jacobson, L.D., Vetter, R.D. 1996. Bathymetric demography and niche separation of thornyhead rockfish: *Sebastolobus alascanus* and *Sebastolobus altivelis*. *Can. J. Fish. Aquat. Sci.* 53, 600– 609.

Jennings, S., Warr, K.J., Mackinson, S. 2002. Use of size-based production and stable isotope analyses to predict trophic transfer efficiencies and predator-prey body mass ratios in food webs. Mar. Ecol. Prog. Ser. 240, 11-20.

Keeling, R.F., Kortzinger, A., Gruber, N. 2010. Ocean deoxygenation in a warming world. Annu. Rev. Mar. Sci. 2, 199–229.

Kelleher, S.D., Livingston, M.B., Hultin, H.O., Aciukewicz, T.J. 2001. Characteristics and storage stability of atlantic hagfish. J. Aquat. Food Prod. Technol. 10, 101–118.

Keller, A.A., Bradburn, M.J., Simon, V.H. 2013. Shifts in condition and distribution of eastern North Pacific flatfish along the U.S. west coast (2003-2010). Deep-Sea Res. I 77, 23-35.

Keller, A.A., Ciannelli, L., Wakefield, W.W., Simon, V., Barth, J.A., Pierce, S.D. 2015. Occurrence of demersal fishes in relation to near-bottom oxygen levels within the California Current large marine ecosystem. Fish. Oceanogr. 24(2), 162–176.

Keller, A.A., Ciannelli, L., Wakefield, W.W., Simon, V., Barth, J.A., Pierce, S.D. 2017. Species-specific responses of demersal fishes to near-bottom oxygen levels within the California Current large marine ecosystem. Mar. Ecol. Prog. Ser. 568, 151-173.

Keller, A.A., Wallace, J.R., Horness, B.H., Hamel, O.S., Stewart, I.J. 2012. Variations in eastern North Pacific demersal fish biomass based on the U.S. west coast groundfish bottom trawl survey (2003-2010). Fishery Bulletin 110(2), 205-222.

Klevjer, T.A., Irigoien, X., Rostad, A., Fraile-Nuez, E., Benitez-Barrios, V.M., Kaartvedt, S. 2016. Large scale patterns in vertical distribution and behavior of mesopelagic scattering layers. Scientific Reports 6, 19873.

Layman, C.A., Araujo, M.S., Boucek, R., Hammerschlag-Peyer, C.M., Harrison, E., Jud, Z.R., Matich, P., Rosenblatt, A.E., Vaudo, J.J., Yeager, L.A., Post, D.M., Bearhop, S. 2011. Applying stable isotopes to examine food-web structure: an overview of analytical tools. Bio. Rev. 87(30), 545-562.

Layman, C.A., Arrington, D.A., Montana, C.G., Post, D.M. 2007. Can stable isotope ratios provide for community-wide measures of trophic structure? Ecology 88(1), 42-48.

Lenarz, T.E., Larson, R.J., Ralston, S. 1991. Depth distributions of late larvae and pelagic juveniles of some fishes of the California current. *CalCOFI Reports* 32, 41–46.

Levin, L.A. 2003. Oxygen minimum zone benthos: adaptation and community response to hypoxia. Ocean. Mar. Biol. Ann. Rev. 41, 1-45.

Levin, L.A. 2018. Manifestation, drivers, and emergence of open ocean deoxygenation. Annu. Rev. Mar. Sci 10, 229–260.

Levin, L.A. Currin, C. 2012. Stable isotope protocols: Sampling and sample processing. *UC San Diego: Scripps Institution of Oceanography*. https://escholarship.org/uc/item/3jw2v1hh

Levin, L.A., Ziebis, W., Mendoza, G.F., Bertics, V.J., Washington, T., Gonzalez, J., Thurber, A.R., Ebbe, B., Lee, R.W. 2013. Ecological release and niche partitioning under stress: Lessons from dorvilleid polychaetes in sulfidic sediments at methane seeps. Deep Sea Res. II 92, 214-233.

Lindeman, R.L. 1942. The trophic-dynamic aspect of ecology. Ecology 23(4), 399-417.

Long, M.C., Deutsch, C., Ito, T. 2016. Finding forced trends in oceanic oxygen. *Global Biogeochem. Cycles* 30, 381–397.

Love, M.S. 1992. Bank rockfish. *In* W. S. Leet, C. M. Dewees, and C. W. Haugen (eds.), California's Living Marine Resources and Utilization. California Sea Grant College Program, Davis, California. UCSGEP-92-12, 129–130, 257 p.

Love, M.S. 1996. Probably more than you want to know about the fishes of the Pacific coast. Really Big Press, Santa Barbara, California. 215 p.

Love, M.S. 2011. Certainly more than you want to know about the fishes of the Pacific Coast: A postmodern experience. Really Big Press, Santa Barbara, California. 649 p.

Love, M.S., B. Axtell, P. Morris, R. Collins, and A. Brooks. 1987. Life history and fishery of the California scorpionfish, *Scorpaena guttata*, within the Southern California Bight. Fish. Bull. 85, 99–116.

Love, M.S., Morris, P., McCrae, M., Collins, R. 1990. Life history aspects of 19 rockfish species (Scorpaenidae: *Sebastes*) from the southern California Bight. U.S. Dept. Commer., NOAA Tech. Rep. NMFS-87, 38 p.

Mauchline, J., Gordon, J.D.M. 1985. Trophic diversity in deep-sea fish. J. Fish Biol. 26, 527-535.

McCain, B.B., Miller, S.D., Wakefield, W.W. 2005. Life history, geographical distribution, and habitat associations of 82 West Coast groundfish species: A literature review. Appendix B. Part 2. Pacific Fishery Management Council, 276 p.

McCarthy, M.D., Benner, R., Lee, C., Fogel, M.L. 2007. Amino acid nitrogen isotopic fractionation patterns as indicators of heterotrophy in plankton, particulate, and dissolved organic matter. Geochimica et Cosmochimica Acta 71, 4727-4744.

McClatchie, S., Goericke, R., Cosgrove, R., Auad, G., Vetter, R. 2010. Oxygen in the Southern California Bight: Multidecadal trends and implications for demersal fisheries. Geophysical Research Letters 37, L19602.

Miller, E.F., Schiff, K.C. 2012. Descriptive trends in SCB demersal fish assemblages since 1994. CalCOFI Reports 53, 107-131.

Miller, E.F., Schiff, K.C. 2011. Spatial distribution of Southern California Bight demersal fishes in 2008. CalCOFI Reports 52, 80-96.

Nam, S., Takeshita, Y., Frieder, C.A., Martz, T., Ballard, J. 2015. Seasonal advection of Pacific Equatorial Water alters oxygen and pH in the Southern California Bight. J. Geophys. Res. Oceans 120: doi:10.1002/ 2015JC010859.

Naqvi, S.W.A., Naik, H., Jayakumar, D.A., Shailaja, M.S., Narvekar, P.V. 2006. Seasonal oxygen deficiency over the western continental shelf of India. Pp. 195-224. Neretin, L.N. (ed.) Past and Present Water Column Anoxia. Springer.

Newsome, S.D., Martinez del Rio, C., Bearhop, S., Phillips, D.L. 2007. A niche for isotopic ecology. Front. Ecol. Environ. 5(8), 429-436.

Netburn, A.N., Koslow, J.A. 2015. Dissolved oxygen as a constraint on daytime deep scattering layer depth in the southern California current ecosystem. Deep-Sea Res. I 104, 149-158.

Nilsson, G.E. 2010. Respiratory physiology of vertebrates: Life with and without oxygen. Cambridge University Press, New York, 334 pgs.

Norris, R.D., Turner, S.K., Hull, P.M., Ridgwell, A. 2013. Marine ecosystem responses to Cenozoic climate change. Science 341, 492-498.

Oschlies, A., Brandt, P., Stramma, L., Schmidtko, S. 2018. Drivers and mechanisms of ocean deoxygenation. Nature Geoscience 11, 476-473.

Pearcy, W.G., Krygier, E.E., Mesecar, R., Ramsey, F. 1977. Vertical distribution and migration of oceanic micronekton off Oregon. Deep-Sea Res. 24(3), 223–245.

Pereyra, W.T., Pearcy, W.G., Carvey, F.E. 1969. *Sebastodes flavidus*, a shelf rockfish feeding on mesopelagic fauna, with consideration of the ecological implications. J. Fish. Res. Bd. Canada 26, 2211-2215.

Pihl, L. 1994. Changes in the diet of demersal fish due to eutrophication-induced hypoxia in the Kattegat, Sweden. Can. J. Fish. Aquat. Sci. 51, 321-336.

Pihl, L., Baden, S.P., Diaz, R.J., Schaffner, L.C. 1992. Hypoxia-induced structural changes in the diet of bottom-feeding fish and Crustacea*. Marine Biology 112, 349-361.

Pörtner, H.O., Langenbuch, M., Michaelidis, B. 2005. Synergistic effects of temperature extremes, hypoxia, and increases in CO_2 on marine animals: From Earth history to global change. Journal of Geophysical Research 110, C09S10.

Pörtner, H.O., Schulte, P.M., Wood, C.M., Schiemer, F. 2010. Niche dimensions in fishes: An integrative view. Physiological and Biochemical Zoology 83(5), 808-826.

Ren, A.S., Chai, F., Xue, H., Anderson, D.M., Chavez, F.P. 2018. A sixteen-year decline in dissolved oxygen in the Central California Current. Scientific Reports 8, 7290.

Rinewalt, C.S., Ebert, D.A., Cailliet, G.M. 2007. Food habits of the sandpaper skate, *Bathyraja kincaidii* (Garman, 1908) off central California: seasonal variation in diet linked to oceanographic conditions. Environ. Biol. Fish 80, 147-163.

Robinson, H.J., Cailliet, G.M., Ebert, D.A. 2007. Food habits of the longnose skate, *Raja rhina* (Jordan and Gilbert, 1880), in central California waters. Environ. Biol. Fish. 80, 165-179.

Sato, K.N., Levin, L.A., Schiff, K. 2017. Habitat compression and expansion of sea urchins in response to changing climate conditions on the California continental shelf and slope (1994-2013). Deep-Sea Res. II 137, 377-389.

Schmidtko, S., Stramma, L., Visbeck, M. 2017. Decline in global oceanic oxygen content during the past five decades. Nature 542, 335-339.

Sedberry, G.R., Musick, J.A. 1978. Feeding strategies of some demersal fishes of the continental slope and rise off the Mid-Atlantic Coast of the USA*. Marine Biology 44, 357-375.

Shipley, O.N., Brooks, E.J., Madigan, D.J., Sweeting, C.J., Grubbs, R.D. 2017. Stable isotope analysis in deep-sea chondrichthyans: recent challenges, ecological insights, and future directions. Rev. Fish Biol. Fisheries 27(3), 481-497.

Sperling, E.A., Frieder, C.A., Raman, A.V., Girguis, P.R., Levin, L.A., Knoll, A.H. 2013. Oxygen, ecology, and the Cambrian radiation of animals. PNAS 110(33), 13446-13451.

Stauffer, G.D. 1985. Biology and life history of the coastal stock of Pacific whiting, *Merluccius productus*. Mar. Fish. Rev. 47(2), 2–9.

Stewart, J.D., Rohner, C.A., Araujo, G., Avila, J., Fernando, D., Forsberg, K., Ponzo, A., Rambahiniarison, J.M., Kurle, C.M., Semmens, B.X. 2017. Trophic overlap in mobulid rays: insights from stable isotope analysis. Mar. Ecol. Prog. Ser. 580, 131-151.

Stramma, L., Johnson, G.C., Sprintall, J., Mohrholz, V. 2008. Expanding oxygen-minimum zones in the tropical oceans. Science 320, 655–58.

Stramma, L., Prince, E.D., Schmidtko, S., Luo, J., Hoolihan, J.P., Visbeck, M., Wallace, D.W.R., Brandt, P., Kortzinger, A. 2011. Expansion of oxygen minimum zones may reduce available habitat for tropical pelagic fishes. Nat. Clim. Change 2, 33–37.

Tinus, C.A. 2012. Prey preference of lingcod (*Ophiodon elongatus*), a top marine predator: implications for ecosystem-based fisheries management. Fish. Bull. 110, 193-204.

Trueman, C.N., Johnston, G., O'Hea, B., MacKenzie, K.M. 2014. Trophic interactions of fish communities at midwater depths enhance long-term carbon storage and benthic production on continental slopes. Proc. R. Soc. B. 281, 20140669.

Vaquer-Sunyer, R., Duarte, C.M. 2008. Thresholds of hypoxia for marine biodiversity. Proc. Natl. Acad. Sci. USA 105, 15452–57.

Vetter, R.D., Lynn, E.A. 1997. Bathymetric demography, enzyme activity patterns, and bioenergetics of deep-living scorpaenid fishes (genera *Sebastes* and *Sebastolobus*): paradigms revisited. Mar. Ecol. Prog. Ser. 155, 173-188.

Wyrtki, K. 1962. The oxygen minima in relation to ocean circulation. Deep-Sea Res. 9, 11-23.

Yang, M.-S., Page, B.N. 1999. Diet of the Pacific sleeper shark, *Somniosus pacificus*, in the Gulf of Alaska. Fish. Bull. 97, 406-409.

Zintzen, V., Rogers, K.M., Roberts, C.D., Stewart, A.L., Anderson, M.J. 2013. Hagfish feeding habits along a depth gradients inferred from stable isotopes. Mar. Ecol. Prog. Ser. 485, 223-234.

Tables

Table 6.1. Demersal fish were sampled from 38 otter trawls ranging from depths of 96-1261 m along the continental margin in the Southern California Bight. The cruise, trawl date, latitude and longitude, depth, near-bottom environmental conditions, and vessel name for each trawl are provided. Entries are organized by depth, from shallowest to deepest.

Cruise	Date	Depth (m)	Temperature (°C)	Oxygen (µmol kg-1)	Salinity (psu)	Latitude	Longitude	Vessel
MV1217	12/14/12	96	11.35	135.40	33.73	32 41.670 N	117 19.725 W	R/V *Melville*
MV1217	12/9/12	98	11.27	128.09	33.71	32 49.001 N	117 21.784 W	R/V *Melville*
MV1217	12/9/12	113	10.51	125.77	33.81	32 59.941 N	117 18.843 W	R/V *Melville*
NH1414	7/27/14	196	10.03	103.16	33.95	32 40.320 N	117 21.251 W	R/V *New Horizon*
NH1414	7/27/14	198	10.17	92.01	34.00	32 49.265 N	117 22.159 W	R/V *New Horizon*
NH1414	7/27/14	205	10.20	88.30	34.03	32 43.867 N	117 21.589 W	R/V *New Horizon*
MV1217	12/12/12	292	8.11	58.38	34.18	32 48.558 N	117 23.077 W	R/V *Melville*
MV1217	12/9/12	306	8.09	50.90	34.19	32 57.407 N	117 19.200 W	R/V *Melville*
MV1217	12/15/12	315	7.73	40.73	34.22	32 41.496 N	117 22.550 W	R/V *Melville*
SP1506	4/18/15	339	8.12	44.39	34.22	32 43.090 N	117 22.512 W	R/V *Sproul*
NH1407	4/20/14	340	8.61	29.67	34.33	32 41.913 N	117 22.539 W	R/V *New Horizon*
NOAA FRAMD_21183	7/18/14	347	8.13	31.08	34.29	32 40.157 N	117 44.751 W	F/V *Last Straw*
NOAA FRAMD_19852	7/17/14	381	8.98	32.94	34.07	33 02.367 N	117 22.951 W	F/V *Noahs Ark*
MV1217	12/14/12	389	7.18	27.13	34.27	32 41.449 N	117 24.133 W	R/V *Melville*
NOAA FRAMD_19291	7/19/14	390	8.30	30.70	34.28	33 14.450 N	117 33.344 W	F/V *Last Straw*
MV1217	12/12/12	403	7.43	32.29	34.25	32 48.600 N	117 24.027 W	R/V *Melville*
MV1217	12/9/12	404	7.36	27.85	34.27	32 57.280 N	117 20.457 W	R/V *Melville*
NOAA FRAMD_19514	7/19/14	443	7.78	25.90	34.28	33 09.212 N	117 30.290 W	F/V *Last Straw*
NOAA FRAMD_21182	7/18/14	451	7.27	15.68	34.33	32 40.828 N	117 46.745 W	F/V *Last Straw*
NOAA FRAMD_20605	7/16/14	474	6.71	16.11	34.18	32 54.115 N	118 37.177 W	F/V *Noahs Ark*
NOAA FRAMD_20871	7/18/14	479	7.36	19.75	34.30	32 44.446 N	117 25.793 W	F/V *Last Straw*
NOAA FRAMD_19850	7/17/14	481	7.55	21.14	34.03	33 02.797 N	117 25.876 W	F/V *Noahs Ark*
NOAA FRAMD_20979	7/18/14	530	7.02	16.70	34.30	32 43.582 N	117 26.227 W	F/V *Last Straw*
NOAA FRAMD_20758	7/17/14	555	6.87	15.77	34.10	32 47.009 N	117 26.247 W	F/V *Noahs Ark*
NOAA FRAMD_18523	7/21/14	566	6.44	12.05	34.18	33 30.743 N	118 11.558 W	F/V *Noahs Ark*
NH1414	7/29/14	697	5.43	8.44	34.39	32 53.446 N	117 28.468 W	R/V *New Horizon*
NH1414	7/29/14	698	5.43	8.44	34.39	32 48.770 N	117 28.054 W	R/V *New Horizon*
NH1414	7/29/14	705	5.39	8.30	34.39	32 52.370 N	117 28.991 W	R/V *New Horizon*
NOAA FRAMD_22499	7/17/14	754	5.35	8.44	34.38	32 19.302 N	118 51.580 W	F/V *Last Straw*
NOAA FRAMD_19276	7/18/14	811	5.15	8.17	34.25	33 16.194 N	118 00.029 W	F/V *Noahs Ark*
NOAA FRAMD_19275	7/18/14	834	5.09	7.38	34.15	33 15.921 N	118 02.477 W	F/V *Noahs Ark*
NOAA FRAMD_19610	7/18/14	877	4.42	12.76	34.46	33 09.718 N	117 59.383 W	F/V *Noahs Ark*
NOAA FRAMD_21569	7/16/14	946	4.46	12.30	34.34	32 36.315 N	118 42.538 W	F/V *Noahs Ark*
NOAA FRAMD_22078	7/17/14	962	4.56	12.85	34.44	32 25.680 N	118 30.253 W	F/V *Last Straw*
NOAA FRAMD_20404	7/18/14	1042	4.33	12.42	34.46	32 54.865 N	117 50.487 W	F/V *Last Straw*
NOAA FRAMD_21975	7/17/14	1073	4.10	19.29	34.47	32 27.824 N	118 32.535 W	F/V *Last Straw*
NOAA FRAMD_19490	7/20/14	1096	4.22	11.05	34.47	33 12.901 N	118 13.430 W	F/V *Last Straw*
NOAA FRAMD_20503	7/16/14	1261	4.21	10.74	34.36	32 55.491 N	118 18.650 W	F/V *Noahs Ark*

Table 6.2. Community metrics for each of the 38 otter trawls, organized from shallowest to deepest. Demersal fish species richness is provided, catch per unit effort (CPUE) is provided for otter trawls conducted during the NOAA groundfish bottom trawl survey, and density is provided for trawls conducted during SIO student cruises. The calculated percent community composition of benthic and pelagic feeders for each trawl sample is indicated. The number of fish individuals sampled and included in the trophic analysis from each trawl, and the species identities are also indicated. Species codes correspond to those provided in Table 6.3.

Cruise	Depth (m)	Demersal Fish Species Richness	Demersal Fish CPUE (kg ha-1)	Demersal Fish Density (fish m-2)	Pelagic Feeders (%)	Benthic Feeders (%)	Number of fish sampled for SIA/GCA	Fish species sampled for SIA/GCA
MV1217	96	5		0.00779	34.21	65.79	9	BP, PSL, ZAN
MV1217	98	16		0.02390	52.76	47.24	26	CT, ES, HA, LIZ, PSL, ZAN, ZR
MV1217	113	16		0.06645	83.46	16.54	29	CT, ES, GR, GSR, HBR, LIZ, SS, STR, ZAN, ZR
NH1414	196	16		0.23490	66.48	33.15	37	BP, DSP, ES, HA, HBR, JROC, LIZ, LYC, PRI, PSL, SS, STR, ZAN
NH1414	198	20		0.16881	86.89	13.11	30	BP, CT, DSP, HA, JROC, LIZ, PSL, RS, SS, STR, ZAN
NH1414	205	15		0.20009	85.27	14.73	33	BP, DSP, ES, HA, HBR, JROC, LIZ, LYC, PSL, SS, STR, ZAN
MV1217	292	5		0.02351	70.00	30.00	8	BP, HFC, ROC
MV1217	306	10		0.20600	22.24	77.58	34	BEP, BP, DSP, HA, HFC, LYC, RS, SPL, SS
MV1217	315	13		N/A	85.01	14.99	35	BEP, BP, DSP, ES, HA, HFC, JROC, LYC, RS, SPL, SS
SP1506	339	12		0.12687	81.10	18.90	33	BEP, BP, DSP, HA, HFC, LD, LYC, RS, SPL, SS, SST
NH1407	340	11		0.06507	94.52	5.48	6	DSP, LYC
NOAA FRAMD_21183	347	9	5.74E-04		74.73	25.27	14	BGR, DSP, LST, SHEL, SPL
NOAA FRAMD_19852	381	16	5.70E-03		60.60	39.40	32	Cmel, DSP, HA, LYC, RS, SBR, SPL, SS, SST
MV1217	389	9		0.10004	47.08	52.92	35	BP, DSP, LD, LYC, RS, SS
NOAA FRAMD_19291	390	14	2.18E-03		54.38	45.62	28	BGR, DSP, HA, HFC, LYC, RS, SAB, SPL, SS, SST
MV1217	403	9		0.05057	27.16	72.84	17	BP, DSP, RS, SPL, SS
MV1217	404	11		0.05088	68.00	32.00	9	BP, DSP, SS
NOAA FRAMD_19514	443	10	2.26E-03		61.45	38.55	27	BGR, Cmel, DSP, HA, LD, RS, SPL, SST
NOAA FRAMD_21182	451	14	2.14E-03		85.18	14.82	20	BGR, DSP, HA, LST, ROC, RS, SHEL, SPL, SST
NOAA FRAMD_20605	474	12	1.11E-03		17.59	82.41	24	BGR, DSP, HA, LST, LYC, PG, SAB, SST
NOAA FRAMD_20871	479	12	5.98E-03		11.12	88.88	18	DSP, HA, LYC, RS, SS, SST
NOAA FRAMD_19850	481	13	6.08E-03		32.65	67.35	28	Cmel, DSP, HA, LD, LST, LYC, RS, SPL, SS, SST
NOAA FRAMD_20979	530	13	4.06E-03		2.13	97.87	20	Cmel, DSP, HA, RS, SPL, SS, SST
NOAA FRAMD_20758	555	11	2.88E-03		0.37	99.63	17	Cmel, DSP, HA, LST, NEZ, SST
NOAA FRAMD_18523	566	10	1.77E-03		20.51	79.49	2	Cmel
NH1414	697	3		0.00620	0.00	100.00	7	LST, NEZ, RNB
NH1414	698	7		0.00587	10.00	90.00	11	BHAG, DSP, LST, PG, RNB
NH1414	705	6		0.02288	0.83	99.17	12	LST, NES, PG, RNB, SST
NOAA FRAMD_22499	754	10	2.34E-03		7.73	92.27	13	CAS, LST, NEZ, PG, TEP
NOAA FRAMD_19276	811	9	3.09E-03		0.32	99.68	19	BHAG, CAS, DSP, EB, LST, NEZ, SST
NOAA FRAMD_19275	834	9	2.01E-03		1.43	98.57	18	CAS, Cmel, DSP, EB, LST, NEZ, SST
NOAA FRAMD_19610	877	10	1.32E-03		17.86	82.14	23	BHAG, CAS, DSP, LST, NEZ, SST, TEP, TSL
NOAA FRAMD_21569	946	10	2.13E-03		18.83	81.17	13	BHAG, CAS, LST, NEZ, SST
NOAA FRAMD_22078	962	13	1.26E-03		4.15	95.85	1	TEP
NOAA FRAMD_20404	1042	13	1.91E-03		2.80	97.20	3	DSP
NOAA FRAMD_21975	1073	16	4.30E-03		5.37	94.63	11	BHAG, CAS, LST, SAB
NOAA FRAMD_19490	1096	12	5.57E-05		38.14	61.86	23	CAS, DSP, HA, LST, NEZ, PG, SST, TEP, TSL
NOAA FRAMD_20503	1261	9	4.90E-04		8.48	91.52	14	CAS, LST, NEZ, SAB, TEP

Table 6.3. Diet data on all demersal fish species that were captured during the 38 otter trawls. For those species that were additionally sampled for stable isotope and gut content analysis, sample numbers are provided, as well as the species category used in figures and tables. Rare and cartilaginous were included in the community analysis but were not sampled for the trophic analysis; these do not have a species category label. Entries are organized alphabetically first by species category, and then by scientific name.

Species	Common name	Category	No. GCA	No. SIA	Benthic or Pelagic	Diet	Diet from GCA	Diet from other references
Lyconema barbatum	Bearded eelpout	BEP	9	12	Benthic	Mainly benthic (B)	Bivalves, polychaetes, crustaceans, gastropods	Bottom-living, nonvisual benthivore (Allen et al. 2006).
Sebastes melanostomus	Blackgill rockfish	BGR	10	11	Pelagic	Mainly pelagic (P)	Midwater teleosts (myctophids), some crustaceans	Blackgill rockfish primarily prey on such planktonic prey as euphausiids and pelagic tunicates, as well as small fishes (e.g., juvenile rockfishes and hake, anchovy, and lantern fishes) and squid (Love et al. 1990, McCain et al. 2005).
Eptatretus deani	Black hagfish	BHAG	0	13	Benthic	Mainly benthic (B)	N/A	Feed on crustaceans, polychaetes, fishes, brittle stars, and decaying whales (Love 2011).
Xeneretmus latifrons	Blacktip poacher	BP	30	33	Benthic	Mixed, but with a preference for benthic prey (MBP)	Decapod shrimp, polychaetes, euphausiids, mysid, copepod, highly digested crustacean tissue is abundant	Feed on gammarids amphipods, euphausiids, and polychaetes, as well as other small crustaceans (Love 2011). Ambushing benthopelagivore (Allen et al. 2006).
Alepocephalus tenebrosus	California slickhead	CAS	24	24	Benthic	Mixed, but with a preference for benthic prey (MBP)	Mainly small crustaceans (unclear if benthic or pelagic), some sediment, polychaetes also present but rarely, some evidence of fish predation	Feed on small crustaceans (FishBase). Fed on isotopically depleted prey, indicative of pelagic items in diet (Boyle et al. 2012).
Careproctus melanurus	Blacktail snailfish	Cmel	20	20	Benthic	Mainly benthic (B)	Crustaceans common, bivalves present, small amounts of teleost, tanaids, mysids, "DB"	Known to feed on polychaete worms, small crustaceans, tiny clams and other invertebrates (FishBase). Feed on crustaceans (shrimp, hermit crabs, and gammarid amphipods), and larger snailfish add fish to their diets (Love 2011). Pursuing benthopelagivore (Allen et al. 2006).
Chilara taylori	Spotted cusk-eel	CT	9	9	Benthic	Mixed, but with a preference for benthic prey (MBP)	Crustaceans most common (stomatopod, euphausiids, decapod shrimp), ophiuroid	Prey on bottom and near-bottom prey. Crabs, gammarid amphipods, euphausiids, and shrimps, along with polychaetes, caprellid amphipods, mysid shrimps, and small fishes (Love 2011). Cruising non-visual benthivore (Allen et al. 2006).
Microstomus pacificus	Dover sole	DSP	77	72	Benthic	Mainly benthic (B)	Bivalves, scaphopods, ophiuroids, gastropods, polychaetes, ostracods, also few crustaceans (mysids, tanaids, amphipods, cumacean)	Eat burrowing organisms and those that live on the seafloor surface, such as polychaetes, various amphipods, brittle stars, and bivalves. Also consumed are ostracods, echiuran, and sipunculid worms, shimps, sea cucumbers, sea urchins, snails, scaphopods, hermit crabs, isopods, and rarely fish (Love 2011). Extracting benthivore (Allen et al. 2006).
Embassichthys bathybius	Deep-sea sole	EB	2	2	Benthic	Mainly benthic (B)	Highly digested reddish tissue	Feed mostly on polychaetes, small crustaceans (mysid shrimps, caprellid and gammarid amphipods), sea anemones, brittle stars, and octopuses (Love 2011).
Parophrys vetulus	English sole	ES	13	11	Benthic	Mainly benthic (B)	*Travisia* polychaetes, ophiuroids, other polychaetes, bivalves, amphipods, tanaids, gastropods, mysids, decapod shrimp	Opportunistic benthic feeders on polychaetes, bivalves (clam and clam siphons), crustaceans (e.g. gammarid and harpacticoid amphipods, mysid shrimps, and shrimps) snails, sand dollars, brachiopods, brittle stars, and fishes (Love 2011). Juveniles feed on harpacticoid copepods and epibenthic crustaceans, adults feed primarily on polychaetes, amphipods, mollusks, cumaceans, ophiuroids, and crustaceans (McCain et al. 2005).
Ophiodon elongatus	Lingcod	GR	3	3	Pelagic	Mixed, but with a preference for pelagic prey (MPP)	Crustacean tissue and carapace	The dominant prey type was Pacific herring, a transient and pelagic species. Numerically, 52% of prey were transient and pelagic, 4% were associated with soft-bottom seafloors, 44% were demersal reef-dwelling species, and of the latter, half were invertebrates (Tinus 2012). Juveniles feed on euphausiids, small fishes, copepods, and crustacean larvae, while larger fish focus on fish, shrimp, octopus, squid, hermit crabs, fish eggs, and hydroids (Love 2011).
Sebastes chlorostictus	Greenspotted rockfish	GSR	3	3	Pelagic	Mainly pelagic (P)	Crustacean tissue and carapace	Prey primarily on planktonic euphausiids and pelagic tunicates, as well as small fishes (e.g., juvenile rockfishes and hake, anchovies, and lanternfishes) and squid (Love et al. 1990).
Merluccius productus	North Pacific hake	HA	46	46	Pelagic	Mainly pelagic (P)	Euphausiids dominant, midwater fish (myctophids), cephalopods, rarely bivalves, ophiuroids, and polychaetes present	Juvenile eat primarily euphausiids and calanoid copepods and minor amounts of other small crustaceans, such as gammarid amphipods and mysid shrimps, as well as small fishes and squids. Larger fishes feed in both midwaters and near the bottom on euphausiids and calanoid copepods and minor amounts of other small crustaceans, as well as a wide range of fishes, and sergestid and pandalid shrimp and squid. Pacific hake can make extensive daily vertical movements; can eat just about everything edible in the water column (Love 2011). Hake take strong diurnal migrations while on feeding grounds, apparently in response to the vertical movements of euphausiids (Stauffer 1985). Juveniles and small adults feed chiefly on euphausiids, and large adults also eat amphipods, squid, herring, smelt, crabs, juvenile Pacific hake, and pelagic schooling fishes (McCain et al. 2005). Schooling pelagivore (Allen et al. 2006).

Table 6.3. Diet data on all demersal fish species that were captured during the 38 otter trawls (continued)

Species	Common name	Category	No. GCA	No. SIA	Benthic or Pelagic	Diet	Diet from GCA	Diet from other references
Sebastes semicinctus	Halfbanded rockfish	HBR	8	6	Pelagic	Mainly pelagic (P)	Euphausiids, copepods, and other crustacean tissue	Water column zooplanktivores (eating euphausiids, copepods, and larvaceans). Can ascend far above the seafloor (Love 2011).
Physiculus rastrelliger	Hundred fathom mora	HFC	11	14	Benthic	Mixed, but with a preference for benthic prey (MBP)	Polychaetes, bivalves, ophiuroids, crustacean tissue	Cruising nocturnal benthopelagivore (Allen et al. 2006).
Sebastes spp. juvenile	Juvenile rockfish	JROC	3	12	Pelagic	Mainly pelagic (P)	N/A	Based on young of the year (YOY) diet data for *Sebastes spp* (Love 2011).
Lycodes diapterus	Black eelpout	LD	7	7	Benthic	Mainly benthic (B)	Bivalves are very common, polychaetes and crustaceans also common, along with harpacticoid copepods	Euphausiids and shrimp (Love 2011). Other *Lycodes spp.* are categorized as excavating benthivores (Allen et al. 2006).
Synodus lucioceps	California lizardfish	LIZ	12	12	Pelagic	Mainly pelagic (P)	Euphausiids dominate, other digested crustacean tissue	Feed primarily on fishes, as well as squid, mysid shrimps, and euphausiids (Love 2011). Categorized as a bottom-living pelagivore (Allen et al. 2006).
Sebastolobus altivelis	Longspine thornyhead	LST	47	48	Benthic	Mainly benthic (B)	Decapod shrimp, tuna crabs, brachyuran crab, polychaetes, ophiuroids, bivalves, mysids, teleost (myctophid or rockfish)	Feed on small invertebrates, such as gammarid amphipods and polychaetes, as they grown they work their way up to fishes, shrimps, crabs, squids, octopuses, and brittle stars (Love 2011). Longspine thornyhead are sit-and-wait predators (Jacobson and Vetter 1996). They consume fish fragments, crustaceans, bivalves, and polychaetes, and occupy a tertiary consumer level in the food web (McCain et al. 2005).
Lycodes spp. (Lycodes cortezianus, Lycodes pacificus)	Eelpout	LYC	33	41	Benthic	Mainly benthic (B)	Bivalves are very common, also polychaetes, crustaceans, gastropods, decapod shrimp, some fish tissue, ophiuroids, cephalopods, euphausiids, mysids, ostracods. Bivalves, ophiuroids, crustaceans, harpacticoid copepod.	Feed on benthic prey such as gammarid amphipods, cumaceans, clams, and polychaetes. Also crabs, shimps, euphausiids, brittle stars, mysid shrimp, and copepods (Love 2011). *Lycodes pacificus* categorized as an excavating benthivore (Allen et al. 2006).
Nezumia spp. (Nezumia liolepis, Nezumia stelgidolepis)	Grenadier	NEZ	29	29	Benthic	Mixed, but with a preference for benthic prey (MBP)	Hyperiid amphipod, amphipod, mysids, decapod shrimp, polychaetes, cephalopod, teleost, "DB", bivalves, copepods, isopods, gastropods	Fed benthically, primarily on crustaceans such as amphipods, shrimp, mysids, crabs, and polychaete worms. Consume snails, bivalves, cephalopods, cumaceans, isopods, hermit crabs, and a few fish (Love 2011). Categorized as a cruising nocturnal benthopelagivore (Allen et al. 2006).
Coryphaenoides acrolepis	Pacific grenadier	PG	7	10	Pelagic	Mixed, but with a preference for pelagic prey (MPP)	Crustaceans common, shrimp, copepods, cephalopods, bivalves also present	Feed in midwaters and bottom. Smaller fish consume primarily polychaetes, amphipods, cumaceans and mysids, while larger individuals consumed increasingly larger, more pelagic prey such as fish, squid, and large crustaceans. Scavenging was also very important for larger individuals (Drazen et al. 2001). Adults often swim well off the bottom, can commonly live 40 m above seafloor.
Plectobranchus evides	Bluebarred prickleback	PRI	3	3	Unknown	Unknown	Crustacean tissue	Unknown
Citharichthys sordidus	Pacific sanddab	PSL	18	15	Pelagic	Mixed, but with a preference for pelagic prey (MPP)	Crustaceans, euphausiids, teleosts, some ophiuroids and polychaetes	Opportunistic predator, feed on wide range of water column and benthic communties. Commonly eaten prey included euphausiids, mysid shrimps, polychaetes, shrimps, gammarid, and hyperiid amphipods, ostracods, crabs, hermit crabs, brittle stars, copepods, clams, pelagic tunicates, squids, and fishes. Swim off the bottom (up to 5 m) (Love 2011). Categorized as pelagobenthivore (Allen et al. 2006).
Cataetyx rubrirostris	Rubynose brotula	RNB	6	9	Benthic	Mainly benthic (B)	Crustacean tissue and carapace, polychaete, amphipod	Unknown
Sebastes spp.	Rockfish	ROC	4	4	Pelagic	Mixed, but with a preference for pelagic prey (MPP)	Highly digested crustacean tissue	Based on other *Sebastes spp.* diets (Love 2011, McCain et al. 2005).
Glyptocephalus zachirus	Rex sole	RS	55	40	Benthic	Mainly benthic (B)	Polychaetes dominant, "DB", bivalves, cehalopod beak, copepods, mysids, crustaceans, amphipods	Polychaetes and gammarid amphipods are most common, also various crabs, euphausiids, cumaceans, fishes, snails, sea urchins, copepods, sipunculids, and the occasional clam. Mostly feeds on or in the seafloor (Love 2011). Categorized as a nonvisual benthivore (Allen et al. 2006).
Anoplopoma fimbria	Sablefish	SAB	9	12	Pelagic	Mixed, but with a preference for pelagic prey (MPP)	Midwater teleosts (myctophids), some crustaceans, a few polychaetes (*Travisia*)	Juveniles are pelagic feeders preying on zooplankton, a few fishes, and squids. Adults are opportunistic feeders, preying on fishes, crustaceans (euphausiids, shimps, crabs, and gammarid amphipods), squids, octopuses, gelatinous zooplankton, polychaetes, and offal (Love 2011). Euphausiids and fish (Pacific herring) are important diet items (McCain et al. 2005). Categorized as a cruising pelagobenthivore (Allen et al. 2006).
Sebastes jordani	Shortbelly rockfish	SBR	3	3	Pelagic	Mainly pelagic (P)	Mostly empty stomachs	Shortbelly rockfish feed primarily on various life stages of euphausiids and calanoid copepods both during the day and night (McCain et al. 2005, Chess et al. 1988, Lenarz et al. 1991). Fish stay near the bottom during the day and then rise up at night to feed (20-70m). Euphausiids are the most important prey, though large numbers of copepods are also eaten. Also taken are larval crustaceans, gammarid and hyperiid amphipods, and arrow worms. Sometimes small fish are also eaten (Love 2006).

Table 6.3. Diet data on all demersal fish species that were captured during the 38 otter trawls (continued)

Species	Common name	Category	No. GCA	No. SIA	Benthic or Pelagic	Diet	Diet from GCA	Diet from other references
Sebastes helvomaculatus	Rosethorn rockfish	SHEL	4	4	Pelagic	Mixed, but with a preference for pelagic prey (MPP)	Tuna crabs, other crustacean tissue and carapace	Off central California, principal prey items are euphausiids and other crustaceans (McCain et al. 2005). Have a varied diet, crabs are very important, and they also eat midwater and benthic shrimp, fishes, hyperiid amphipods, copepods, euphausiids, squids, and pelagic tunicates (Love 2011).
Sebastes diploproa	Splitnose rockfish	SPL	31	31	Pelagic	Mainly pelagic (P)	Euphausiids dominant, midwater fish (hatchetfish), calanoid copepod, amphipods, mysids, salps, *Phronema*	Adult splitnose rockfish off southern California feed on midwater plankton, primarily euphausiids (Allen 1982). Feed almost entirely on midwater and epibenthic crustaceans, translating to a diet heavy in euphausiids and copepods. Pelagic tunicates and pteropods are also consumed but less important. Can swim up off the seafloor up to 100 m (Love 2011).
Lyopsetta exilis	Slender sole	SS	46	45	Pelagic	Mixed, but with a preference for pelagic prey (MPP)	Pelagic crustaceans, euphausiids, tuna crabs, decapod shrimp, bivalves, teleosts, polychaetes, ophiuroids, myctophids, isopods, "DB"	Feed on the bottom and in the water column, preying on crustaceans (e.g. copepods, euphausiids, gammarid amphipods, and shrimps) and polychaetes, and fishes and pelagic tunicates (Love 2011). Categorized as a pelagobenthivore (Allen et al. 2006).
Sebastolobus alascanus	Shortspine thornyhead	SST	32	47	Benthic	Mixed, but with a preference for benthic prey (MBP)	Tuna crabs, brachyuran crabs, decapod shrimp, teleosts, euphausiids, mysids, bivalves, gastropods, polychaetes	Feed on shrimps, mysid shrimps, polychaetes, and amphipods. Larger fish tend to eat fishes and larger crustaceans. Other prey include squid, octopus, brittle stars, hermit crabs, copepods, and arrow worms (Love 2006). Benthic individuals are sit-and-wait predators that rest on the bottom and remain motionless for extended periods of time (Jacobson and Vetter 1996). Variety of benthic invertebrates included in diet such as shrimp, crabs, calanoid copepod, gammarid amphipods, as well as worms. Longspine thornyheads are commonly found in the stomachs of shortspine thornyhead (McCain et al. 2005).
Sebastes saxicola	Stripetail rockfish	STR	13	12	Pelagic	Mainly pelagic (P)	Mainly euphausiids, also crab zoae, and other crustacean tissue	Adult stripetail rockfish pursue pelagic prey such as euphausiids, and juveniles off southern California feed primarily on calanoid copepods (Allen 1982). Maonly planktivores, feeding primarily on euphausiids and calanoid copepods, and occasionally on pelagic tunicates, ctenophores, and other pelagic animals (Love 2011).
Bothrocara brunneum	Twoline eelpout	TEP	10	10	Benthic	Mixed, but with a preference for benthic prey (MBP)	Crustacean tissue and carapace common, small amounts of teleost tissue, decapod	The stomach contents indicate that it feeds upon a wide variety of bottom-dwelling organisms, probably eating anything it encounters that has food value and is small enough to ingest (FishBase). Feed on benthic and epibenthic crustaceans (ie. euphausiids, gammarid amphipods, shrimp, and mysid shrimp), fishes and squid (Love 2011).
Talismania bifurcata	Threadfin slickhead	TSL	5	5	Benthic	Mixed, but with a preference for benthic prey (MBP)	Small teleost, crustacean, "DB"	Unknown
Zaniolepis spp. (Zaniolepis frenata, Zaniolepis latipinnis)	Combfish	ZAN	18	18	Benthic	Mixed, but with a preference for benthic prey (MBP)	Polychaetes, crustacean tissue	Eat a wide range of benthic and epibenthic organisms, such as gammarid amphipods, mysid shrimps, cumaceans, euphausiids, gnathiid isopods, fish eggs, and polychaetes. Also eat scallops, snails, fishes, hydroids, shrimps, nudibranchs, copepods, and crabs (Love 2011). Categorized as a pursuing bottom-living benthopelagivore (Allen et al. 2006).
Zalembius rosaceus	Pink surfperch	ZR	6	6	Benthic	Mixed, but with a preference for benthic prey (MBP)	Bivalves, gastropods, crustacean tissue, amphipod	Feed on planktonic and epibenthic organisms; ostracods, gammarid amphipods, cumaceans are the most important prey items but calanoid copepods, polychaetes, shrimps, brittle stars, and caprellid amphipods, and an occasional fish are also consumed (Love 2011). Categorized as a cruising diurnal benthopelagivore (Allen et al. 2006).
Albatrossia pectoralis	Giant grenadier		0	0	Pelagic	Mixed, but with a preference for pelagic prey (MPP)	N/A	Adults feed mainly on cephalopods, fish and shrimps; other food items include ctenophores, echinoderms, worms, crabs, and amphipods (Cohen et al. 1990). Adults feed on a very wide variety of organisms living both on the bottom and in the water column. Fishes are very important, and other commonly consumed prey include mysid shrimp, euphausiids, brittle stars, octopus, shrimp, crabs, and sea cucumbers (Love 2011).
Antimora microlepis	Finescale mora		0	0	Benthic	Mainly benthic (B)	N/A	Feeds on benthic invertebrates (FishBase).
Apristurus brunneus	Brown catshark		0	0	Pelagic	Mainly pelagic (P)	N/A	Feeds on small true shrimps, euphausiid shrimps, squids, and small fishes (FishBase). Brown cat sharks feed on large numbers of crustaceans (primarily shrimps and pelagic red crabs), fishes and squids, along with isopods, mysid shrimps, and euphausiids (Love 2011).
Bathyraja abyssicola	Deepsea skate		0	0	Benthic	Mixed, but with a preference for benthic prey (MBP)	N/A	Deepwater skates feed on benthic organisms, including annelid worms, cephalopods, tanner crabs, shrimps, and bony fishes (Wikipedia).
Bathyraja kincaidii	Sandpaper skate		0	0	Pelagic	Mixed, but with a preference for pelagic prey (MPP)	N/A	Euphausiids, but shrimps, polychaetes and squids were also important secondary prey (Rinewalt et al. 2007). Diet includes crabs, euphausiids, fishes, hermit crabs, shrimps, octopus, squid, polychaetes, and amphipods (Love 2011).

Table 6.3. Diet data on all demersal fish species that were captured during the 38 otter trawls (continued)

Species	Common name	Category	No. GCA	No. SIA	Benthic or Pelagic	Diet	Diet from GCA	Diet from other references
Bathyraja trachura	Roughtail skate		0	0	Benthic	Mixed, but with a preference for benthic prey (MBP)	N/A	Diet consistes mainly of organisms from benthic (44%) and benthopelagic (39%) habitats, with smaller contributions from pelagic (9%) and infaunal (8%) organisms (Boyle et al. 2012). Polychaetes are a very important part of their diet, also eat fishes, squid, octopus, pandalid shrimp, mysid shrimp, and isopods (Love 2011).
Centroscyllium nigrum	Combtooth dogfish		0	0	Pelagic	Mainly pelagic (P)	N/A	Feeds chiefly on other fishes and invertebrates (FishBase). Feeds on deepwater shrimps, cephalopods, and small mesopelagic bony fishes. Based on the presence of mesopelagic prey items this species may migrate into the water column to feed (Ebert 2003).
Eptatretus stoutii	Pacific hagfish		0	0	Benthic	Mixed, but with a preference for benthic prey (MBP)	N/A	Pacific hagfish feed on a variety of dead or dying organisms, including fish and mammals, but also probably include marine invertebrates in their diet. Consume shrimp, octopuses, sergestiid shrimp, fish parts, polychaetes, amphipods, eggs, and euphaudiids (Love 2011).
Facciolella equatorialis	Dogface witch eel		0	0	Benthic	Mainly benthic (B)	N/A	Feeds on small deep-sea crustaceans. Dives in the mud looking for crustaceans (Love 2011).
Genyonemus lineatus	White croaker		0	0	Benthic	Mixed, but with a preference for benthic prey (MBP)	N/A	Polychaetes are a very important part of their diet, other commonly encountered foods include various crustaceans (gammarid amphipods, crabs, isopods, mysid shrimp, hermit crabs, and shrimp), and fishes, arrow worms, larvaceans, ctenophores, brittle stars, and clam siphons (Love 2011).
Hydrolagus colliei	Spotted ratfish		0	0	Benthic	Mainly benthic (B)	N/A	Feed on mollusks, crustaceans and fishes, also echinoderms and worms (FishBase). Opportunistic feeders with diets on benthic and epibenthic animals -- common prey include fishes, brachyuran and hermit crabs, shrimps, gastropods, sea urchins, polychaetes, bivalves, clam siphons, and isopods (Love 2011).
Kathetostoma averruncus	Smooth stargazer		0	0	Pelagic	Mainly pelagic (P)	N/A	Feeds on ctopus/squid/cuttlefish and bony fishes (Encyclopedia of Life). Feeds mainly on other fishes (FishBase).
Liparidae sp.	Snailfish		0	0	Benthic	Mainly benthic (B)	N/A	Based on other demersal snailfish diets (Love 2011).
Paraliparis cephalus	Swellhead snailfish		0	0	Benthic	Mainly benthic (B)	N/A	Unknown for this species. The diet of snailfish consists primarily of benthic crustaceans, mollusks, polychaete worms (Love 2011).
Pleuronichthys verticalis	Hornyhead turbot		0	0	Benthic	Mainly benthic (B)	N/A	Feed on polychaetes, clam siphons, crabs, amphipods, sea anemones, brachiopods, snails, nemerteans, and fishes (Love 2011).
Porichthys notatus	Plainfin midshipman		0	0	Pelagic	Mainly pelagic (P)	N/A	Nocturnal predators that feed primarly on midwater crustaceans: euphuasiids, gammarid amphipods, mysid shrimps, ostracods, and copepods. Also squids, crabs, polychaetes and fishes are consumed (Love 2011). Categorized as a bottom-refuge, nonvisual pelagivore (Allen et al. 2006).
Raja rhina	Longnose skate		0	0	Pelagic	Mixed, but with a preference for pelagic prey (MPP)	N/A	Five most important prey items in 618 stomachs of *R. rhina* were unidentified teleosts (31.6% IRI), unidentified shrimps (19.6% IRI), unidentified euphausiids (10.9% IRI), Crangonidae (7.4% IRI), and *Neocrangon resima* (6.0% IRI) (Robinson et al. 2007). Eat a lot of fishes, crabs, shrimps, and hermit crabs, along with some euphausiids, mantis shrimp, snails, squids, and octopuses (Love 2011). Characterized as a nonvisual benthivore (Allen et al. 2006).
Scorpaena guttata	California scorpionfish		0	0	Benthic	Mixed, but with a preference for benthic prey (MBP)	N/A	The main food items of the California scorpionfish are juvenile cancer crabs, small fishes such as the northern anchovy, octopus, isopods, the ridgeback prawn and shrimp (Love et al. 1987, McCain et al. 2005).
Sebastes aurora	Aurora rockfish		0	0	Pelagic	Mixed, but with a preference for pelagic prey (MPP)	N/A	Unknown, but assumed to be similar to other rockfish species
Sebastes dallii	Calico rockfish		0	0	Pelagic	Mixed, but with a preference for pelagic prey (MPP)	N/A	Feed on benthic and epibenthic crustaceans (copepods, shrimps, mysiid shrimps, gnathiid isopods, hyperiid amphipods). Also consume crabs, fishes, bivalves, octopuses. Adults feed on larger crustaceans such as euphausiids, fishes, and cephalopods (Love 2011).
Sebastes elongatus	Greenstriped rockfish		0	0	Pelagic	Mixed, but with a preference for pelagic prey (MPP)	N/A	Juvenile and adult greenstriped rockfish prey upon planktonic prey such as euphausiids, copepods, and pelagic tunicates, as well as small fishes (e.g., hake, anchovies, and lanternfishes), shrimp, and squid (Allen 1982). Feed both on water column and benthic prey: midwater shrimp (sergestiids), euphausiids, fishes, crabs, and shrimps are most important. Hyperiid amphipods, copepods, mysid shrimp, crustacean larvae, and squid are also diet items (Love 2011). Feed on euphausiids (mostly *E. pacifica*) in the Southern CA Bight (Genin et al. 1988).

Table 6.3. Diet data on all demersal fish species that were captured during the 38 otter trawls (continued)

Species	Common name	Category	No. GCA	No. SIA	Benthic or Pelagic	Diet	Diet from GCA	Diet from other references
Sebastes goodei	Chilipepper rockfish		0	0	Pelagic	Mainly pelagic (P)	N/A	Are somewhat opportunistic feeders, preying on copepods and euphausiids. In California, adults prey on large euphausiids, squid, and small fishes such as anchovy, lanternfishes, and young hake (Love et al. 1990, McCain et al. 2005). Can swim well up into the water column or sit on the bottom. Appear to more or less feed exclusively in the water column - fishes, euphausiids, and squids make up most of their diet (Love 2011). Feed on euphausiids (mostly *E. pacifica*) in the Southern CA Bight (Genin et al. 1988).
Sebastes rosaceus	Rosy rockfish		0	0	Benthic	Mixed, but with a preference for benthic prey (MBP)	N/A	Rosy rockfish primarily eat small, bottom-dwelling animals, such as shrimp and crabs (Love 1996). Feed on both benthic and midwater prey including shrimps, euphausiids, gelatinous zooplankton, and small fishes (Love 2011).
Sebastes rufus	Bank rockfish		0	0	Pelagic	Mainly pelagic (P)	N/A	Bank rockfish are midwater feeders, eating mostly gelatinous planktonic organisms such as tunicates, but also preying on small fishes and krill (Love 1992). Feed on euphausiids (mostly *E. pacifica*) in the Southern CA Bight (Genin et al. 1988).
Somniosus pacificus	Pacific sleeper shark		0	0	Benthic	Mixed, but with a preference for benthic prey (MBP)	N/A	Arrowtooth flounder, *Atheresthes stomias* , was the most important prey, representing 67% of the total stomach content weight (Yang and Page 1999). Squids are very important in their diets, fishes, octopuses, some marine mammals, crabs, snails, sponges, hermit crabs (Love 2011).
Symphurus atricaudus	California tonguefish		0	0	Benthic	Mainly benthic (B)	N/A	Nocturnal feeders that focus on soft-bottom small crustaceans (gammarid amphipods, crabs, polychaetes, harpacticoid and caprellid amphipods, gnathiid isopods, cumaceans, isopods, snails, and brittle stars) (Love 2011). Categorized as a nonvisual benthivore (Allen et al. 2006).
Torpedo californica	Pacific electric ray		0	0	Benthic	Mixed, but with a preference for benthic prey (MBP)	N/A	The Pacific electric ray feeds mainly on bony fishes, including anchovies, herring, hake, mackerel, croakers, rockfishes, surfperches, kelp bass, and flatfishes, but will also take cephalopods and invertebrates given the opportunity (Wikipedia, Ebert 2003).

Table 6.4. Compound-specific stable isotope (CS-SIA) results ± Sd (n). * shows significance between oxygen zones at the 0.02 level.

	Shortspine thornyhead	**California slickhead**	**Longspine thornyhead**	**Hundred fathom codling**	**Rubynose brotula**
Phenylalanine					
Not OMZ	8.22 ± 1.26 (3)			8.04 ± 0.4 (3)	
Outer OMZ	8.46 ± 0.38 (6)	9.42 ± 1.05 (4)	7.77 ± 0.57 (6)		
OMZ Core	9.17 ± 0.56 (3)	9.04 ± 0.62 (4)	8.1 ± 0.72 (3)		8.05 ± 0.96 (4)
Glycine					
Not OMZ	7.78 ± 0.11 (3)			8.88 ± 0.67 (4)	
Outer OMZ	6.96 ± 1.49 (6)	6.87 ± 0.9 (4)*	5.16 ± 0.73 (6)		
OMZ Core	6.96 ± 0.15 (3)	9.99 ± 0.96 (4)*	5.01 ± 0.7 (3)		7.72 ± 0.65 (4)
Glutamic Acid - Phenylalanine					
Not OMZ	19.37 ± 0.41 (3)*			20.5 ± 0.76 (3)	
Outer OMZ	21.7 ± 1.32 (6)	22.85 ± 1.06 (4)*	20.85 ± 0.65 (6)		
OMZ Core	22.74 ± 1.65 (3)*	20.12 ± 0.36 (4)*	21 ± 0.59 (3)		20.84 ± 0.6 (4)
Glutamic Acid - Glycine					
Not OMZ	19.81 ± 0.96 (3)*			19.78 ± 1.79 (3)	
Outer OMZ	23.2 ± 2.42 (6)	25.4 ± 0.92 (4)*	23.46 ± 1.11 (6)		
OMZ Core	24.95 ± 1.04 (3)*	19.18 ± 0.89 (4)*	24.1 ± 1.1 (3)		21.16 ± 0.65 (4)

Figures

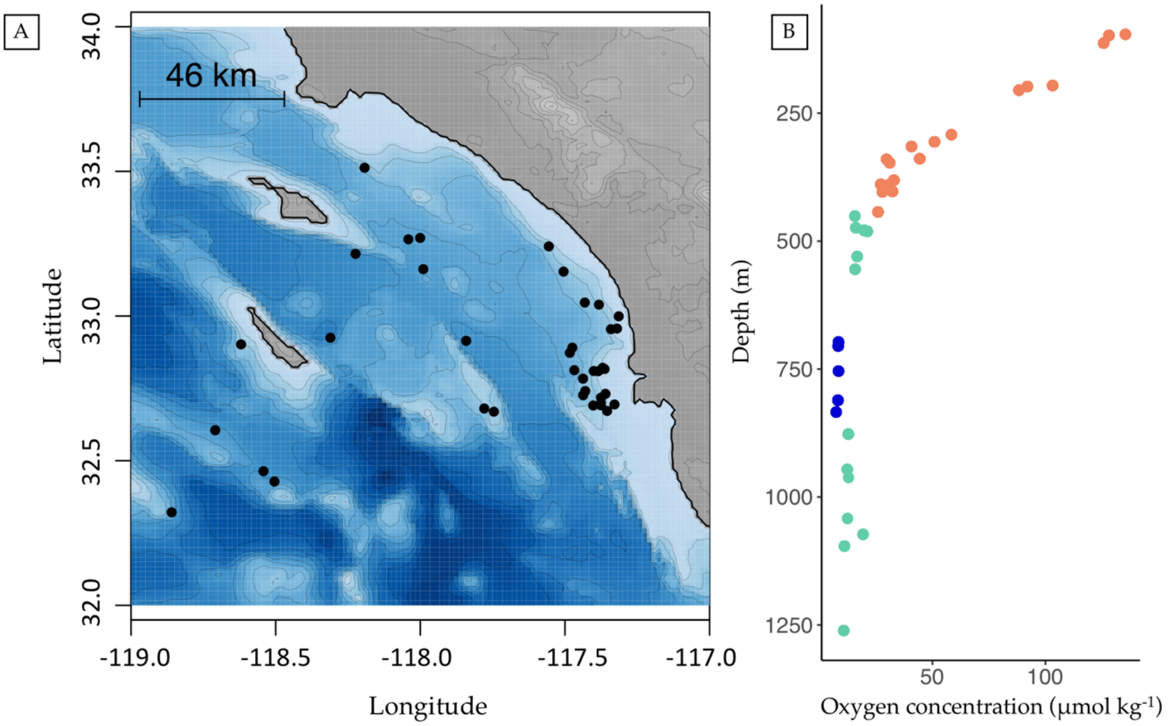


Figure 6.1. Location and oxygen conditions for all otter trawls included in this study. All otter trawls included in this study (n = 38) were done in the Southern California Bight (A) at depths between 96-1261 m (Table 6.1). This region is characterized by the presence of an oxygen minimum zone (OMZ), with an upper boundary around 450 m. The near-bottom oxygen conditions for each trawl are shown (B), color-coded by non-OMZ samples (salmon), OMZ samples (turquoise), and OMZ core samples (dark blue). Trawl samples capture the oceanographic dissolved oxygen profile characteristic for this region.

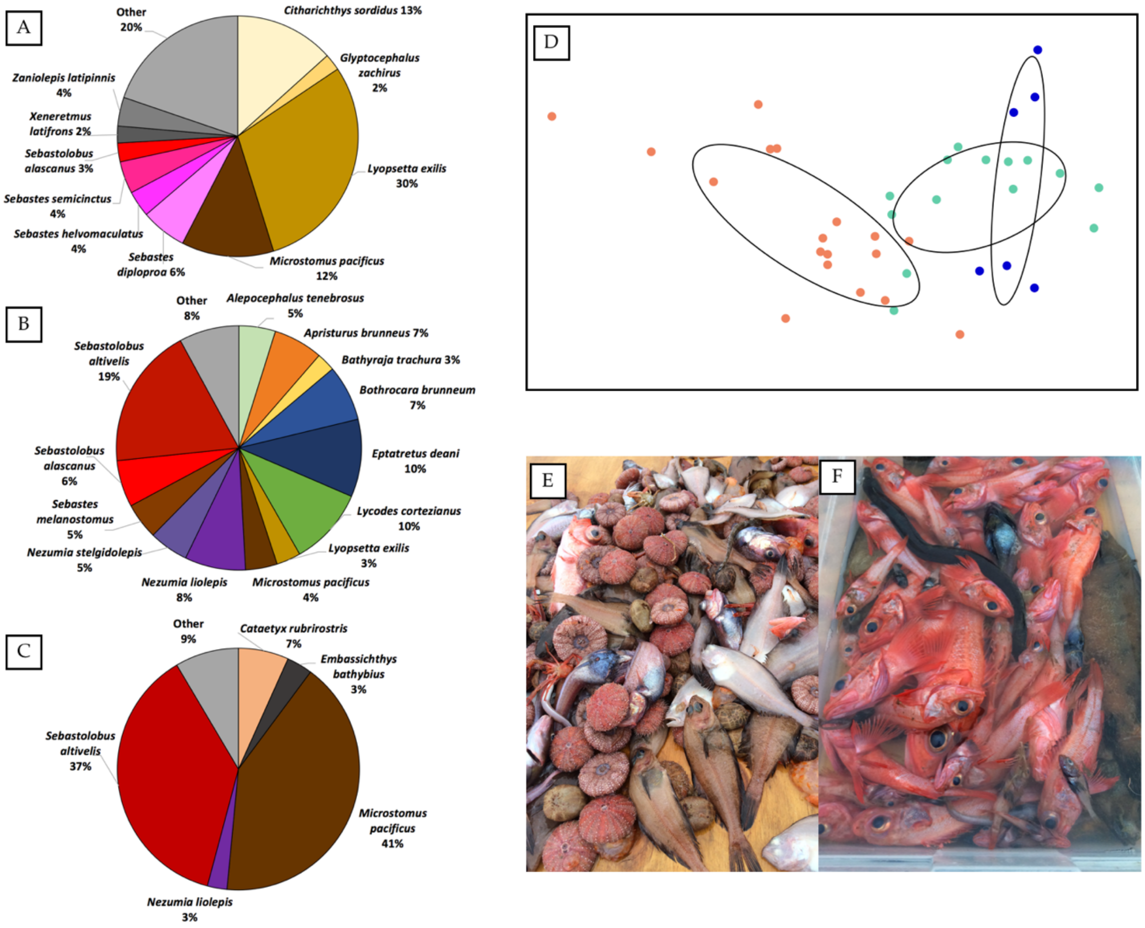


Figure 6.2. Demersal fish community composition differs across oxygen gradients in the Southern California Bight. Pie charts show community composition of different species for trawls outside of the oxygen minimum zone (OMZ) (A), within the upper and lower boundary of the OMZ (B) and within the OMZ core (C). Non-metric multidimensional scaling (D) shows that demersal fish communities in the OMZ upper and lower boundary (turquoise) and the OMZ core (dark blue), are distinct from communities outside of the OMZ (salmon). Ellipses represent 50% confidence intervals and points represent the demersal fish community from each otter trawl (n=38). Photographs show a representation of the demersal fish community at 340 m (E) outside of the OMZ, and at 700 m (F), from the OMZ core.

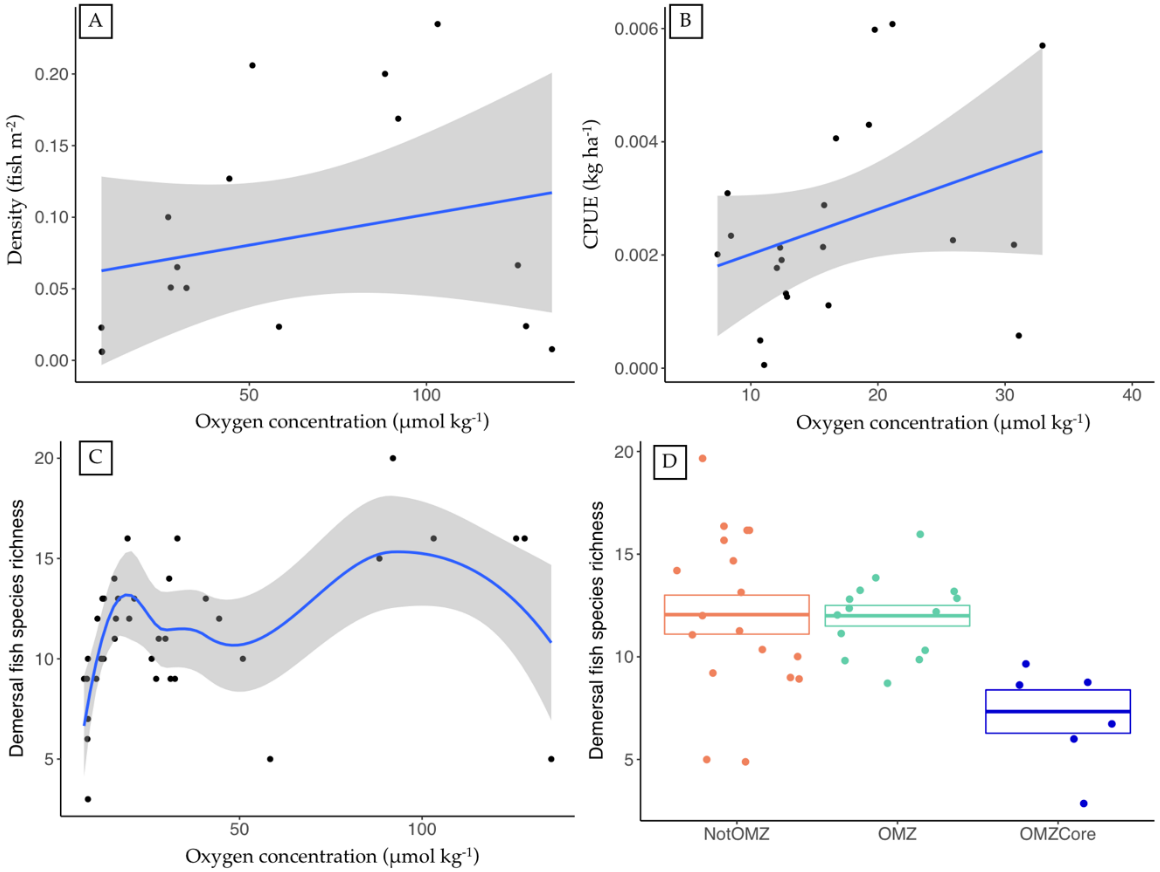


Figure 6.3. Relationship between demersal fish community metrics and oxygen exposure regime in the Southern California Bight. The density (A) and catch per unit effort (CPUE) (B) of the demersal fish community exhibit a positive, though non-significant, relationship with dissolved oxygen (LR, $p = 0.36$ and $p = 0.12$ respectively). Demersal fish density is provided for otter trawls conducted on SIO cruises (n=17) and CPUE is provided for trawls conducted as part of the NOAA groundfish trawl survey (n=21). The species richness of the demersal fish community declines under low oxygen conditions within the oxygen minimum zone (OMZ) (C), though this difference is only statistically significant within the OMZ core ($O_2 <$ 10 µmol kg^{-1}) (D) (Tukey HSD, $p < 0.05$). Points represent community metrics from individual otter trawls (n=38).

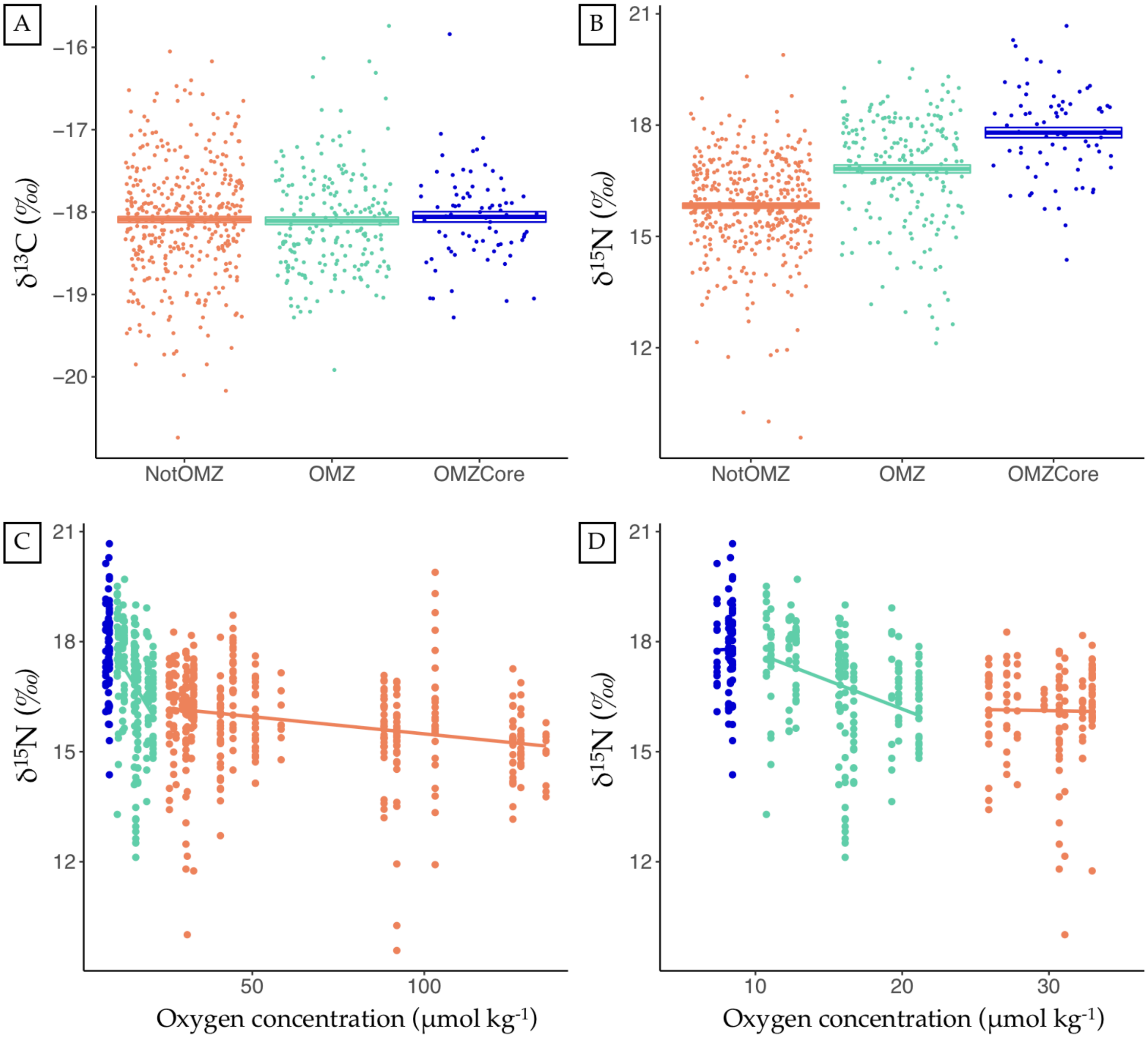


Figure 6.4. Relationship between demersal fish isotopic signatures and oxygen exposure regimes. The mean carbon isotopic signature of the demersal fish community does not change within the oxygen minimum zone (OMZ) or OMZ core (A) (ANOVA, $p = 0.866$), suggesting that the base of the food web does not change and that chemosynthetic production is not being utilized by the demersal fish community in the OMZ or OMZ Core. In contrast, the mean nitrogen isotopic signature of the demersal fish community does become enriched in the OMZ and the OMZ core (B) (ANOVA, $p < 0.001$, Tukey's HSD $p < 0.001$ for all comparisons). Upper panels show mean +/- se, and points are individual datapoints for each individual fish (n=660). Bottom panels show δ^{15}N signatures for individuals ($n = 660$), regressed with respect to the oxygen environment they were captured in (C, D). The enrichment in δ^{15}N appears to be strongly correlated with oxygen conditions, however this relationship is non-linear across the range of oxygen values sampled across, and seems to be especially pronounced within the oxygen gradient between 10-20 μmol kg^{-1} (D).

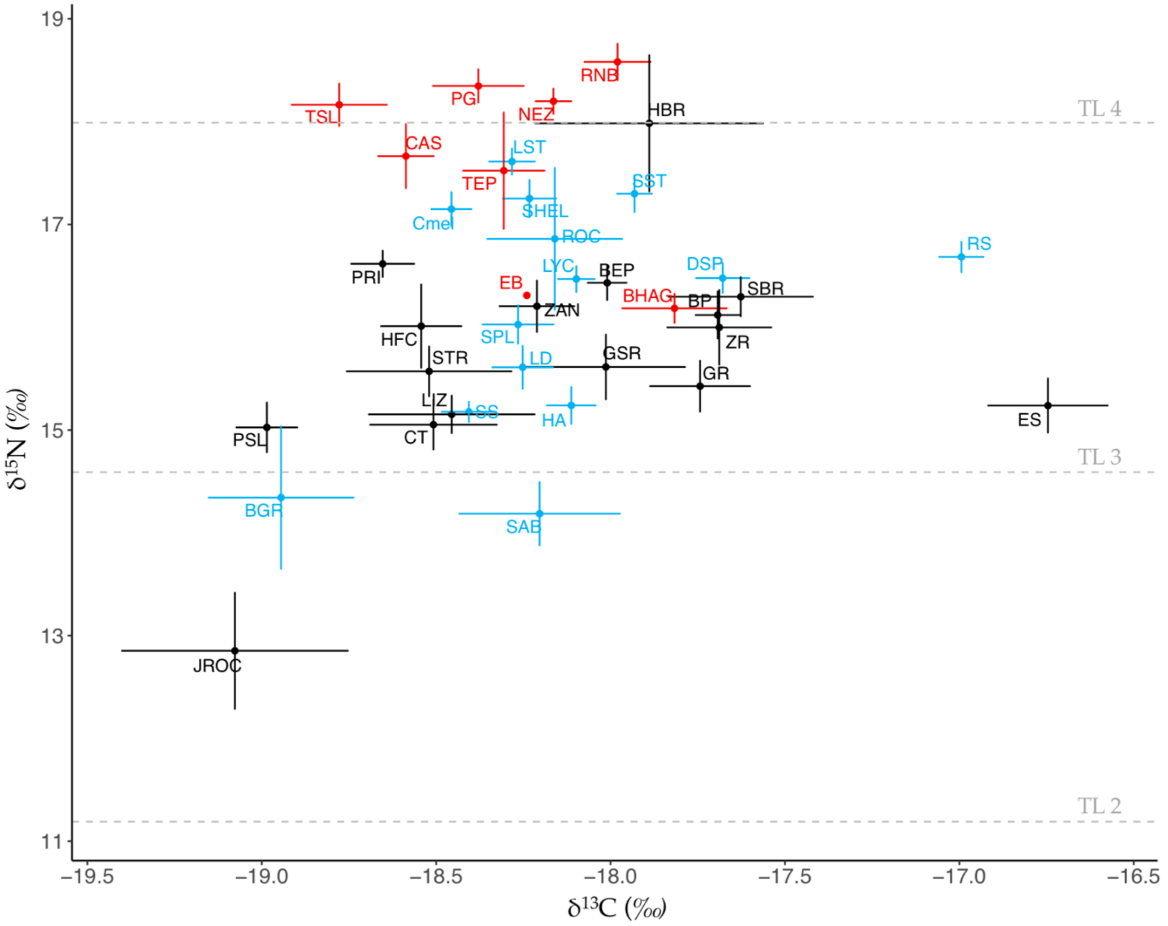


Figure 6.5. Mean δ^{13}C and δ^{15}N signatures for demersal fish species included in the study. Demersal fish species that only live in the OMZ (red), have more enriched δ^{15}N signatures than species that were captured only outside of the OMZ (black), or species that were captured both inside and outside of the OMZ (blue). These OMZ-dwelling species appear to be feeding at a higher trophic level. Data points represent species means, error bars represent standard error of the mean. See Table 6.2 for species codes and sample numbers. Dashed grey lines represent an average calculated trophic position, based on the average isotopic signature of the fish species relative to the average isotopic signature of filtered POM.

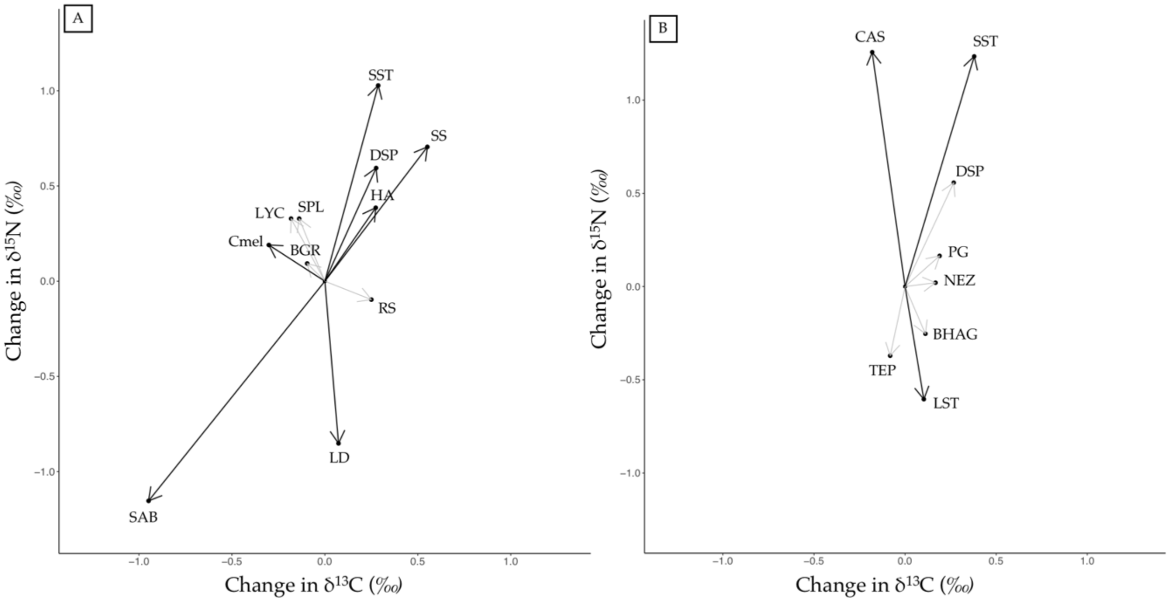


Figure 6.6. Intraspecies isotopic shifts across oxygen exposure regimes. Demersal fish species that span the OMZ had enriched isotopic signatures in the lower oxygen habitats of their range, consistent with community-level patterns. Figures show the intra-species shift in $\delta^{13}C$ and $\delta^{15}N$ between higher and lower oxygen habitats, calculated as the difference between mean isotopic signature in the OMZ compared to outside of the OMZ (A) and difference between mean isotopic signature in the OMZ core compared to the upper and lower OMZ (B). Darker lines represent shifts that were statistically significant for either $\delta^{13}C$ and $\delta^{15}N$ at the $p < 0.1$ significance level, using a non-parametric Kruskal-Wallis rank sums test. See Table 2 for species codes. Axis ranges are the same for both figure panels.

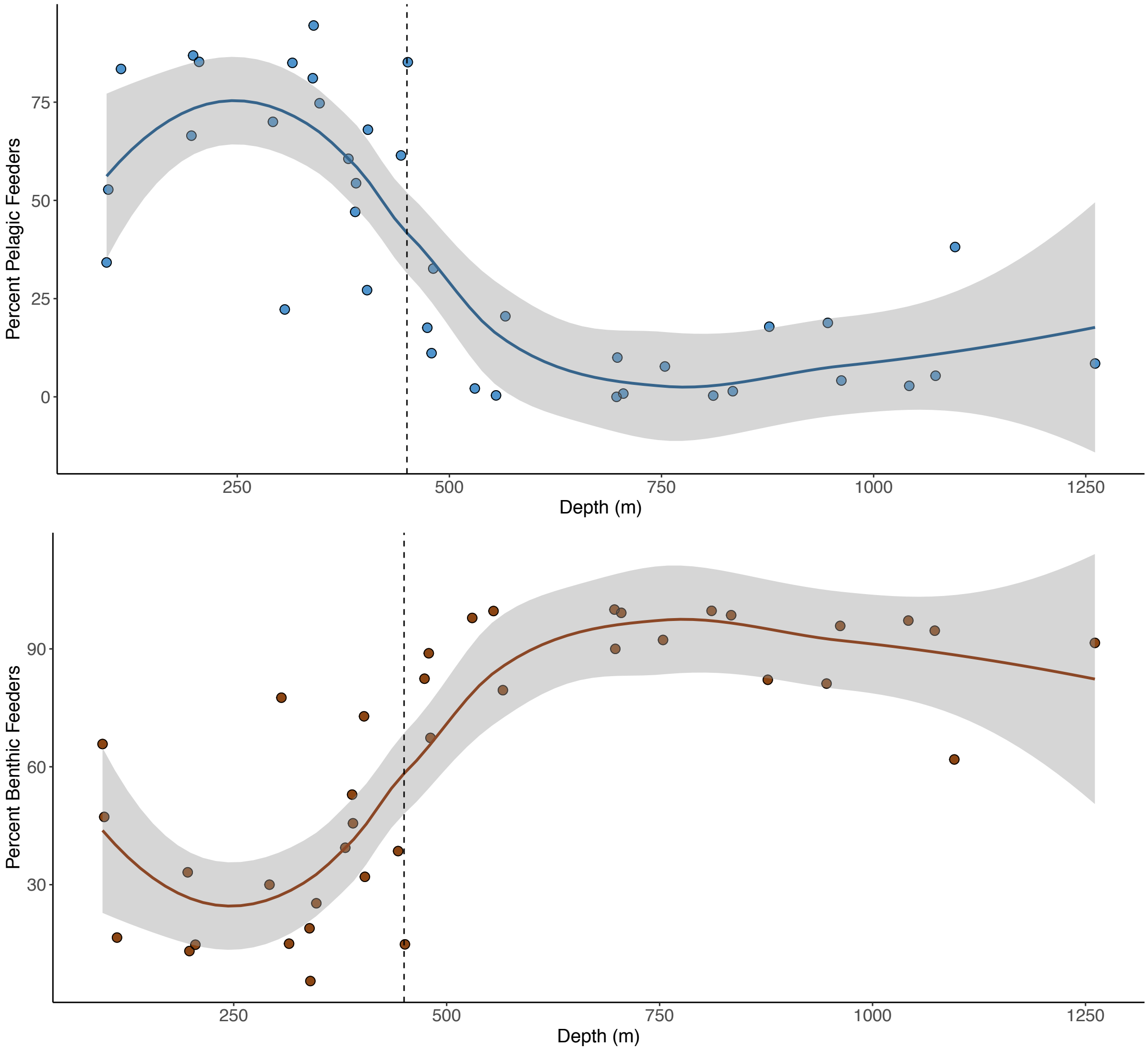


Figure 6.7. Cross-margin shift in the importance of pelagic or benthic feeding for the demersal fish community. The dominant feeding mode of the demersal fish community changes from primarily pelagic to primarily benthic. This change in dominant feeding mode coincides with the upper boundary of the oxygen minimum zone (OMZ), indicated with a dashed line. Each point represents a trawl sample (n = 38), with the percent benthic or pelagic feeders within the whole demersal fish community sampled by each trawl indicated.

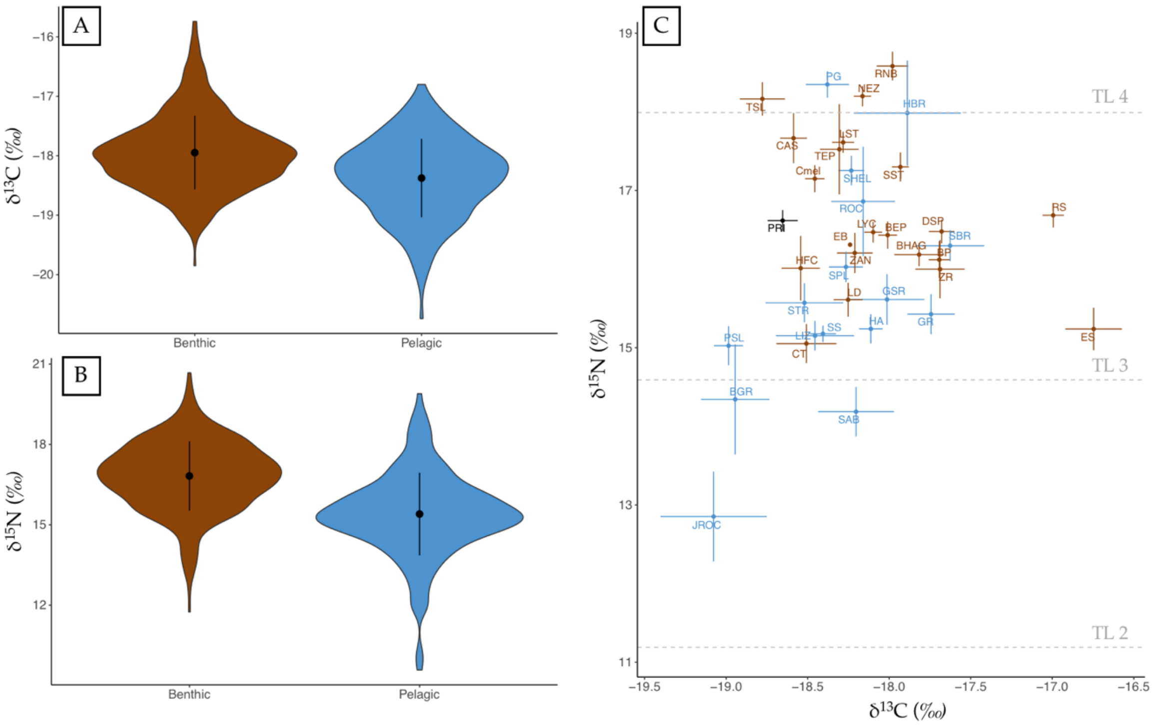


Figure 6.8. Relationship between isotopic signatures and benthic- or pelagic-feeding demersal fish species. Demersal fish that are predominantly benthic feeders show a more enriched carbon (A) and nitrogen (B) isotopic signature than the pelagic feeders. Violin plots with mean +/- 1 SD shown for all individual fish categorized by species *a priori* as benthic or pelagic feeders. Differences are statistically significant for both $\delta^{13}C$ (ANOVA, $p < 0.001$) and $\delta^{15}N$ (ANOVA, $p < 0.001$) between benthic ($n = 440$) and pelagic ($n = 217$) feeders. Species that were *a priori* categorized as benthic feeders (brown) have more enriched $\delta^{15}N$ signatures on average than those categorized as pelagic feeders (blue), and appear to be feeding at a higher trophic level (C). C-N biplot shows the mean value for each species ± 1 standard error. Species names are shown in Table 6.2.

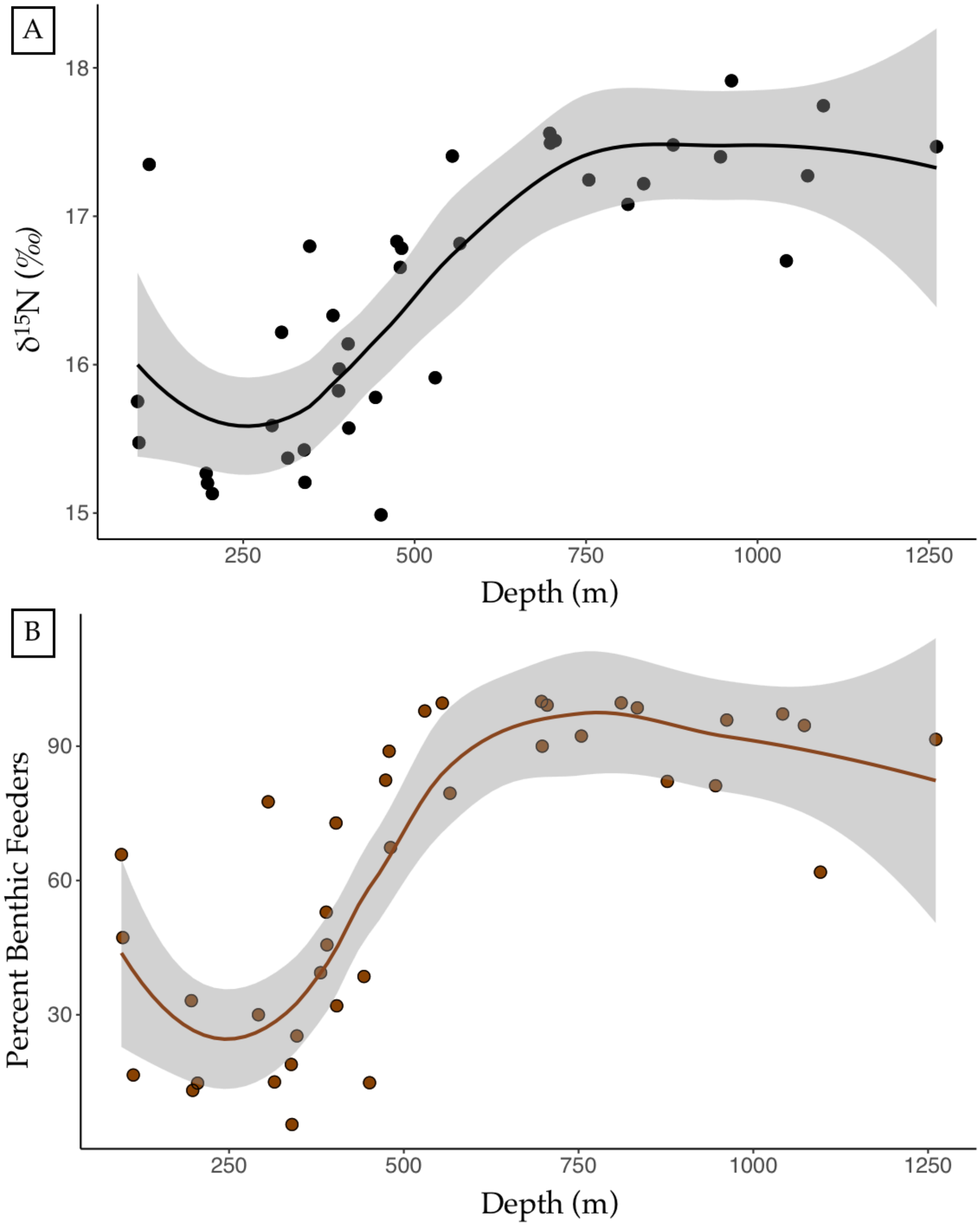


Figure 6.9. Cross-margin shift in mean isotopic signatures and dominant feeding type. The enrichment in δ^{15}N with depth observed for the demersal fish community (A), coincides with a shift in feeding mode from predominantly pelagic to predominantly benthic (B). Points represent community composition from otter trawls (n = 38). For (A), a mean δ^{15}N isotopic signature was calculated for each demersal fish community, using community composition data and mean δ^{15}N isotopic signatures for species in the community. For (B), the percentage of benthic feeders in each otter trawl sample is shown.

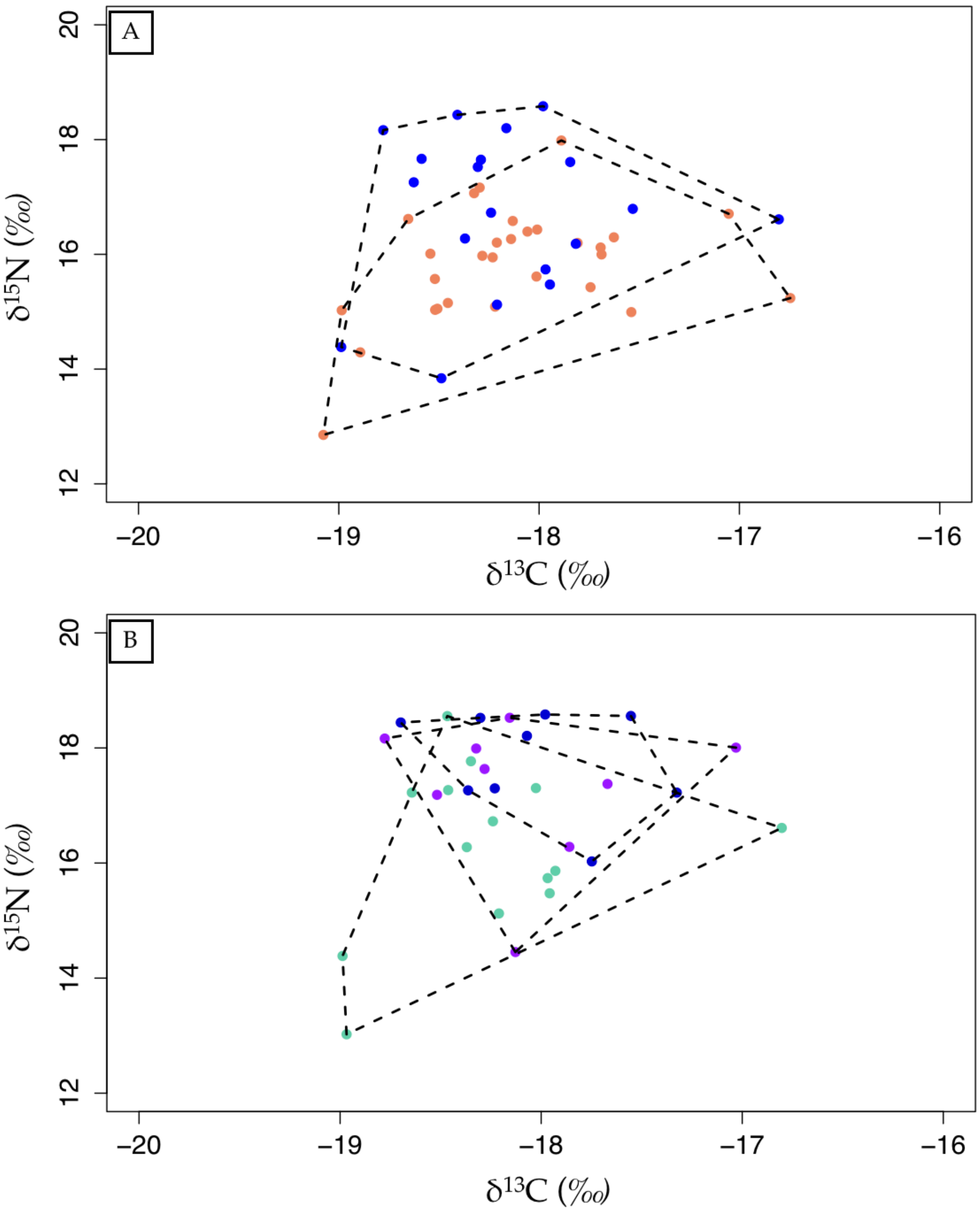


Figure 6.10. Layman convex hulls demarcate the trophic niches of demersal fish communities across different oxygen habitats. Contrary to our hypothesis, we found that the convex hull area is similar (A) between the demersal fish community above the OMZ (coral) and within the OMZ (blue). However, when looking more closely at different zones within the OMZ (B), we find that the trophic niche breadth of the demersal fish community in the OMZ core is smaller (blue points), than that in the OMZ lower boundary (purple dots), and the OMZ upper boundary (green dots). Points represent individual species means.

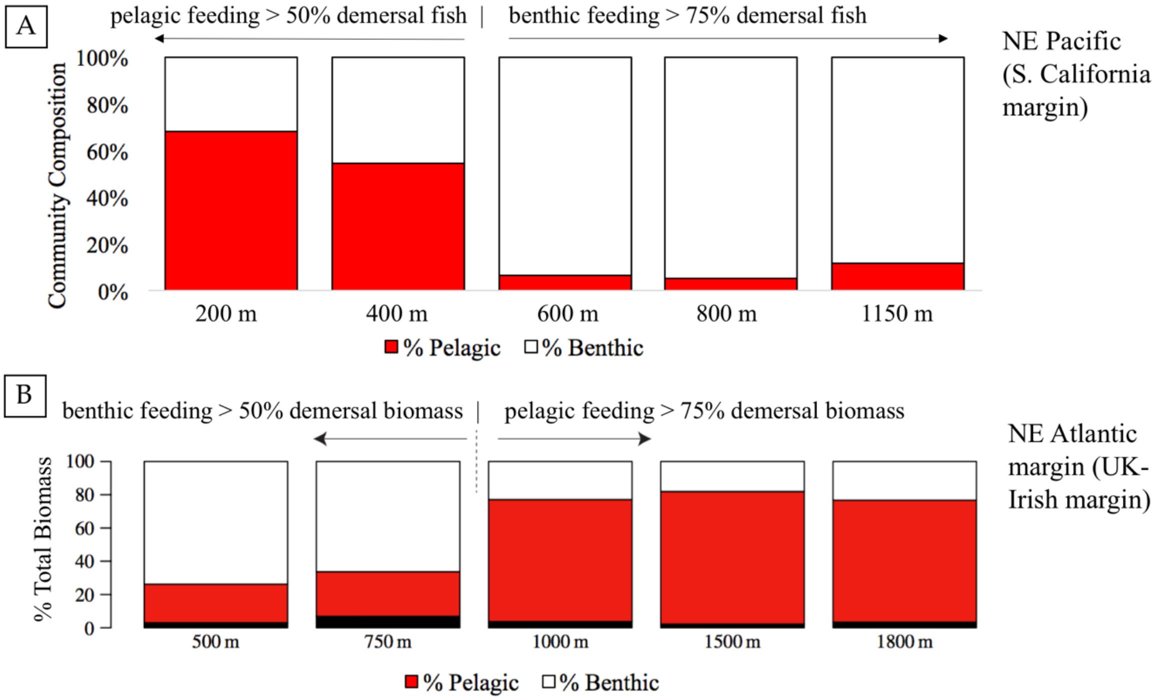


Figure 6.11. Comparison of demersal fish community trend in dominant feeding types for an upwelling margin compared to a non-upwelling margin. In the Southern California Bight, the dominant feeding mode used by demersal fish shifts from being pelagic to benthic with increasing water depth across the margin (A). This pattern contrasts with the more typical pattern described for continental margins without OMZs, where reliance of the demersal fish community on pelagic production increases at depths below 500 m, as shown for the NE Atlantic margin by Trueman et al. (2014) (B). We hypothesize that this difference is related to the shallowing of the daytime depth of the DVM community in areas with OMZs, which prevents demersal fish living deeper than the upper OMZ boundary from accessing the abundant midwater prey items that sustain deeper demersal fish communities on margins without OMZs. For panel (A) an average community composition of pelagic or benthic feeders was calculated for each depth zone, based on otter trawl data (n = 38), and the median depth for each zone is indicated. Note that the Trueman et al. (2014) study shown in panel (B) looks at a deeper depth range (500-1800 m) than this study (100-1300 m).

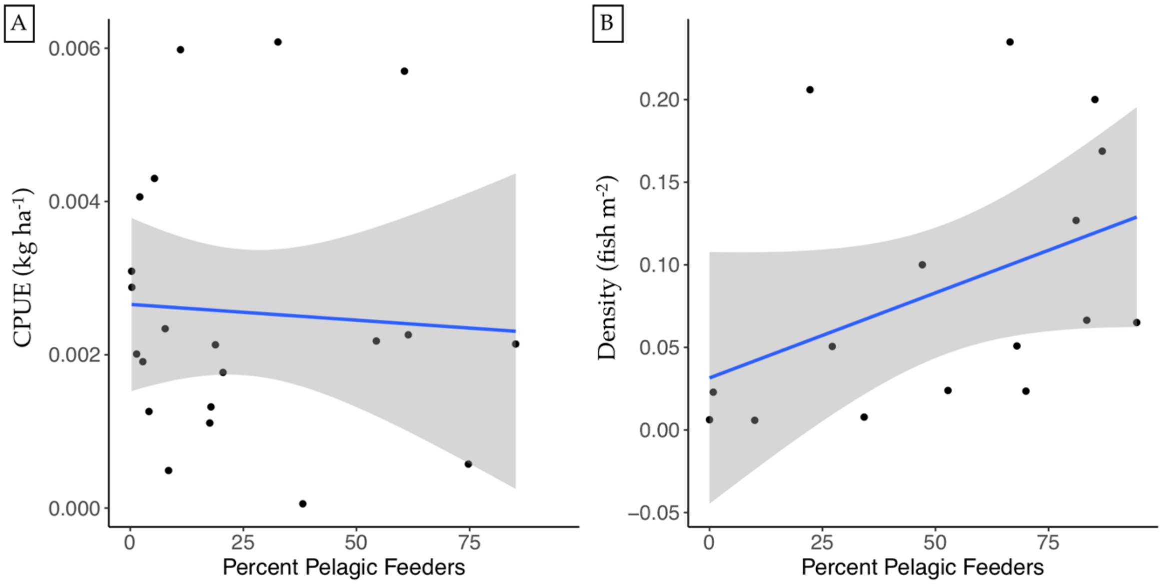


Figure 6.12. The relationship between proportion of pelagic feeders and (A) catch per unit effort (CPUE) and (B) fish density. No statistically significant linear relationship was found (LR, $p > 0.05$).

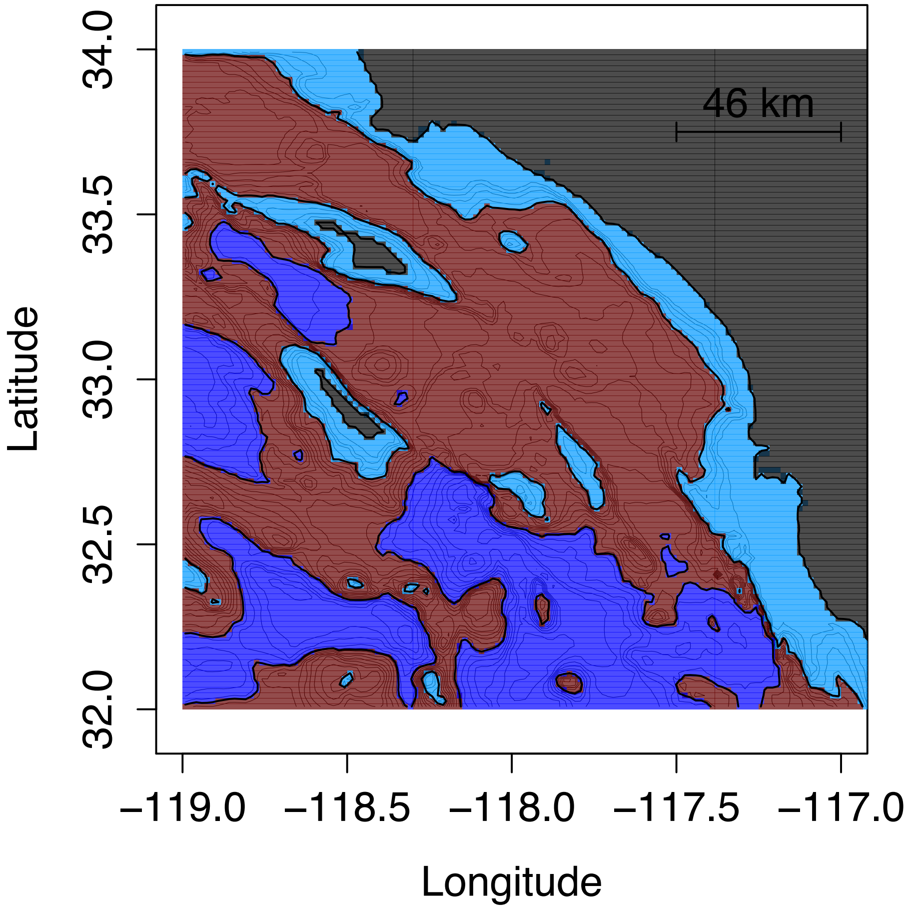
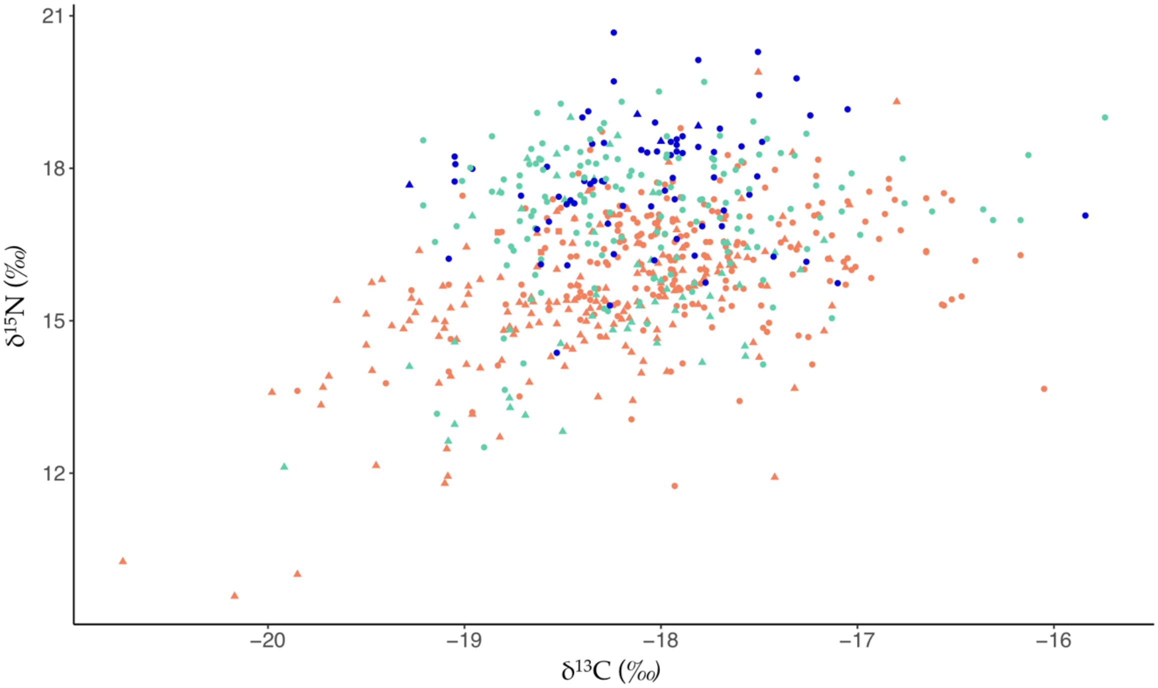


Figure 6.13. Seafloor area in the Southern California Bight exposed to different oxygen conditions. More than 50% of the seafloor in the Southern California Bight is exposed to oxygen minimum zone (OMZ) conditions (brown). Only ~20% of the seafloor in the Southern California Bight is at depths shallower than the upper boundary of the OMZ (light blue), and in these areas the DVM community likely plays an important role in supporting demersal fish production. The OMZ was defined as occurring between depths of 450-1250 m, and total bathymetric surface area was calculated between pre-assigned depth zones. The surface area determined for above the OMZ (light blue), within the OMZ (brown), and below the OMZ (purple) is 6,076 km^2, 17,412 km^2, and 8,354 km^2, respectively. Land area is shown in gray.

Chapter 6 Appendix



Supplementary Figure 6.1. Carbon and nitrogen isotopic signatures for all demersal fish individuals included in the stable isotope analysis (n = 660). δ^{13}C are lipid corrected for individuals that had a C:N ratio > 3.8 and outliers are removed. Data points are color coded by oxygen habitat that individuals were captured from (salmon = outside of the OMZ (n = 384), turquoise = in the upper or lower boundary of the OMZ (n = 201), and dark blue = within the OMZ core (n = 75)). Point shapes represent if individuals were from species categorized as predominantly benthic feeders (circles, n = 440), predominantly pelagic feeders (triangles, n = 217), or unknown (squares, n = 3).

CHAPTER 7

Ocean commitments under the Paris Agreement

Natalya D. Gallo, David G. Victor, Lisa A. Levin

nature climate change

ARTICLES

Ocean commitments under the Paris Agreement

Natalya D. Gallo[1,2]*, David G. Victor[3,4,5] and Lisa A. Levin[1,2]

Under the Paris Agreement nations made pledges known as nationally determined contributions (NDCs), which indicate how national governments are evaluating climate risks and policy opportunities. We find that NDCs reveal important systematic patterns reflecting national interests and capabilities. Because the ocean plays critical roles in climate mitigation and adaptation, we created a quantitative marine focus factor (MFF) to evaluate how governments address marine issues. In contrast to the past, when oceans received minimal attention in climate negotiations, 70% of 161 NDCs we analysed include marine issues. The percentage of the population living in low-lying areas—vulnerable to rising seas—positively influences the MFF, but negotiating group (Annex 1 or small island developing states) is equally important, suggesting political motivations are crucial to NDC development. The analysis reveals gaps between scientific and government attention, including on ocean deoxygenation, which is barely mentioned. Governments display a keen interest in expanding marine research on climate priorities.

The decision by 195 countries to adopt the Paris Agreement[1] at the 21st Conference of the Parties (COP) on 12 December 2015 marked a historic turning point for climate change policy and a major success in multilateral diplomacy[2]. Unlike the Kyoto Protocol adopted nearly two decades earlier, the Paris Agreement includes prominent focus on impacts of climate change and adaptation[3]. This shift is potentially auspicious for policy attention to the oceans and marine ecosystems. Despite the central role the ocean plays in regulating the climate and absorbing anthropogenic CO_2 emissions[4,5], prior to Paris, climate diplomacy devoted scant attention to the ocean[6,7]. Although the 1992 UNFCCC formally recognized the importance of marine ecosystems as sinks and reservoirs of greenhouse gases[8], ocean, marine, or coastal ecosystems were largely left out of subsequent COP negotiations[6,7]. Paris represented a significant turning point for recognition of the oceans within the climate negotiations[9], evidenced by an increase in ocean-related side events, greater participation of ocean scientists and non-governmental organizations, and the signing of the 'Because the Ocean' declaration by 22 Parties[10]. Furthermore, in contrast to the Kyoto Protocol (1997)[11] in which marine systems are not formally recognized, the Paris Agreement[1] explicitly includes the ocean within the Preamble.

We assess empirically whether and how the Parties to the Paris Agreement are focusing on the ocean and marine ecosystems. To do that, we take advantage of a novel institutional feature at the centre of the Paris Agreement: pledge and review, covered in Article 4 of the Paris Agreement[1]. Unlike earlier attempts to negotiate climate accords, prior to the Paris meeting nearly all countries submitted 'intended nationally determined contributions (INDCs)' to indicate their national strategies for climate action[12]. Countries were encouraged to submit their strategies for reducing greenhouse gas emissions (that is, mitigation component) and invited to communicate undertakings in climate adaptation planning (that is, adaptation component) in their INDCs. These INDCs—which become simply NDCs as each country formally joins the Paris Agreement—are the basic building blocks for implementing the Paris Agreement and reflect the highest possible ambition. Parties may adjust their NDCs at any time, but must revise and update NDCs every five years. The NDCs provide a window into how governments view their climate policy priorities, thus opening a gold mine of information with nearly global coverage that was previously unavailable to scholars, who have struggled to obtain reliable, systematic information about national preferences[12].

As of June 2016, 161 governments had filed NDCs[13], of which 70% include some mention of marine issues (Fig. 1). This group of 161 covers 188 nations, since the NDC from the European Union spans all 28 EU members[14]. The majority (103) of ocean-inclusive NDCs focus on climate change impacts and adaptation needs in marine areas. Of those Parties that ignore the oceans in their NDCs, 14 are coastal, some with very large Exclusive Economic Zones (EEZs) such as Australia, Brazil, the European Union, Micronesia, New Zealand, Norway, the Russian Federation, and the United States of America.

Marine-focused sections of NDCs were read and specific categories involving marine ecosystems intersection with climate change policy were identified. The dominant concerns raised by governments were coastal impacts (95 NDCs), ocean warming impacts (77 NDCs), and fisheries impacts (72 NDCs) (Fig. 2). Some NDCs provided specific plans to address these impacts, whereas others include them more generally as adaptation needs. Mangrove conservation, restoration, and management plans are included in 45 NDCs, and are included in both mitigation and adaptation sections. Coral reefs are included in 28 NDCs, but are typically included as adaptation components (Table 1). Mangroves and coral reefs are both habitat-forming marine species that provide key ecosystem services[15,16], including fisheries production and coastal buffering, but sustain negative impacts from climate change[5]. Blue carbon[17,18] mitigation contributions were included in 27 NDCs (Table 1), encompassing ocean carbon storage and the protection, replantation, or management of mangroves, salt marshes, sea grass

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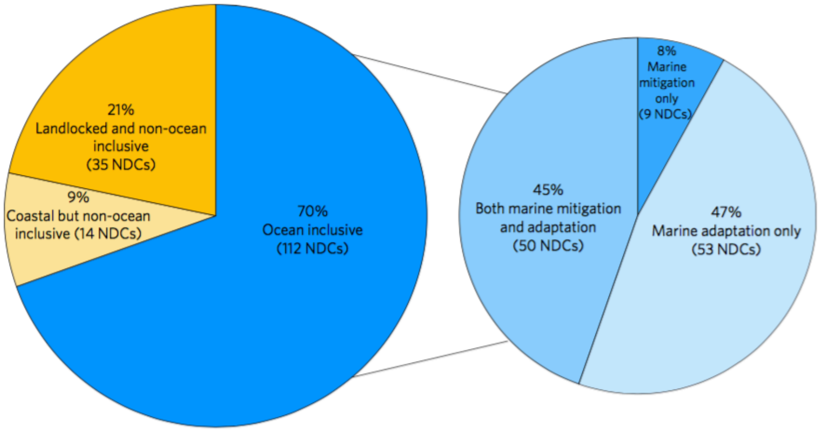

Figure 1 | Inclusion of ocean issues in NDCs. Of 161 NDCs (left) most are ocean-inclusive (right). Most NDCs that exclude oceans are from landlocked states. Most ocean-inclusive NDCs focus on climate impacts and adaptation (103 NDCs), but 59 Parties include marine topics in the mitigation section. A list of which Parties included marine issues as adaptation or mitigation components is provided in Supplementary Section 1, and a map visualizing the MFFs of different countries' NDCs is provided in Supplementary Section 2.

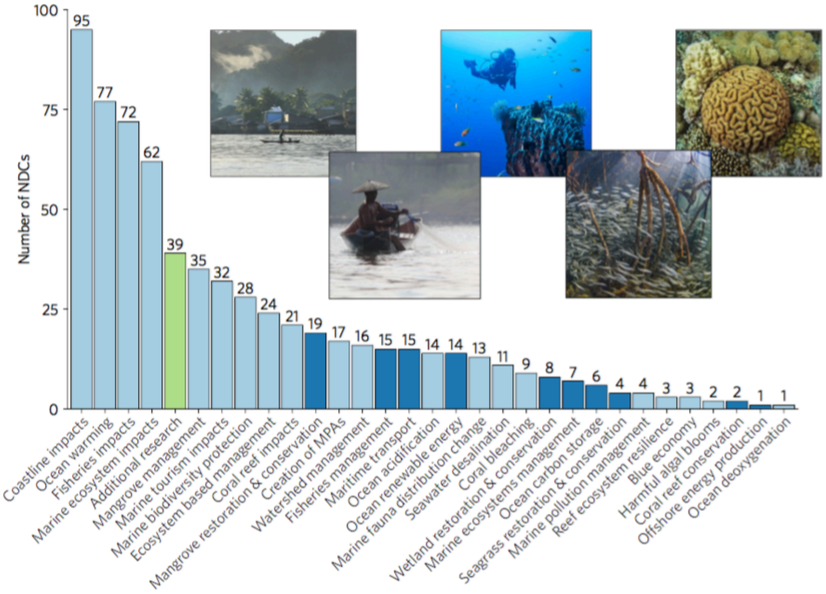

Figure 2 | Frequency of marine mitigation and adaptation categories in NDCs. Bar graph shows the frequency of different marine mitigation (dark blue) and marine impacts and adaptation (light blue) categories included in NDCs. Number of NDCs requesting additional marine research shown in green. Marine impacts and adaptation actions and concerns received much greater attention across NDCs than marine mitigation actions. Categories selected were based on multiple occurrences in NDCs and in the marine climate science literature.

beds, or other marine ecosystems. Significant opportunities exist to further expand the carbon mitigation potential of blue carbon ecosystems[19]. Several NDCs contained an ecosystem approach to climate change adaptation and included marine biodiversity preservation, creation of marine protected areas (MPAs), and utilization of conservation and ecosystem-based management in their adaptation plans (Fig. 2).

Ocean warming, acidification, deoxygenation, and changes in primary productivity are considered the four main climate change stressors of marine ecosystems[20], and occur simultaneously, creating high risk for synergistic impacts[21,22]. These effects will arise even with aggressive mitigation of global emissions—under the RCP2.5 scenario, model-mean sea surface temperature will increase 0.71 (±0.45) °C, sea surface pH will decrease 0.07 (±0.001) pH units, and global oxygen content will decrease 1.81 (±0.31)% by the 2090s compared to the 1990s[20]. As shown in Fig. 2, general concerns about ocean warming are widespread (77 NDCs), but a much smaller number of NDCs (mostly from small island developing states (SIDS)) specifically address ocean acidification as an additional stressor from anthropogenic CO_2 emissions (14 NDCs).

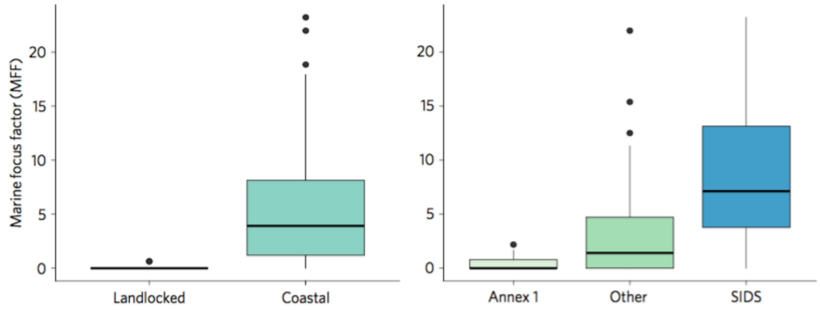

Figure 3 | Differences in marine focus factor across NDCs. Boxplots show differences in marine focus factor (MFF) between NDCs from landlocked ($n=37$) and coastal countries ($n=124$) (left); and between NDCs from Annex 1 ($n=15$), SIDS ($n=39$) and Parties that are neither Annex 1 nor SIDS ($n=107$) (right). Coastal countries had a significantly higher MFF than landlocked countries (Kruskal–Wallis, $H=67.053$, 1 d.f., $p<0.0001$). The difference in MFF between negotiating groups is also significant (Kruskal–Wallis, $H=41.741$, 2 d.f., $p<0.0001$). Comparisons between other negotiating groups were not possible because most Parties belong to more than one negotiating group.

Table 1 | Occurrence of specific marine topics in NDCs.

Ocean warming ($n=76$)	Angola, Antigua and Barbuda, Bahamas, Bahrain, Bangladesh, Barbados, Belize, Benin, Brunei Darussalam, Cabo Verde, Cambodia, Cameroon, China, Comoros, Congo, Costa Rica, Cuba, Democratic Republic of Congo, Djibouti, Dominica, Egypt, El Salvador, Eritrea, Equatorial Guinea, Fiji, Gambia, Georgia, Grenada, Guinea, Guinea-Bissau, Guyana, Haiti, Honduras, India, Indonesia, Iraq, Kiribati, Kuwait, Lebanon, Liberia, Madagascar, Malaysia, Maldives, Marshall Islands, Mauritania, Mauritius, Morocco, Mozambique, Myanmar, Nauru, Nigeria, Niue, Oman, Palau, Papau New Guinea, Qatar, Saint Kitts and Nevis, Saint Lucia, Saint Vincent and the Grenadines, Sao Tome and Principe, Saudi Arabia, Senegal, Seychelles, Singapore, Solomon Islands, Somalia, South Africa, Sudan, Suriname, Tonga, Trinidad and Tobago, Tunisia, Tuvalu, United Republic of Tanzania, Vietnam, Yemen
Ocean acidification ($n=14$)	Antigua and Barbuda, Bangladesh, Comoros, Dominica, Eritrea, Iraq, Kiribati, Marshall Islands, Mauritania, Nauru, Niue, Palau, Seychelles, Tonga
Ocean deoxygenation ($n=1$)	Mauritania
Mangroves ($n=45$)	Angola, Bahamas, Bahrain, Bangladesh, Benin, Brunei Darussalam, Cambodia, Cameroon, Congo, Côte d'Ivoire, Cuba, Djibouti, El Salvador, Fiji, Gabon, Grenada, Guinea, Guinea-Bissau, Guyana, Haiti, Honduras, India, Kiribati, Liberia, Madagascar, Marshall Islands, Mauritius, Mexico, Myanmar, Saint Kitts and Nevis, Saint Lucia, Saint Vincent and the Grenadines, Saudi Arabia, Senegal, Seychelles, Sierra Leone, Singapore, Somalia, Sudan, Suriname, Thailand, United Republic of Tanzania, United Arab Emirates, Vietnam, Yemen
Coral reefs ($n=28$)	Barbados, Belize, Brunei Darussalam, Cuba, Djibouti, Dominica, Egypt, Eritrea, Grenada, Honduras, Iraq, Kiribati, Madagascar, Maldives, Mauritius, Mexico, Nauru, Niue, Palau, Papau New Guinea, Qatar, Saint Vincent and the Grenadines, Saudi Arabia, Solomon Islands, Somalia, Sudan, Tonga, Yemen
Blue carbon ($n=27$)	Angola, Antigua and Barbuda, Armenia, Bahamas, Bahrain, Bangladesh, Brunei Darussalam, China, Dominica, El Salvador, Guinea, Guyana, Haiti, Iceland, Kiribati, Madagascar, Marshall Islands, Mexico, Philippines, Saudi Arabia, Senegal, Seychelles, Solomon Islands, Suriname, Ukraine, United Arab Emirates, Vietnam

Certain marine climate impacts and marine ecosystems were recognized in many NDCs, whereas others received little attention. The table specifies which Parties have included specific mention of the three main climate change stressors for marine ecosystems (warming, acidification and deoxygenation) within their NDCs. Many Parties also included mangroves and coral reef ecosystems in their NDCs. Coral reefs were typically included as adaptation components, whereas mangroves received attention as both adaptation and mitigation components, with Parties recognizing the carbon sequestration service of mangroves. Carbon sequestration in marine ecosystems is called 'Blue Carbon' and 27 NDCs reference management of mangroves, sea grass beds, salt marshes, wetlands or ocean carbon as mitigation strategies. The number of NDCs including each category is indicated under the category name.

Only Mauritania raised concerns about ocean deoxygenation in its NDC, even though a greater than 2% loss in the global ocean oxygen inventory has already been observed since 1960[23]. This suggests a lack of knowledge at the international policy level about ocean deoxygenation, which is a result of warming-induced changes in seawater solubility, stratification, and respiration[24], and carries significant ecosystem consequences[25].

To better understand the variance in how countries have identified marine issues in their NDCs, we first compute a marine focus factor (MFF)—a quantitative metric of the frequency and diversity of marine-related topics in each NDC. The NDCs with the highest MFF were Maldives, Oman, St. Kitts and Nevis, Kiribati, Bahrain, Seychelles, Mauritania, Mauritius, St. Vincent and the Grenadines, and Nauru—several of which are members of the SIDS designation that has become a powerful bloc in the climate negotiations[26]. Coastal countries ($n=124$) had a higher MFF than landlocked countries ($n=37$) ($H=67.053$, 1 d.f., $p<0.0001$) and MFF differed significantly among negotiating groups ($H=41.741$, 2 d.f., $p<0.0001$), with NDCs from Annex 1 Parties having the lowest MFF (Fig. 3).

Next we identified a host of factors that would plausibly influence MFF. These are: how much marine and coastal territory a country has, how much of the country's land area and population is vulnerable to sea-level rise, the importance of marine sectors for the economy, the country's commitment to marine conservation, the economic situation, and the country's political negotiating history within the UNFCCC. We then selected global data sets for variables that represented these factors. EEZ size, ratio of EEZ to land area, and coastline length were selected to reflect how much marine and coastal territory countries had. Percentage of land area below 5 m above sea level (%Land Area < 5 m) and percentage of population living in these low-lying areas (%Pop < 5 m) were selected to reflect vulnerabilities to sea-level rise. Domestic fisheries landing value was selected to reflect the value of marine resources. Percentage of territorial areas that are marine protected areas (MPAs) was selected to reflect commitment to marine conservation. Gross domestic product (GDP) was selected to reflect the economic situation. The UNFCCC negotiating group that Parties belonged to provided a reflection of their political negotiating history.

We hypothesized a priori that variables that would be positively related to MFF were: total EEZ area, ratio of EEZ to land area, coastline length, percentage of territorial waters that are marine protected areas, value of domestic fisheries landings, percentage of low-lying land area, percentage of the population living in low-lying areas, and whether the country is a SIDS. By contrast, we hypothesized that two closely related factors would be negatively correlated with MFF: whether the country is a member of Annex 1 of the UNFCCC and its gross domestic product (GDP). We chose these variables with possible negative correlation with MFF to reflect that the advanced industrialized countries have framed the climate issue as one of mitigation[27] and been reluctant to focus on climate impacts and adaptation[28], particularly for the ocean. We were unable to include other explanatory variables based on political system or administrative competence, because Annex 1 countries represent the developed countries where these are highly collinear. Scatterplots showing the relationship between each explanatory variable and MFF are provided in Supplementary Section 6.

These hypotheses were tested empirically in a multiple linear regression analysis, yielding a significant regression equation ($F_{10,107} = 6.676$, $p < 0.0001$) with a model that explains 38% of the variance in MFF for NDCs of coastal countries ($R^2 = 0.384$). Selecting the best model fit with Akaike's information criterion modified for small sample sizes (AICc) (Supplementary Section 4) yields:

$$\begin{aligned} \mathrm{MFF}^{0.5} = {} & 1.672 + 5.534\mathrm{e}^{-1}(\mathrm{SIDS}) + 3.362\mathrm{e}^{-2}\,(\%\mathrm{Pop} < 5\,\mathrm{m}) \\ & + 2.191^{-2}\,(\%\mathrm{Land\ Area} < 5\,\mathrm{m}) - 1.310\,(\mathrm{Annex\ 1}) \\ & - 1.215\mathrm{e}^{-4}\,(\mathrm{EEZ{:}Land}) \end{aligned}$$

Figure 4 summarizes the standardized coefficients and significance for each of the hypothesized variables. Two factors have a significant positive influence on MFF ($p < 0.05$): the percentage of the country's population that lives in low-lying areas and being a SIDS. Many other factors, including fisheries catch and coastline length, have no significant effect. The result that the percentage of the population living in low-lying areas positively influences the MFF, whereas other coastal factors (for example, coastline length) do not, suggests that sea-level rise vulnerabilities are particularly important in shaping climate policy priorities. As hypothesized, being an Annex 1 Party negatively influences MFF (Figs 3 and 4), although GDP does not. Despite Annex 1 countries having large marine territories, economically important fisheries, and a commitment to marine conservation, indicated by having large MPAs (Supplementary Section 7), their NDCs have a low MFF (Fig. 3).

Contrary to our hypothesis, the value of domestic fisheries landings had no significant influence on MFF. This is striking because national economies are vulnerable to the impacts of climate change on fisheries[29,30] and 72 Parties include fisheries impacts in the adaptation sections of their NDCs (Fig. 2). The fisheries sector is also included by 15 NDCs within the mitigation section, showing that fisheries concerns are relevant to both climate mitigation and adaptation plans. However, the results of the analysis show that the value of fisheries is not statistically influencing the amount of focus dedicated to marine topics in NDCs. Two additional fisheries-related explanatory variables were also tested and had no significant influence on MFF (Supplementary Section 8), suggesting this result is robust.

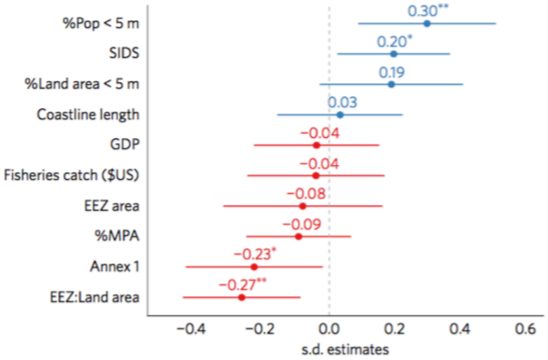

Figure 4 | Ability of different explanatory variables to explain variance in NDC marine focus. Standardized coefficients from the multiple linear regression with Marine Focus Factor (MFF) as the dependent variable. Variables with positive (blue) and negative (red) impacts on MFF shown, with bars indicating two standard deviations in the error estimate. Asterisks denote statistically significant variables (*$p < 0.05$, **$p < 0.01$). Explanatory variables tested were: percentage of the population living in areas less than 5 m above sea level (%Pop < 5 m), whether the country was a SIDS, percentage of land area that was less than 5 m above sea level (%Land Area < 5 m), the coastline length (m), the GDP, the domestic fisheries landing value (Fisheries Catch ($US)), the total EEZ Area, the percentage of the marine territory that was protected (%MPA), whether the country was an Annex 1 Party, and the ratio of EEZ to land area (EEZ:Land Area).

Although we had initially hypothesized that increasing marine territory would positively influence MFF, we found no significant relationship between EEZ Area and NDC MFF. We also found a significant negative relationship between the ratio of EEZ to land area and the NDC MFF (Fig. 4). Since the SIDS represent a large negotiating bloc of countries and have large EEZ to land areas (Supplementary Section 7), we additionally tested this finding in the SIDS alone and found that the result was consistent (Supplementary Section 10). This trend was largely driven by Tuvalu and the Marshall Islands, which have extremely high EEZ to land area ratios, but submitted NDCs with relatively low MFFs. This result suggests that the marginal value of marine territory may decrease as EEZ size increases relative to land area.

Also unexpected is the finding that percentage of marine territory that was protected (%MPA) was negatively (but not significantly) correlated with MFF (Fig. 4). To further assess if countries with better marine management and healthier ocean ecosystems were more inclusive of marine issues in their climate pledges, we used the Ocean Health Index[31,32] as an additional explanatory variable. We found that the Ocean Health Index was not significantly correlated with MFF ($p > 0.05$) for all coastal countries (Supplementary Section 9) as well as for the SIDS-only negotiating bloc (Supplementary Section 10). When the MFF was deconstructed into a coastal and ocean component, percentage of protected marine territory still had no significant influence on either of these (Supplementary Section 11). Although the explanatory variables tested here accounted for 38% of the variance in MFF, the way NDCs were developed (with input from international consultants who are well acquainted with scientific issues versus a more government-driven process) may also be an important factor influencing marine focus and may account for a component of the variance not explained by the model.

The results of the multiple linear regression analysis suggest that historical political behaviours may be an important driving factor in influencing how countries are including oceans in their NDCs.

We hypothesized that variables relating to ocean value (that is, fisheries, EEZ area, coastline length) and ocean conservation and governance (that is, %MPA, Ocean Health Index) would have a positive influence on marine inclusion in NDCs, but found this not to be the case. Instead, we found a stark difference in how countries in Annex 1 and SIDS included oceans in their NDCs (Fig. 4). This difference may be attributed to the different historical roles these two groups have played within the international climate negotiations[27,33]. Annex 1 Parties represent countries with highly developed economies that have contributed the most to climate change and have historically focused on mitigation of emissions. That focus was reflected in the Kyoto Protocol, which concentrated on emission reduction goals only for Annex 1 Parties, while marginalizing the adaptation needs of developing countries[34]. SIDS are developing coastal countries that contribute minimally to global emissions but are some of the most vulnerable to climate change impacts. To represent their shared vulnerabilities, these countries organized into the Alliance of Small Island States (AOSIS) around 1990, and rapidly emerged as a powerful voice within the UNFCCC negotiations[35,36]. Throughout the negotiations, AOSIS has advocated for a greater emphasis on adaptation, with a special focus on climate impacts on oceans[26]. The strong influence of negotiating group (Annex 1 or SIDS) on MFF that we find in the present study suggests political and not principally scientific motivations are largely driving current patterns of ocean inclusion in NDCs. Even though attention to climate impacts and adaptation have risen in the past decade, the Annex 1 countries remain systematically focused on climate change as a problem of mitigating emissions, and under-represent oceans in their NDCs, whereas the SIDS are increasingly focused on marine climate impacts and adaptation.

We also assessed if Parties were including information on additional marine research needs in their NDCs, and found this to be the case in 39 NDCs (Fig. 2). These needs can roughly be divided into four categories: improve scientific climate models and marine observations; strengthen the capacity of local marine and resource management institutions; conduct additional studies on marine climate change vulnerabilities, losses, and damages to improve management plans and national development frameworks; and conduct research on mitigation potential of marine ecosystems, specifically, carbon storage, development of renewable ocean energy, and low-carbon fisheries practices. In their NDCs, least developed countries (LDCs) and SIDS largely look to the international community to provide the financial support to meet their NDC goals. It is likely that additional financing streams, in addition to the Green Climate Fund, will be necessary to support stated ocean and climate research needs. One possibility may be the proposed Ocean Bank for Sustainability and Development[37]. Increased cooperation and collaboration between marine institutions in developing and developed countries may help address capacity building challenges raised in NDCs. Climate impacts in certain marine ecosystems, such as the deep sea[38], remain poorly understood and will require additional international cooperation.

The Paris Agreement commits nations to limit global temperature rise to well below 2 °C, while pursing efforts to limit to 1.5 °C; however, marine ecosystems experience impacts even under the most ambitious mitigation scenarios[39,40]. Concrete financial incentives exist for meeting the goals of the Paris Agreement, especially for countries reliant on marine fisheries[41]. The results of this analysis show that oceans are not only becoming more prominent in the climate negotiations, but that countries are actively including marine ecosystems in their national climate plans. However, we find a large spread in the marine focus of NDCs, with Annex 1 Parties showing a lack of focus on marine issues. Certain marine impacts, such as ocean deoxygenation and acidification, continue to receive limited attention from governments, emphasizing the need for additional scientific engagement and education. Secondary impacts from climate mitigation and adaptation plans should also be considered. For example, 11 NDCs include seawater desalination plans, which carry environmental risks including larval entrainment and outflow of chemical-contaminated brine[42].

Over half a billion of the world's poorest people rely heavily on the ocean for food, jobs, and revenue and live in countries that will be impacted by simultaneous changes in ocean biogeochemistry from climate change[21]. Not considering the ocean in NDCs has several consequences, including missed mitigation opportunities involving marine ecosystems and the development of national climate adaptation plans that fall short of addressing the needs and vulnerabilities of coastal communities[43]. Certain Parties have stated that including oceans in NDCs is necessary for the successful implementation of the Paris Agreement[44]. Since the high seas experience climate impacts but remain outside of the legal jurisdiction of the UNFCCC, it is important to consider how action under the Paris Agreement interacts with other UN treaties, including the UN Convention on the Law of the Sea, the Convention on Biological Diversity, and the Sustainable Development Goals. Climate impacts may also shape the biodiversity treaty under development in areas beyond national jurisdiction. Under the Paris Agreement, NDCs are reviewed and communicated anew every five years, allowing for improvements to be made on identified gaps. The Intergovernmental Panel on Climate Change (IPCC) special report on the ocean and cryosphere (due out in 2019) could provide additional guidance on marine impacts in time to inform the next round of NDC revisions. Engagement of ocean scientists is essential to ensure that marine ecosystems are being appropriately considered in national climate action plans[45].

Methods

Methods, including statements of data availability and any associated accession codes and references, are available in the online version of this paper.

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References

1. *Paris Agreement* (UNFCCC, 2016).
2. Bodansky, D. The Paris Climate Change Agreement: A new hope? *Am. J. Int. Law* **110,** 288–319 (2016).
3. Lesnikowski, A., Ford, J., Biesbroek, R., Berrang-Ford, L. & Heymann, S. J. National-level progress on adaptation. *Nat. Clim. Change* **6,** 261–264 (2016).
4. Pörtner, H.-O. *et al*. in *IPCC Climate Change 2014: Impacts, Adaptation, and Vulnerability* (eds Field, C.B. *et al*.) 411–484 (IPCC, Cambridge Univ. Press, 2014).
5. Hoegh-Guldberg, O. & Bruno, J. F. The impact of climate change on the world's marine ecosystems. *Science* **328,** 1523–1528.
6. Eddebbar, Y. A., Gallo, N. D. & Linsmayer, L. B. The oceans and the UN framework convention on climate change. *L&O Bull.* **5,** 69–72 (2015).
7. Galland, G., Harrould-Kolieb, E. & Herr, D. The ocean and climate change policy. *Clim. Policy* **12,** 764–771 (2012).
8. *United Nations Framework Convention on Climate Change* (UNFCCC, 1992).
9. Gattuso, J. P. An Ocean Scientist at COP21. *L&O Bull.* **25,** 15–17 (2016).
10. Chilean Ministry of Foreign Affairs. Because the Ocean Declaration (Institute for Sustainable Development (IDDRI), 2015); http://www.iddri.org/Themes/Because-the-Ocean-ENG.pdf
11. *Kyoto Protocol* (UNFCCC, 1997).
12. Keohane, R. O. & Victor, D. G. Cooperation and discord in global climate policy. *Nat. Clim. Change* **6,** 570–575 (2016).
13. *INDC Portal* (UNFCCC, 2015); http://www4.unfccc.int/submissions/indc/Submission%20Pages/submissions.aspx
14. *The Intended Nationally Determined Contribution Submission by Latvia and the European Commission on Behalf of the European Union and Its Member States* (UNFCCC, 2015).
15. Costanza, R. *et al*. The value of the world's ecosystem services and natural capital. *Nature* **387,** 253–260 (1997).
16. Barbier, E. B. *et al*. The value of estuarine and coastal ecosystem services. *Ecol. Monogr.* **81,** 169–193.

17. Mcleod, E. *et al*. A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO_2. *Front. Ecol. Environ.* **9,** 552–560 (2011).
18. Alongi, D. M. Carbon sequestration in mangrove forests. *Carbon Manage.* **3,** 313–322 (2012).
19. Herr, D. & Landis, E. *Coastal Blue Carbon Ecosystems: Opportunities for Nationally Determined Contributions* (International Union for Conservation of Nature, The Nature Conservancy, 2016).
20. Bopp, L. *et al*. Multiple stressors of ocean ecosystems in the 21st century: projections with CMIP5 models. *Biogeosciences* **10,** 6225–6245 (2013).
21. Mora, C. *et al*. Biotic and human vulnerability to projected changes in ocean biogeochemistry over the 21st Century. *PLoS Biol.* **11,** e1001682 (2013).
22. Gruber, N. Warming up, turning sour, losing breath: ocean biogeochemistry under global change. *Phil. Trans. R. Soc. A* **369,** 1980–1996 (2011).
23. Schmidtko, S., Stramma, L. & Visbeck, M. Decline in global oceanic oxygen content during the past five decades. *Nature* **542,** 335–339 (2017).
24. Keeling, R. F., Körtzinger, A. & Gruber, N. Ocean deoxygenation in a warming world. *Annu. Rev. Mar. Sci.* **2,** 199–229 (2010).
25. Gilly, W. F., Beman, J. M., Litvin, S. Y. & Robison, B. H. Oceanographic and biological effects of shoaling of the oxygen minimum zone. *Annu. Rev. Mar. Sci.* **5,** 393–420 (2013).
26. Wong, P. P. Small island developing states. *WIREs Clim. Change* **2,** 1–6 (2011).
27. Schipper, E. L. F. Conceptual history of adaptation in the UNFCCC process. *RECIEL* **15,** 82–92 (2006).
28. Pielke, R., Prins, G., Rayner, S. & Sarewitz, D. Lifting the taboo on adaptation. *Nature* **445,** 597–598 (2007).
29. Allison, E. H. *et al*. Vulnerability of national economies to the impacts of climate change on fisheries. *Fish Fish.* **10,** 173–196 (2009).
30. Lam, V. W. Y., Cheung, W. W. L., Reygondeau, G. & Sumaila, U. R. Projected change in global fisheries revenues under climate change. *Sci. Rep.* **6,** 32607 (2016).
31. Halpern, B. S. *et al*. An index to assess the health and benefits of the global ocean. *Nature* **488,** 615–620 (2012).
32. Halpern, B. S. *et al*. Patterns and emerging trends in global ocean health. *PLoS ONE* **10,** e0117863 (2015).
33. Gupta, J. A history of international climate change policy. *WIREs Clim. Change* **1,** 636–653 (2010).
34. Najam, A., Huq, S. & Sokona, Y. Climate negotiations beyond Kyoto: developing countries concerns and interests. *Clim. Policy* **3,** 221–231 (2003).
35. Ashe, J. W., Lierop, R. V. & Cherian, A. The role of the Alliance of Small Island States (AOSIS) in the negotiation of the United Nations Framework Convention on Climate Change (UNFCCC). *Nat. Resour. Forum* **23,** 209–220 (1999).
36. Betzold, C. "Borrowing" power to influence international negotiations: AOSIS in the climate change regime, 1990–1997. *Politics* **30,** 131–148 (2010).
37. Thiele, T. Accelerating impact, the promise of blue finance. *Cornerstone J. Sustain. Financ. Bank.* **II,** 21–22 (2015).
38. Levin, L. A. & Le Bris, N. The deep ocean under climate change. *Science* **350,** 766–768 (2015).
39. Magnan, A. K. *et al*. Implications of the Paris agreement for the ocean. *Nat. Clim. Change* **6,** 732–735 (2016).
40. Gattuso, J.-P. *et al*. Contrasting futures for ocean and society from different anthropogenic CO_2 emissions scenarios. *Science* **349,** aac4722 (2015).
41. Cheung, W. W. L., Reygondeau, G. & Frölicher, T. L. Large benefits to marine fisheries of meeting the 1.5 °C global warming target. *Science* **354,** 1591–1594 (2016).
42. Elimelech, M. & Phillip, W. A. The future of seawater desalination: energy, technology, and the environment. *Science* **333,** 712–717 (2011).
43. Cicin-Sain, B. *et al*. *Towards a Strategic Action Roadmap on Oceans and Climate: 2016 to 2021* (Global Ocean Forum, 2016).
44. Submission from Chile to the UNFCCC *Submission on the Relevance of the Ocean in the Global Response to Climate Change* (2016); http://go.nature.com/2yi47y8
45. Petes, L. E., Howard, J. F., Helmuth, B. S. & Fly, E. K. Science integration into US climate and ocean policy. *Nat. Clim. Change* **4,** 671–677 (2014).

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Author contributions

N.D.G. performed the analysis and wrote the manuscript, D.G.V. and L.A.L. contributed equally in providing guidance on the analysis and revising the manuscript.

Additional information

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Competing financial interests

The authors declare no competing financial interests.

Methods

All 161 pledges submitted to the UNFCCC Secretariat[13] by June 2016 were analysed for inclusion of marine keywords and categories (Supplementary Section 3). These pledges were known as intended nationally determined contributions (INDCs), but became nationally determined contributions (NDCs) once the Paris Agreement came into force in November 2016, and are therefore referred to as NDCs throughout the manuscript. The total NDC data set represented 1,997 pages of NDC text and a text mining approach was used. For this analysis, marine ecosystems include estuarine, coastal, and open ocean ecosystems.

A core set of 23 marine keywords (Supplementary Section 3) was selected and a standardized search for this core set of keywords was carried out for each NDC. Marine keywords were determined based on the authors' knowledge of terms commonly used in the marine and climate science, marine conservation, and marine policy fields, and represent general terms that reference specific marine habitats, climate impacts, and ocean industries or economic sectors. The core set of keywords represented a balance between being broad enough to appropriately identify marine-focused sections of text, while reducing the number of keywords required for the standardized search applied to all NDCs. Sections of text in which these core keywords were found were then read to identify other marine keywords (ex. 'beach', 'desalination', 'fishermen'). The frequency of use of all marine keywords in each NDC was then tabulated. In some cases, such as 'fisheries,' the authors evaluated whether the use of this keyword in the NDC referred to freshwater or marine sectors, and only included keywords in the total count that were marine-focused. A total marine word count was then determined for each NDC. To account for differences in NDC length (Supplementary Section 5), the marine word count was standardized to total NDC word count.

Sections where marine keywords appeared were extracted, read in their entirety, and were used to determine if Parties were including marine ecosystems as mitigation or adaptation contributions in their NDCs. Although NDCs varied considerably in length and content, they did follow a format that, although not consistent across all NDCs, was similar for many submitted NDCs. The format included an introductory section, a section on mitigation contributions and (for some) a section on adaptation contributions. If specific marine topics were included in the mitigation section or annexes to the mitigation section, they were considered as mitigation components, and are referenced this way in the manuscript. Mitigation refers to actions that result in reductions to national greenhouse gas emissions. If marine topics were included in the adaptation section of the NDC or if marine impacts or vulnerabilities were discussed within other components of the NDC, these were considered adaptation components and are referenced this way in the manuscript. Adaptation refers to vulnerabilities from climate change and actions that reduce climate impacts. Descriptions of marine impacts were categorized as adaptation components, despite these sections not always containing specific adaptation plans. A total of 31 specific marine categories were identified across NDCs (Fig. 2 and Supplementary Section 3) based on marine concepts that were included in NDCs; these represent a general grouping of ways in which marine issues were included.

Using the tabulated marine keywords and categories, a Marine Focus Factor (MFF) was then calculated for each NDC.

$$\mathrm{MFF} = 1{,}000 \times \left(\frac{\text{Marine Keywords in NDC}}{\text{Total NDC Word Count}}\right) \times \left(1 + \frac{\text{Marine Categories in NDC}}{\text{Total Marine Categories}}\right)$$

The MFF is meant to be used as a comparative metric for evaluating how much marine consideration different countries are including in their climate pledges, across all submitted NDCs. The MFF does not differentiate between marine activities that are environmentally beneficial (for example, mangrove replanting) or potentially environmentally detrimental (for example, seawater desalination), so the MFF should not be used alone as a metric to evaluate how beneficial an NDC is for the marine environment. Twenty NDCs were randomly selected, read in their entirety, and marine components summarized to provide a qualitative assessment of how well the MFF was capturing actual differences in marine focus (Supplementary Section 12).

Although most NDCs were available in English, those that did not have an English translation available (Spanish (8), French (12), and Arabic (2)) were analysed by native language speakers who were also fluent in English, following the same protocol. Specifically, the core set of 23 marine keywords were translated into the native language, with care taken to ensure that the translation was accurately capturing the concept. The core keywords were then used to identify sections of marine-focused text, and these sections were translated into English. Additional marine keywords were then identified and a count was obtained for all marine keywords in the NDC. The author who processed all of the English NDCs also utilized Google Translate to translate the foreign language NDCs in their entirety, and this rough translation was read through to ensure that the keyword count and identification of marine categories was consistent across the English and non-English NDCs. We also tested NDC language as an additional explanatory variable in the multiple linear regression analysis and found no statistically significant influence on MFF ($p > 0.05$) (Supplementary Section 5).

Developing the MFF as a comparative metric allowed us to test which factors give rise to differences in the amount of marine consideration in NDCs. We hypothesized a priori that factors that influence how likely Parties are to include marine issues in their NDCs were: total EEZ area, ratio of EEZ to land area, coastline length, percentage of territorial waters that are marine protected areas, value of domestic fisheries landings, percentage of low-lying land area, percentage of the population living in low-lying areas, gross domestic product (GDP), and whether the country is a SIDS or Annex 1 Party. Data for continuous explanatory variables were obtained from the World Bank[46] and the Sea Around Us Project[47]. Data for GDP originated from the World Bank national accounts data and the OECD National Accounts data files and represent GDP at market prices (in constant 2005 $US) for the year 2010. Data for MPAs originated from the United Nations Environmental Program and the World Conservation Monitoring Center, and represent percentage of territorial intertidal and subtidal terrain and overlying water that have been protected by law or other effective means, for the year 2014. Data for percentage of low-lying land area and percentage of the population living in low-lying areas originated from the Center for International Earth Science Information Network and measure the percentage of total land area where the elevation is 5 m or less and the percentage of the total population living in these areas, for year 2010. Data for domestic fisheries landing values were obtained from the Sea Around Us project on 6 September 2016 and represent fisheries landed value reconstructed domestic catch in constant 2005 $US.

All data were collected in an Excel spreadsheet and all statistical analyses were performed in R[48], a free software environment for statistical computing and graphics. Since the data for MFF were not normally distributed, we used a nonparametric one-way analysis of variance (ANOVA) (Kruskal–Wallis) to test if there was a significant difference in marine inclusion between coastal and landlocked countries, and among Annex 1, SIDS, and all Other Parties for the whole NDC data set ($n = 161$). We then tested the influence of all the hypothesized explanatory variables on the MFF using a multiple linear regression analysis to determine which explanatory variables had a significant effect on an NDC's MFF. Only coastal countries with data for all explanatory variables were included in the multiple regression analysis ($n = 118$), which excluded all landlocked countries and Montenegro, EU, Cook Islands, Monaco, Nauru, and Niue, for which data on the full-suite of explanatory variables were not available. Since the dependent variable was not normally distributed, we first square-root-transformed the MFF to meet the assumptions of normality. As a robustness check, both absolute marine word count and standardized marine word count were also tested as dependent variables in the model (Supplementary Section 5) and an additional analysis deconstructed the MFF into a coastal and ocean component (Supplementary Section 11). Additional explanatory variables including the Ocean Health Index[31,32] and the government effectiveness index were also tested and included in the multiple linear regression model (Supplementary Sections 9 and 10).

Results for the significance of each explanatory variable and the overall model fit were reported for the multiple linear regression analysis. The best model was then selected using a stepwise algorithm using Akaike's Information Criterion, modified for small sample size (AICc)[49] employing the AICc function in the AICcmodavg package for R[50]. Although AICc allows us to select the best model, we acknowledge the limitations of the data set, specifically the small sample size ($n = 118$) and the large number of degrees of freedom. Candidate models are provided in Supplementary Section 4. Multicollinearity and variance inflation factors were checked for the explanatory variables tested (Supplementary Section 5). Standardized coefficients for each explanatory variable from the multiple linear regression analysis were extracted using the lm.beta function in the QuantPsyc package for R[51] and plotted using the sjPlot package[52]. An additional multiple linear regression analysis was also carried out for the SIDS-only data set (Supplementary Section 10). Additional figures were produced using the ggplot2 package[53] in R.

Data availability. The authors declare that all data supporting the findings of this study are available within the Zenodo data repository with the identifier (http://dx.doi.org/10.5281/zenodo.845500)[54] and within the article's Supplementary Information files.

References

46. *Indicators: World Bank* (accessed 20 September 2016); http://data.worldbank.org/indicator
47. *Sea Around Us: Fisheries, Ecosystems and Biodiversity* (accessed 15 September 2016); http://www.seaaroundus.org/data/#/eez

48. R Development Core Team *R: A Language and Environment for statistical computing. R Foundation for Statistical Computing* ISBN 3-900051-07-0 (2008).
49. Symonds, M. R. E. & Moussalli, A. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behav. Ecol. Sociobiol.* **65,** 13–21 (2011).
50. Mazerolle, M. J. *AICcmodavg: Model Selection and Multimodel Inference Based on* (Q)*AIC*(*c*)*. R Package Version* 2.0-4 (2016).
51. Fletcher, T. D. *QuantPsych: Quantitative Psychology Tools. R Package Version* 1.5 (2012).
52. Lüdecke, D. *sjPlot: Data Visualization for Statistics in Social Science. R Package Version* 2.1.1 (2016).
53. Wickham, H. *ggplot2: Elegant Graphics for Data Analysis* (Springer, 2009).
54. Gallo, N. D., Victor, D. G. & Levin, L. A. *Raw Dataset for Ocean Commitments under the Paris Agreement* (Zenodo, 2017); http://dx.doi.org/10.5281/zenodo.845500

Chapter 7 Appendix

nature climate change

SUPPLEMENTARY INFORMATION

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In the format provided by the authors and unedited.

Ocean commitments under the Paris Agreement

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Supplementary Material for Gallo et al. Ocean Commitments Under the Paris Agreement

Table of Contents for Supplementary Material

Supplementary Material for Gallo et al. Ocean Commitments Under the Paris Agreement

S1. The calculated Marine Focus Factor (MFF) for each submitted NDC and whether marine topics were included as mitigation or adaptation components

List of Parties that have included marine ecosystems in their Nationally Determined Contributions (NDCs) and the calculated marine focus factor (MFF) for each NDC. Asterisks represent inclusion and indicate if marine ecosystems have been included as a mitigation or adaptation component in the NDC. If specific marine topics were included in the mitigation section or annexes to the mitigation section, they were considered as mitigation components and are referenced this way in the manuscript. Mitigation refers to actions that result in reductions to national greenhouse gas emissions. If marine topics were included in the adaptation section of the NDC or if marine impacts or vulnerabilities were discussed within other components of the NDC, these were considered adaptation components and are referenced this way in the manuscript. Adaptation refers to vulnerabilities from climate change and actions that reduce climate impacts. Descriptions of marine impacts were categorized as adaptation components, despite these sections not always containing specific adaptation plans.

The MFF is a quantitative metric of the standardized marine word count and diversity of marine-related topics in each NDC (see manuscript methods for description of how the MFF was calculated). Parties are ordered from those with NDCs with the highest MFF to those with the lowest MFF. The MFF is meant to be used as a comparative metric for evaluating how much marine consideration different countries are including in their climate pledges, across all submitted NDCs. The MFF does not differentiate between marine activities that are environmentally beneficial (ex. mangrove replanting) or potentially environmentally detrimental (ex. seawater desalination), so the MFF should not be used alone as a metric to evaluate how beneficial an NDC is for the marine environment.

Party	Marine Mitigation	Marine Adaptation	Marine Focus Factor
Maldives	*	*	23.209
Oman		*	21.981
Saint Kitts and Nevis		*	18.846
Kiribati	*	*	17.915
Bahrain	*	*	17.841
Seychelles	*	*	15.415
Mauritania	*	*	15.382
Mauritius	*	*	15.323
Saint Vincent and the Grenadines		*	14.844
Nauru		*	14.243
Bahamas	*	*	13.908
Belize	*	*	13.478
Dominica	*	*	12.785
Honduras		*	12.506
Suriname	*	*	12.471
Senegal	*	*	11.314
United Arab Emirates	*	*	11.000
Haiti	*	*	10.932
Madagascar	*	*	10.898
Eritrea		*	10.675
Somalia	*	*	10.494
Qatar	*	*	10.379
Indonesia	*	*	9.802
Solomon Islands	*	*	9.281

United Republic of Tanzania	*	*	9.195
Grenada	*	*	9.004
Saudi Arabia	*	*	8.838
Djibouti	*	*	8.778
Kuwait		*	8.777
Cabo Verde	*	*	8.694
Sudan		*	8.265
Vietnam	*	*	8.088
Egypt		*	8.044
Sao Tome and Principe		*	7.992
Liberia		*	7.925
Antigua and Barbuda	*	*	7.651
Tunisia		*	7.551
Palau		*	7.413
Cook Islands	*	*	7.123
Yemen	*	*	6.838
Equatorial Guinea	*	*	6.659
Guinea-Bissau		*	6.496
Guinea	*	*	6.328
Mozambique		*	6.192
Barbados		*	6.184
Fiji	*	*	6.147
Singapore		*	5.873
Côte d’Ivoire	*	*	5.606
Marshall Islands	*	*	5.490
Mexico	*	*	5.202
Angola	*	*	5.116
Cambodia		*	4.822
Malaysia		*	4.620
Georgia		*	4.556
Niue		*	4.531
Cuba		*	4.526
Saint Lucia	*	*	4.439
Togo		*	4.304
Gabon	*	*	4.127
Brunei Darussalam	*	*	4.097
Tonga	*	*	4.079
Congo	*	*	3.938
Democratic Republic of the Congo		*	3.888
Bangladesh	*	*	3.745
Morocco	*	*	3.625
Vanuatu		*	3.473
Jamaica		*	3.367
India	*	*	3.350
Tuvalu	*	*	3.317
Thailand		*	3.245
Cameroon	*	*	3.032
Sierra Leone		*	2.713
Ecuador		*	2.687
Gambia		*	2.665
Guyana	*	*	2.659
Peru		*	2.656
Papua New Guinea		*	2.582

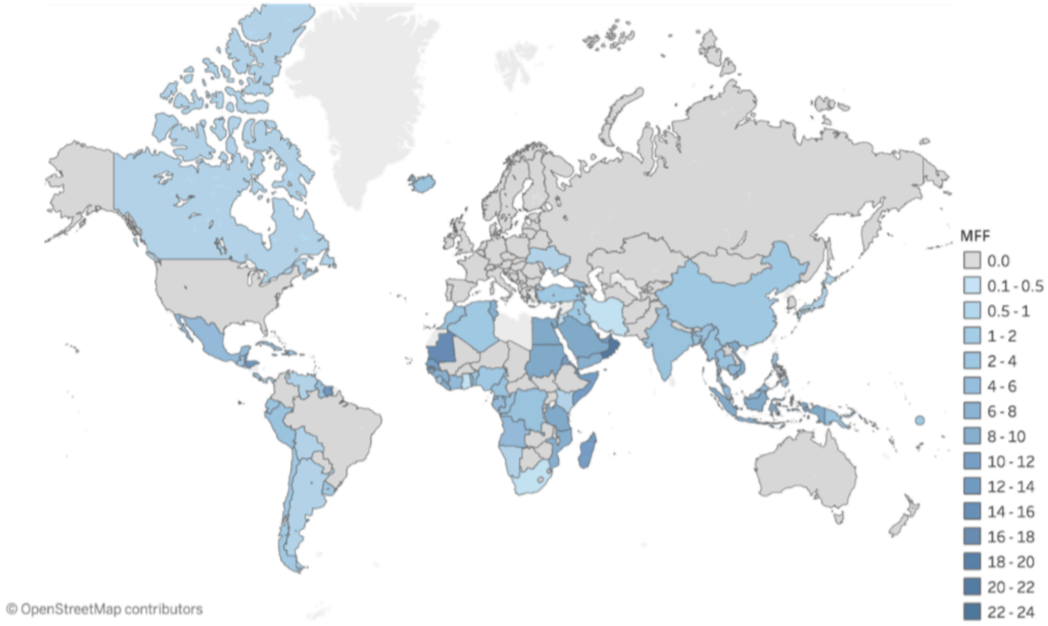
Myanmar		*	2.487
Benin		*	2.467
Lebanon		*	2.446
Iceland	*		2.195
Philippines	*	*	2.189
Comoros		*	2.012
El Salvador	*	*	1.991
Nigeria	*	*	1.854
Guatemala		*	1.845
Iraq		*	1.726
Dominican Republic		*	1.706
China	*	*	1.686
Turkey	*		1.664
Costa Rica		*	1.575
Chile		*	1.415
Uruguay		*	1.230
Trinidad and Tobago		*	1.093
Algeria		*	1.030
Venezuela	*	*	0.941
Kenya		*	0.932
Monaco	*		0.893
Ukraine	*		0.860
Namibia		*	0.848
Israel	*		0.844
Argentina		*	0.733
Japan	*		0.712
Canada	*		0.670
Armenia	*		0.655
Bolivia		*	0.626
Panama	*		0.556
Ghana		*	0.492
Iran		*	0.475
Samoa		*	0.436
South Africa		*	0.416
Jordan		*	0.356
Montenegro			0.000
Afghanistan			0.000
Albania			0.000
Andorra			0.000
Australia			0.000
Azerbaijan			0.000
Belarus			0.000
Bhutan			0.000
Bosnia and Herzegovina			0.000
Botswana			0.000
Brazil			0.000
Burkina Faso			0.000
Burundi			0.000
Chad			0.000
Colombia			0.000
Ethiopia			0.000
EU			0.000
Micronesia			0.000

Kazakhstan			0.000
Kyrgyzstan			0.000
Lao			0.000
Liechtenstein			0.000
Lesotho			0.000
Malawi			0.000
Mali			0.000
Mongolia			0.000
Nepal			0.000
New Zealand			0.000
Niger			0.000
Norway			0.000
Pakistan			0.000
Paraguay			0.000
Korea			0.000
Macedonia			0.000
Moldova			0.000
Serbia			0.000
Central African Republic			0.000
Russia			0.000
Rwanda			0.000
San Marino			0.000
South Sudan			0.000
Swaziland			0.000
Switzerland			0.000
Tajikistan			0.000
Turkmenistan			0.000
Uganda			0.000
United States of America			0.000
Zambia			0.000
Zimbabwe			0.000

Supplementary Material for Gallo et al. Ocean Commitments Under the Paris Agreement

S2. A map visualizing the Marine Focus Factor (MFF) of different countries' NDCs

This figure provides a global look at the Marine Focus Factors (MFFs) of the 161 submitted Nationally Determined Contributions (NDCs). Countries shown in blue included some mention of marine issues in their NDCs; lighter blue colors indicate a lower MFF and darker blue colors indicate a higher MFF. Countries shown in grey with a black border did not include any mention of marine issues in their NDCs. Countries shown in grey with no border did not submit NDCs at the time of this analysis. Small Island Developing States (SIDS), which frequently included marine topics and concerns in their NDCs, are not visible in this figure but their MFFs are presented in Supplementary Section 1.



S3. The keywords used in the standardized word search and the marine categories developed

This table shows keywords used to identify marine-focused sections of text (left) with the total number of times these keywords were found in all 1997 pages of NDC text. Asterisks indicate that all words with the indicated root were counted. “Ocean warming” represents a concept and was counted even if different words were used, such as “rising ocean temperatures.” Sections of marine-focused text were then read to develop specific marine mitigation (middle) and marine adaptation and impact (right) categories across NDCs. We present the identified categories and the total number of NDCs that included these categories. While the keyword “deoxygenation” was not found in any of the 161 NDCs, Mauritania’s NDC referenced oxygen depletion impacts due to climate warming, which was categorized as “Ocean Deoxygenation Impacts.”

Keywords Used for Standardized Search	Total Number of Uses in All NDCs
"coast*"	630
"sea level"	261
"marine"	167
"fisheries"	152
"mangrove"	108
"ocean*"	100
"wetland"	72
"fishery"	70
"coral"	69
"reef"	57
"sea"	51
"ocean warming**"	37
"aquaculture"	35
"maritime"	30
"acidification"	26
"blue economy"	25
"wave"	16
"seagrass"	14
"blue carbon"	8
"marsh"	6
"offshore"	6
"oxygen"	4
"deoxygenation"	0

Marine Mitigation Categories	Number of NDCs
Mangrove Restoration and Conservation	19
Fisheries Management	15
Maritime Transport	15
Ocean Renewable Energy	14
Wetland Restoration and Conservation	8
Management of Watersheds and Marine Ecosystems	7
Ocean Carbon Storage	6
Seagrass Restoration and Conservation	4
Coral Reef Conservation	2
Offshore Energy Production	1

Marine Adaptation Categories (Including Impacts)	Number of NDCs
Coastline Impacts	95
Ocean Warming Impacts	77
Fisheries Impacts	72
Marine Ecosystem Impacts	62
Additional Research Requirements	39
Mangrove Restoration and Management	35
Marine Tourism Impacts	32
Protecting Marine Biodiversity	28
Conservation and Ecosystem Based Management	24
Coral Reef Impacts	21
Creation of Marine Protected Areas	17
Management of Watersheds	16
Ocean Acidification Impacts	14
Marine Fauna Distribution Change	13
Seawater Desalination	11
Coral Bleaching	9
Marine Pollution Management	4
Reef Ecosystem Resilience	3
Promote Ocean-Based ‘Blue’ Economy	3
Harmful Algal Blooms	2
Ocean Deoxygenation Impacts	1

S4. The best-ranked regression models by AICc explaining Marine Focus Factor (MFF) of Nationally Determined Contributions (NDCs)

This table shows the 95% confidence set of best-ranked regression models (the 4 models whose cumulative Akaike weight, acc *w*i < 0.95) examining the effects of possible explanatory variables on marine focus factor (MFF) of nationally determined contributions (NDCs). Explanatory variables included in the best-ranked models include: Annex1, %POP, SIDS, EEZ:Land, %LAND, %MPA, and FISH$. Annex1 refers to if the country is a member of Annex 1 of the United Nations Framework Convention on Climate Change (UNFCCC). %POP refers to the percentage of the total population living in low-lying areas (less than 5 m above sea level). SIDS refers to if the country is a member of the Small Island Developing States (SIDS) negotiating bloc. EEZ:Land represents the ratio of the area of national marine territory (the Exclusive Economic Zone) to the national land area. %LAND refers to the percentage of low-lying land area (less than 5 m above sea level). %MPA refers to the percentage of the total marine territory that is protected. FISH$ refers to the annual fisheries landing value. For more information on how data for explanatory variables was obtained, please see manuscript methods.

	Candidate Model	**K**	**RSS**	**AICc**	**Δi**	***w*i**	**acc *w*i**
1	MFF ~ Annex1 + %POP + SIDS + EEZ:Land + %LAND	7	104.020	335.007	0.000	0.299	0.299
2	MFF ~ Annex1 + %POP + SIDS + EEZ:Land + %LAND + %MPA	8	102.353	335.404	0.397	0.245	0.545
3	MFF ~ Annex1 + %POP + SIDS + EEZ:Land	6	106.654	335.698	0.690	0.212	0.757
4	MFF ~ Annex1 + %POP + SIDS + EEZ:Land + %LAND + %MPA + FISH$	9	101.249	336.470	1.463	0.144	0.901

S5. The robustness of the multiple linear regression results

The Nationally Determined Contributions (NDCs) reviewed varied considerably in length and focus, the shortest being 1 page long (Pakistan), the longest being 51 pages long (Burkina Faso), and the average being 12 pages long. To account for the substantial differences in length, we standardized the marine word count for each NDC to the total NDC word count (Fig S5a).

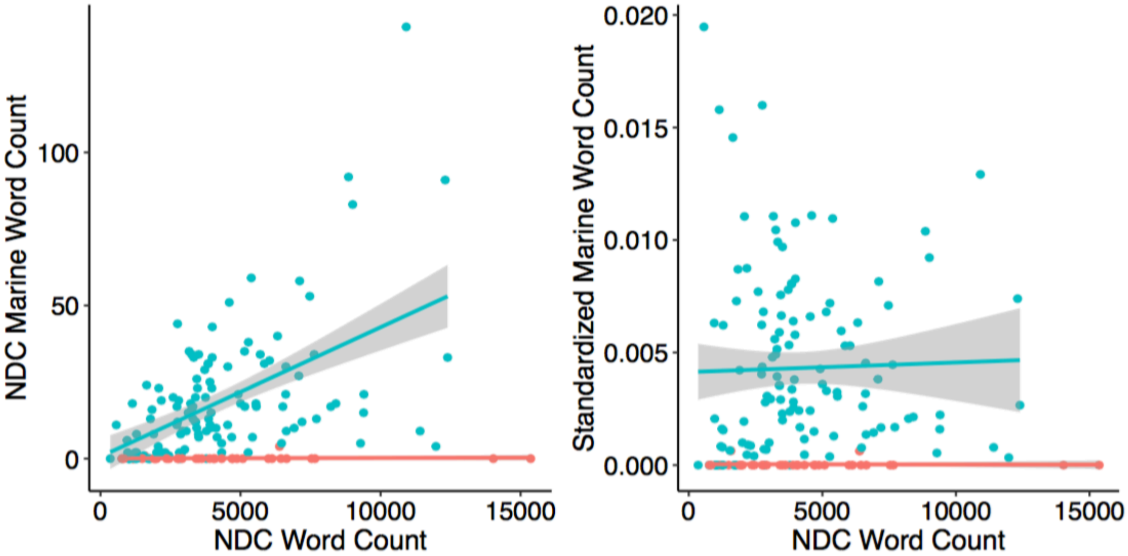


Figure S5a. Both figures show the large range in word count of NDCs (reflecting differences in length) and show that for coastal countries (blue), marine word count is a linear function of total NDC word count (left). No linear relationship is observed between total NDC word count and marine word count for landlocked nations (red). Since NDC length is not a meaningful explanatory variable, we remove this relationship by standardizing marine word count in NDCs to total NDC word count (right), thus allowing for the variance in marine focus to be explained by explanatory variables which are policy relevant.

The Marine Focus Factor (MFF) utilizes the marine word count standardized to total NDC word count but also rewards countries for having NDCs that incorporate a greater diversity of marine topics in their NDCs. The MFF is a multiplicative metric of the standardized word count and the marine topic diversity and reflects how much focus is given to marine topics, as well as how comprehensive this focus is. Parties whose NDCs included more marine categories (of a possible 31 categories, all possible categories annotated are shown in manuscript Figure 2) thus receive a higher MFF than those that have the same standardized word count, but include fewer categories. We tested the raw word count, standardized word count, and MFF as dependent variables in a multiple linear regression analysis to insure that the results were robust and were not being biased by countries producing long, detailed NDCs on a number of issues (including marine topics) that diluted the perceived marine focus, compared to less comprehensive NDCs. We see that the model fit is improved by using the MFF but that the results are robust across the dependent variables tested (Fig S5b), with the same explanatory variables being selected as significant in almost all cases.

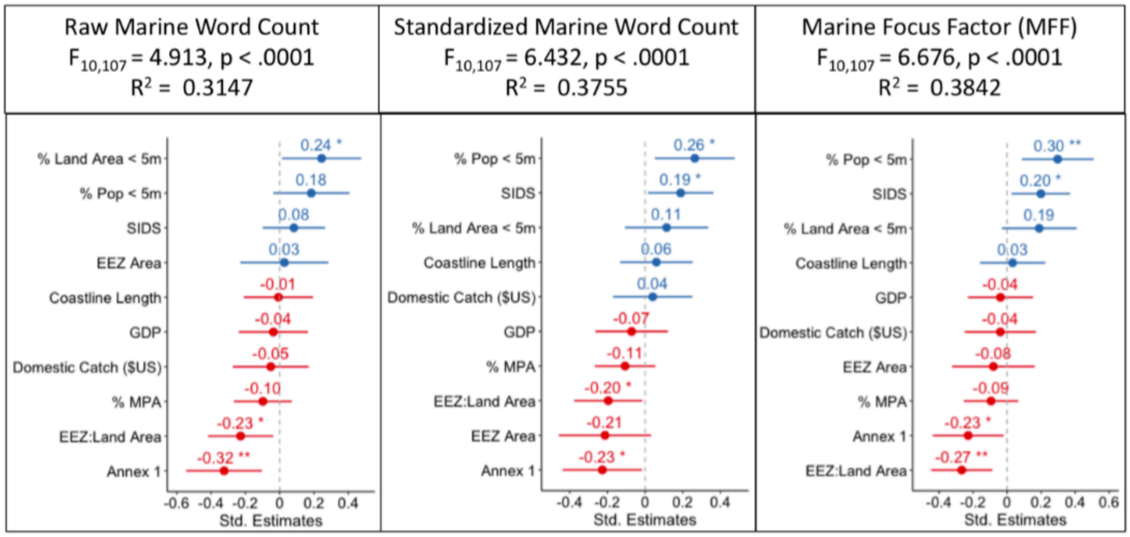


Figure S5b. Standardized coefficients from the multiple linear regression analysis with raw marine word count (left), standardized marine word count (middle), and Marine Focus Factor (MFF) (right) as the dependent variables. Raw marine word count and MFF were square root transformed and standardized marine word count was logit transformed to fit a multiple linear regression model to the data. Variables with positive (blue) and negative (red) influence on the dependent variable shown, with bars indicating two standard deviations in the error estimate. Asterisks denote statistically significant variables (* $p < 0.05$, ** $p < 0.01$).

Since several of the explanatory variables likely co-varied (ex. being a Small Island Developing State and having a large EEZ:Land Area ratio), we also tested the covariance of all explanatory variables utilized in the multiple linear regression model and present the Correlogram (Fig S5c) and correlation matrix (Table S5) below. Variance inflation factors (VIFs) were checked and were less than 3 for all explanatory variables (ranging from 1.15 for % MPA to 2.67 for EEZ Area). Based on the relatively low VIFs, we do not believe multicollinearity is an issue.

SIDS refers to if the country is a member of the Small Island Developing States (SIDS) negotiating bloc. EEZ:Land represents the ratio of the area of national marine territory (the Exclusive Economic Zone) to the national land area. %LAND refers to the percentage of low-lying land area (less than 5 m above sea level). %POP refers to the percentage of the total population living in low-lying areas (less than 5 m above sea level). %MPA refers to the percentage of the total marine territory that is protected. FISH ($US) refers to the annual fisheries landing value. GDP refers to the gross domestic product. COAST refers to the total coastline length. EEZ Area refers to the total area of national marine territory (the Exclusive Economic Zone). Annex1 refers to if the country is a member of Annex 1 of the United Nations Framework Convention on Climate Change (UNFCCC). For more information on how data for explanatory variables was obtained, please see manuscript methods.

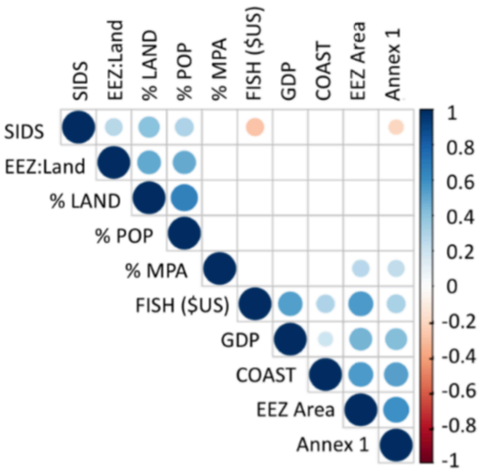


Figure S5c. Correlogram showing statistically significant ($p < 0.05$) positive (blue) and negative (red) correlation between explanatory variables used in the multiple linear regression model. The color scale represents correlation coefficients, with light colors representing small but significant correlations. Most statistically significant correlations are positive.

Var1	Var2	cor	p
% LAND	% POP	0.6699	0.0000
% LAND	% MPA	-0.0712	0.4436
% POP	% MPA	-0.0058	0.9502
% LAND	FISH ($US)	-0.1008	0.2773
% POP	FISH ($US)	-0.0541	0.5606
% MPA	FISH ($US)	0.0478	0.6075
% LAND	COAST	-0.0614	0.5087
% POP	COAST	-0.0761	0.4129
% MPA	COAST	0.1298	0.1611
FISH ($US)	COAST	0.2994	0.0010
% LAND	EEZ Area	0.0484	0.6030
% POP	EEZ Area	-0.0369	0.6913
% MPA	EEZ Area	0.2634	0.0040
FISH ($US)	EEZ Area	0.5589	0.0000
COAST	EEZ Area	0.5558	0.0000
% LAND	EEZ:Land	0.5079	0.0000
% POP	EEZ:Land	0.4914	0.0000
% MPA	EEZ:Land	-0.0694	0.4550
FISH ($US)	EEZ:Land	-0.0793	0.3933
COAST	EEZ:Land	-0.0442	0.6347
EEZ Area	EEZ:Land	0.0549	0.5545
% LAND	GDP	-0.0629	0.4988
% POP	GDP	-0.0528	0.5704
% MPA	GDP	0.1603	0.0830
FISH ($US)	GDP	0.5404	0.0000
COAST	GDP	0.1934	0.0359
EEZ Area	GDP	0.4660	0.0000
EEZ:Land	GDP	-0.0404	0.6637
% LAND	Annex 1	-0.0939	0.3117
% POP	Annex 1	-0.0872	0.3480
% MPA	Annex 1	0.2498	0.0064
FISH ($US)	Annex 1	0.3121	0.0006
COAST	Annex 1	0.5345	0.0000
EEZ Area	Annex 1	0.6079	0.0000
EEZ:Land	Annex 1	-0.0550	0.5543
GDP	Annex 1	0.4294	0.0000
% LAND	SIDS	0.4031	0.0000
% POP	SIDS	0.3090	0.0007
% MPA	SIDS	-0.1133	0.2219
FISH ($US)	SIDS	-0.2850	0.0018
COAST	SIDS	-0.1479	0.1099
EEZ Area	SIDS	-0.1053	0.2563
EEZ:Land	SIDS	0.2743	0.0026
GDP	SIDS	-0.1427	0.1231
Annex 1	SIDS	-0.2016	0.0286

Table S5d. Table shows correlation coefficients (cor) and significance values (p) between all explanatory variables utilized in the multiple linear regression model.

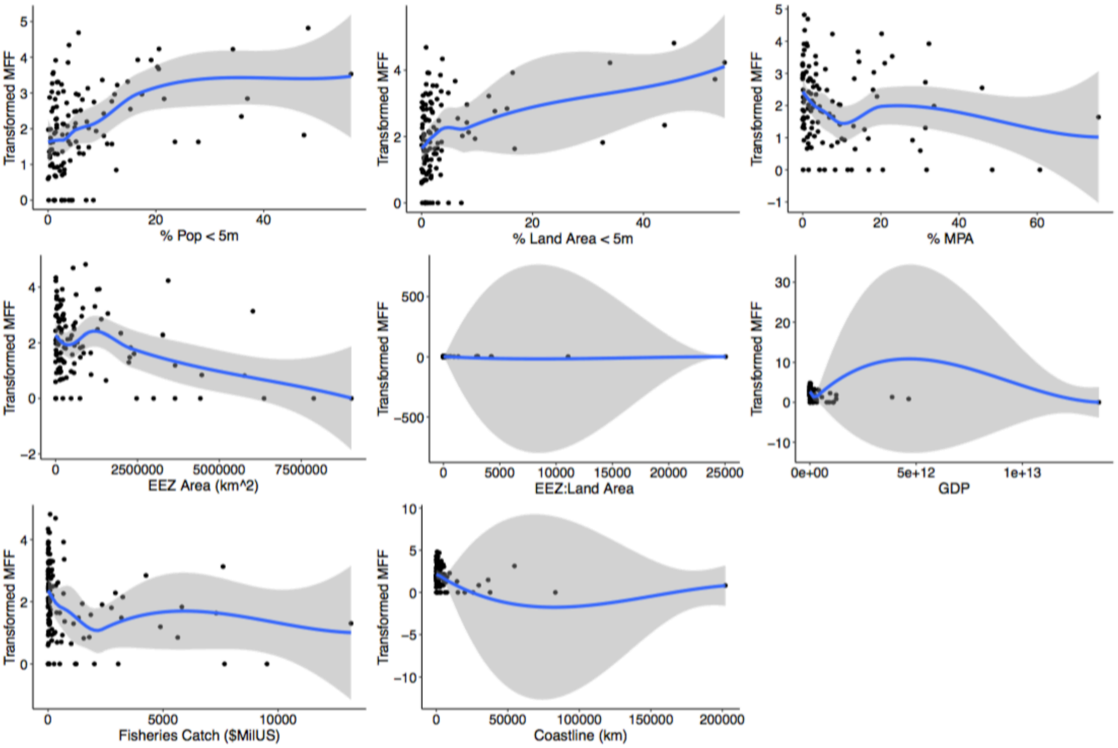
While most NDCs were available in English, those that did not have an English translation available (Spanish (8), French (12), and Arabic (2)) were analyzed by native language speakers who were also fluent in English, following the same protocol. To ensure that differences in calculated MFF were not influenced by the person coding the NDCs, we included the language of the NDC as an additional variable in the multiple linear regression analysis. We found that there was no significant influence of NDC language on NDC MFF ($p > 0.05$). The table below presents a summary of the model output with NDC language added as additional explanatory variables. Adding NDC language also did not change the model results with respect to any of the other explanatory variables.

Explanatory Variable	**p-value**	**Significance**
% LAND	0.085	
% POP	**0.005**	**
% MPA	0.166	
FISH ($US)	0.695	
COAST	0.751	
EEZ Area	0.603	
EEZ:Land	**0.004**	**
GDP	0.699	
Annex 1	**0.038**	*
SIDS	**0.032**	*
English NDC	0.332	
French NDC	0.117	
Spanish NDC	0.400	
Arabic NDC	N/A	N/A

Table S5e. This table shows the results for the multiple linear regression analysis when NDC language is added as an additional explanatory variable ($F_{13,104} = 5.427$, $p < 0.0001$). Asterisks denote statistically significant variables (* $p < 0.05$, ** $p < 0.01$) and statistically significant variables are also indicated in bold. Language of the NDC was not found to have a significant influence on calculated marine focus factor (MFF).

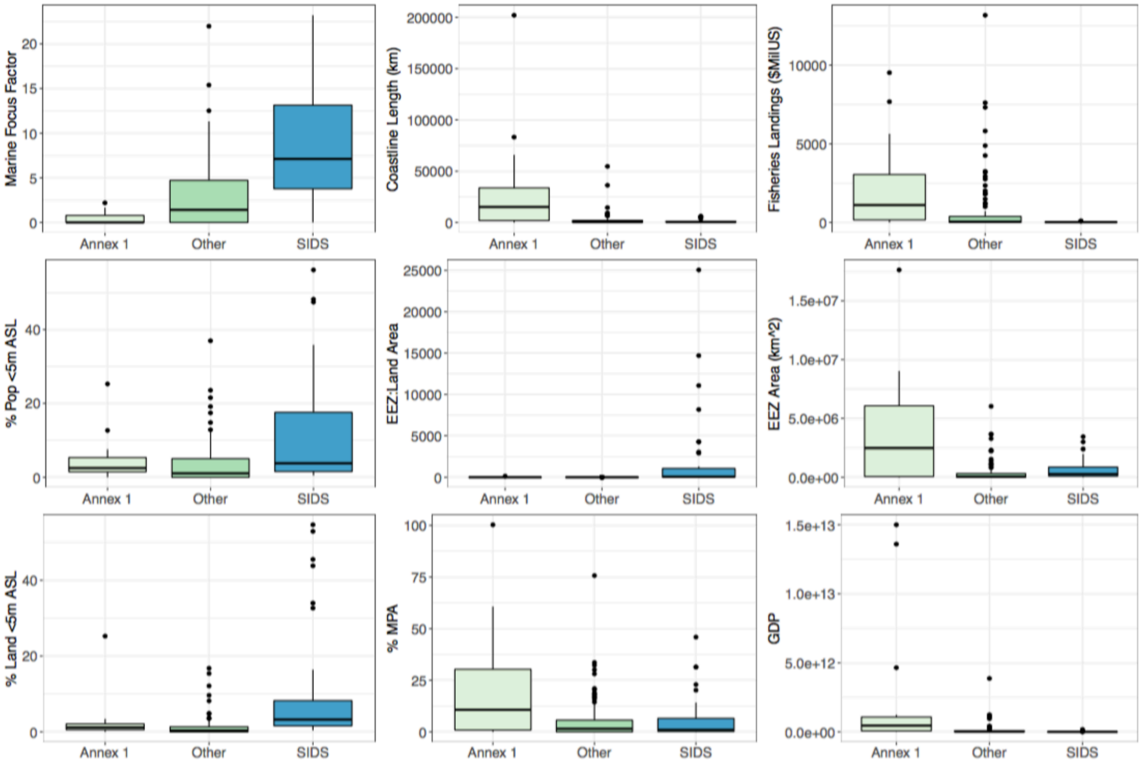
S6. Scatterplot relationships between the continuous explanatory variables tested in the multiple linear regression analysis and the Marine Focus Factor (MFF)

Scatterplots show the relationship between the continuous explanatory variables used in the multiple linear regression analysis and the Marine Focus Factor (MFF) (square-root transformed). Displayed dataset includes the 118 NDCs included for the multiple linear regression analysis (landlocked countries are excluded, as well as Montenegro, EU, Cook Islands, Monaco, Nauru, and Niue for which data on the full-suite of explanatory variables were not available). The blue line shows an estimate of the conditional mean function, with the shaded band representing 95% point-wise confidence intervals. Explanatory variables are: percentage of the population living in areas less than 5 m above sea level (% Pop < 5m), percentage of land area that was less than 5 m above sea level (% Land Area < 5m), the percent of the marine territory that was protected (% MPA), the total exclusive economic zone (EEZ) area (EEZ Area (km^2)), the ratio of EEZ to land area (EEZ:Land Area), the gross domestic product (GDP), domestic fisheries landing value (Fisheries Catch ($MilUS)), and the coastline length (km) (Coastline (km)). Information on where data for explanatory variables were obtained is provided in the manuscript methods.



S7. Boxplots of how tested continuous explanatory variables differ across negotiating blocs (Annex 1, SIDS, Other)

Boxplots show how the Marine Focus Factor (MFF) and all tested continuous explanatory variables differ across negotiating blocs (Annex 1, Small Island Developing States (SIDS), and Parties that are neither Annex 1 nor SIDS). Displayed dataset includes the 161 NDCs analyzed in this study. Explanatory variables are: percentage of the population living in areas less than 5 m above sea level (% Pop <5m ASL), percentage of land area that was less than 5 m above sea level (% Land < 5m ASL), the value of the annual fisheries catch (Fisheries landings ($MilUS)), the coastline length (km) (Coastline Length (km)), the gross domestic product (GDP), the percent of the marine territory that was protected (% MPA), the total exclusive economic zone (EEZ) area (EEZ Area (km^2)), and the ratio of EEZ to land area (EEZ:Land Area). Information on where data for explanatory variables were obtained is provided in the manuscript methods.



S8. Influence of additional fishery-related variables on Marine Focus Factor (MFF)

Two additional fisheries-related explanatory variables were tested to ensure that the non-significant influence of the domestic fisheries landing value on marine focus factor (MFF) of national climate pledges was robust. These additional variables were capture fisheries production (in metric tons) for 2014 and domestic fisheries landing values (in millions of $US) for 2010 standardized to national GDP. Data for capture fisheries production were obtained from the World Bank and originate from the Food and Agriculture Organization. Capture fisheries production measures the volume of fish catches landed by a country for all commercial, industrial, recreational and subsistence purposes. Data for domestic fisheries landing values were obtained from the Sea Around Us project on September 6, 2016 and represent fisheries landed value reconstructed domestic catch in constant 2005 $US. These data were then standardized to 2010 GDP (in constant 2005 $US) for the fisheries:GDP variable. Scatterplot relationships between these three fisheries-relevant explanatory variables and MFF are shown (Figure S8a).

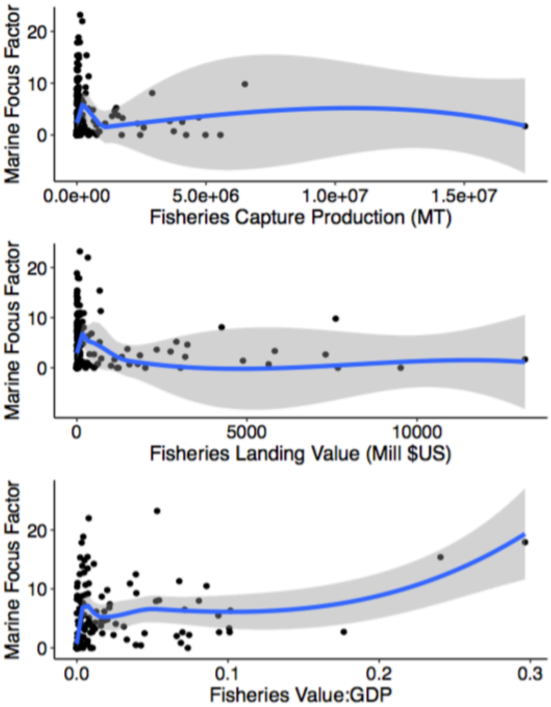


Figure S7a. Scatterplots show the relationship between the continuous fisheries explanatory variables used in the multiple linear regression analysis and the Marine Focus Factor (MFF). The blue line shows an estimate of the conditional mean function, with the shaded band representing 95% point-wise confidence intervals.

All three fisheries-relevant explanatory variables were found to have no significant relationship with MFF ($p > 0.05$) in a multiple linear regression model (Fisheries Production ($p = 0.88$), Fisheries Landing Value ($p = 0.94$), Fisheries Landing Value Standardized to GDP ($p = 0.30$)). Model fit was also not improved by adding these additional fisheries variables ($F_{12,105} = 5.611$, $p < .0001$, $R^2 = 0.39$). The updated figure of standardized coefficients from the multiple linear regression model that includes all three fisheries-related explanatory variables is shown (Figure S8b).

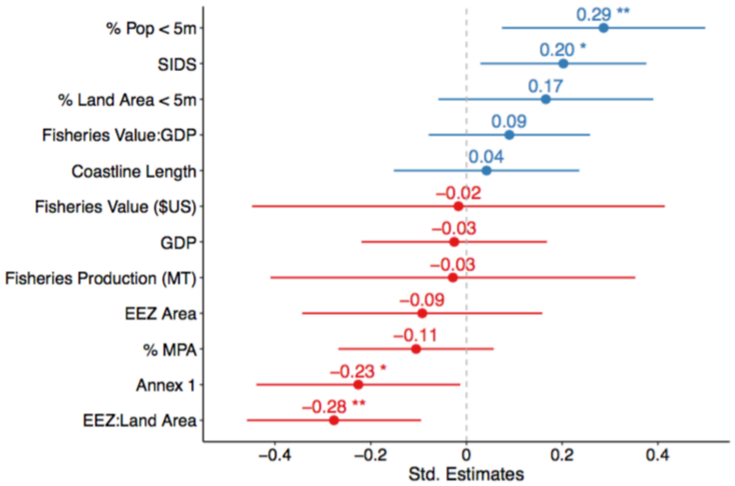


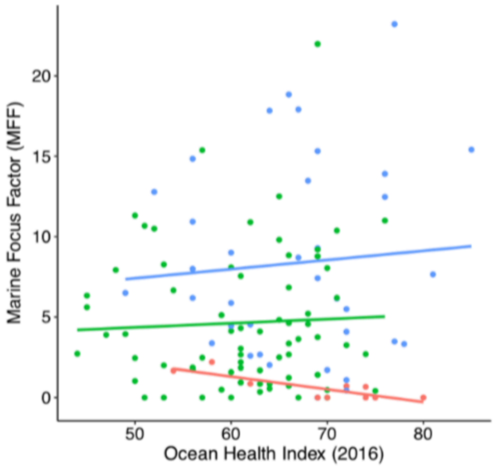
Figure S8b. Standardized coefficients from the multiple linear regression analysis, which includes all three fisheries-related explanatory variables in addition to the other explanatory variables tested in the manuscript. Marine Focus Factor (MFF) is the dependent variable. Variables with positive (blue) and negative (red) impacts on MFF shown, with bars indicating two standard deviations in the error estimate. Asterisks denote statistically significant variables (* $p < 0.05$, ** $p < 0.01$).

While the lack of correlation between fisheries value and MFF of climate pledges is surprising, the result appears to be robust. Potential explanations for this finding may be that while fisheries impacts are of broad concern to climate policy-makers, as revealed by the fact that 72 countries included fisheries impacts within the adaptation section of their NDCs, the actual value of the fishery may not be considered if climate policy-makers are not directly interacting with fisheries managers in developing NDCs. Getting accurate data on fisheries landings and landing value, especially for developing countries, has many recognized challenges, which could also introduce more error into these explanatory variables.

S9. Influence of the Ocean Health Index on Marine Focus Factor (MFF)

To further explore the difference in marine focus of NDCs between Annex 1 and other Parties, we sought out available marine-focused governance indices that could be added to the core analysis. While a standardized marine-governance index was unavailable, we decided to test the Ocean Health Index in our multiple regression mode. The Ocean Health Index measures ocean health across countries and an index is calculated for every coastal country using a composite of ten public goals: food provision, artisanal fishing opportunity, natural products, carbon storage, coastal protection, tourism and recreation, coastal livelihoods and economies, sense of place, clean waters, and biodiversity. We assume that countries with a higher Ocean Health Index (OHI) may also have better marine governance in place and better marine management schemes. In support of this assumption, developed countries generally score higher on this index than developing countries[31].

We hypothesized that countries with a higher Ocean Health Index score, and thereby hypothetically better marine governance, would be more likely to include a greater focus on marine issues in their NDCs. However, we found this not to be the case. No significant relationship was found between Ocean Health Index and Marine Focus Factor ($p = 0.483$) when this additional explanatory variable was added to the multiple linear regression and the model was not improved ($F_{11,106} = 6.085, p < .0001, R^2 = 0.39$). Adding OHI did not change the model results with respect to any of the other explanatory variables. The relationship between OHI and MFF is shown as a scatterplot with fitted linear regressions below, with colors representing countries that are Annex 1 Parties (red), Small Island Developing States (SIDS) Parties (blue), and other Parties that are neither Annex 1 nor SIDS (green). Results of the multiple linear regression analysis with OHI added as an additional explanatory variable are shown in the table on the right.



Explanatory Variable	p-value	Significance
% LAND	0.089	
% POP	**0.005**	**
% MPA	0.277	
FISH ($US)	0.702	
COAST	0.725	
EEZ Area	0.674	
EEZ:Land	**0.005**	**
GDP	0.688	
Annex 1	**0.034**	*
SIDS	**0.021**	*
OHI (2016)	0.483	

S10. The influence of explanatory variables on Marine Focus Factor (MFF) of the Small Island Developing States (SIDS) Parties

The Small Island Developing States (SIDS) are an important negotiating group in the UNFCCC and, in the manuscript analysis, we found that being a SIDS had a significant positive effect on the Marine Focus Factor (MFF) of NDCs. Given that the full dataset of explanatory variables was available for 36 SIDS Parties that submitted NDCs, we were able to examine whether the explanatory variables that were explaining trends in MFF overall were consistent with those explaining trends in MFF within the SIDS. Parties included in this analysis were: Antigua and Barbuda, Bahamas, Barbados, Belize, Cabo Verde, Comoros, Dominica, Dominican Republic, Micronesia, Fiji, Grenada, Guinea-Bissau, Guyana, Haiti, Jamaica, Bahrain, Kiribati, Maldives, Marshall Islands, Mauritius, Palau, Papua New Guinea, Cuba, St. Lucia, Samoa, Seychelles, Singapore, Solomon Islands, St. Vincent and the Grenadines, St. Kitts and Nevis, Sao Tome and Principe, Suriname, Tonga, Trinidad and Tobago, Tuvalu, and Vanuatu. MFFs ranged from 0 (Micronesia) to 23.209 (Maldives). The median MFF for the SIDS group was 6.955 and the mean MFF was 8.358, and the distribution was right-skewed (Fig S10a), with more NDCs having a lower MFF.

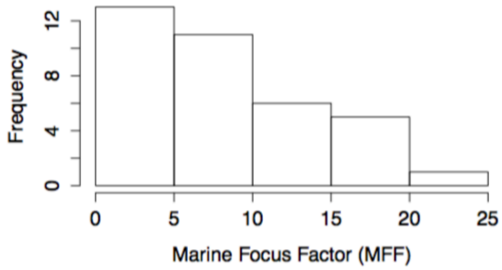


Figure S10a. Histogram of the distribution of NDC Marine Focus Factors (MFFs) for the Small Island Developing States (SIDS).

Largely the same explanatory variables were used for this analysis, with a few differences. These include that SIDS and Annex1 were no longer included as explanatory variables because the analysis only includes SIDS. We also added two additional explanatory variables (GE 2015 and OHI 2016) to try and better explain factors that were giving rise to differences in ocean focus within this negotiating bloc. GE 2015 is a metric for government effectiveness for 2015. These data were obtained from the Worldwide Governance Indicators 2016 Update (www.govindicators.org). OHI 2016 measures ocean health across countries, and calculated values from 2016 were used (http://data.oceanhealthindex.org/data-and-downloads).

A significant regression equation was found ($F_{10,25} = 2.5$, $p = 0.031$), and the model explains 50% of the variance in MFF for NDCs of SIDS Parties ($R^2 = 0.5$). Variance inflation factors were checked for all explanatory variables and all were below 4, ranging from 1.30 (% MPA) to 3.61 (% POP). We found that EEZ:Land Area has a significant negative influence on NDC MFF ($p < 0.01$). This is consistent with the result for the overall NDC dataset and suggests the larger ratio between marine national territory and land territory was not equating to a higher focus on marine topics, but was having the opposite effect. EEZ size itself was found to have no influence on MFF ($p = 0.98$). We also found that both the percent of land area below 5 m above sea level (ASL) and the percent of population living below 5 m ASL had a significant positive effect on NDC MFF ($p < 0.05$). The positive correlation between MFF and the percentage of low-lying area and percentage of the population living in low-lying areas was also consistent with the results of the overall analysis. Interestingly, the Ocean Health Index had no significant influence on MFF ($p = 0.23$) and the government effectiveness index had no significant influence on MFF ($p = 0.77$). These results show that similar explanatory variables are influencing the level of marine focus in the NDCs of SIDS as for the NDCs of all Parties in the UNFCCC.

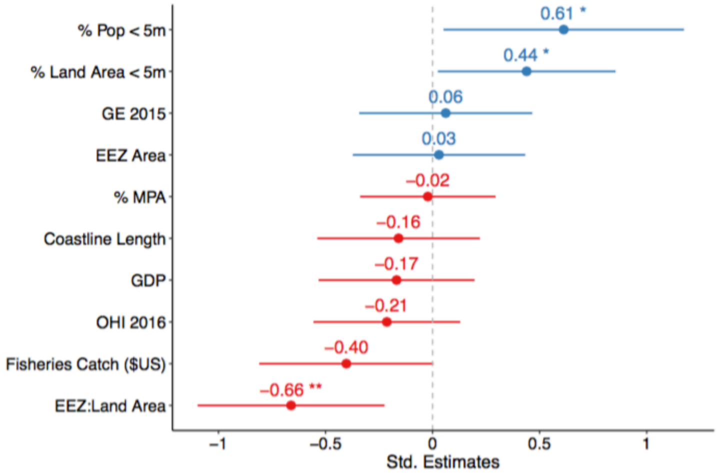


Figure S10b. Standardized coefficients from the multiple linear regression with Marine Focus Factor (MFF) as the dependent variable for only the Small Island Developing States (SIDS) (n = 36). Variables with positive (blue) and negative (red) impacts on MFF shown, with bars indicating two standard deviations in the error estimate. Asterisks denote statistically significant variables (* $p < 0.05$, ** $p < 0.01$).

S11. Deconstructing the Marine Focus Factor (MFF) into coastal and ocean components

To further explore the influence of the explanatory variables on the marine focus of Nationally Determined Contributions (NDCs), we deconstructed the Marine Focus Factor (MFF) into a coastline-related and an ocean-related component. For the coastal component, we included keywords "coast*", "mangrove", "marsh", "wetland", and "sea level", as well as any additional keywords that referred to coastal infrastructure (ex. "sea ports"), coastal vulnerabilities (ex. "saltwater intrusion"), and land-based activities (ex. "seawater desalination"). For the ocean component, we included keywords "ocean", "marine", "coral", "reef", "fish*", "acidification", "deoxygenation", "blue economy", "seagrass", "blue carbon", "sea", "oxygen", "aquaculture", "offshore", "ocean warming", "maritime", and "wave" as well as any additional keywords that referred to ocean activities (ex. "shipping") and ocean concerns (ex. "bleaching" and "aragonite saturation").

Totaled across all 161 NDCs, the number of coastal and ocean keywords used was similar (1237 coastal keywords and 1027 ocean keywords). The marine word count for each of these two components (coastal and ocean) was then standardized to the total word count for each NDC, and used as the metric to further evaluate the explanatory power of certain predictor variables on the marine focus of NDCs. To more closely meet the assumptions of normality, an epsilon value representing half of the lowest standardized ocean or coastal word count value was added to each of the standardized word counts, and the data were then logit transformed. We utilized the same multiple linear regression approach with the same explanatory variables as used in the main manuscript, but performed the analysis for these deconstructed ocean and coastal components of the MFF.

We found that for the coastal component, the results were similar to the results of the main model presented in the manuscript: the percentage of the total population living in low-lying areas (< 5m above sea level) had a significant positive effect on coastal focus ($p < 0.01$), while the ratio of Exclusive Economic Zone area to land area and whether the country was an Annex 1 Party both had a significant negative effect on coastal focus ($p < 0.01$ and $p < 0.05$, respectively). Being a Small Island Developing State (SIDS) also positively influenced coastal focus ($p = 0.07$). This model was able to explain 39% of the variance in coastal focus ($F_{10,107} = 6.866$, $p < 0.001$). In contrast, the only explanatory variable that significantly influenced ocean focus was whether the country was a SIDS, which was positively correlated with ocean focus ($p < 0.05$). The model was only able to explain 23% of the variance in ocean focus ($F_{10,107} = 3.227$, $p = 0.001$), suggesting that other untested explanatory variables may be more important for influencing how much ocean focus is included in NDCs. This result is intriguing and suggests that other factors, such as how the NDCs were developed, may be particularly important in explaining differences in the amount of attention devoted to ocean-related topics in NDCs.

S12. Summaries of 20 randomly selected Nationally Determined Contributions (NDCs) and discussion of their calculated Marine Focus Factor (MFF)

These summaries are provided to offer a qualitative view of what ocean elements the Marine Focus Factor is capturing. NDC summaries are organized from high to low MFF and summaries present an overview of all marine topics included within the NDC. All information included in these summaries (except for the county's location) is found within the NDCs. It should be noted that when information about other national policies is included, the information is taken directly from the NDC and does not represent additional research into these policy documents. This was done to standardize the gathering of information for this analysis. We assume that topics that are explicitly included in the NDC are those that are nationally prioritized and viewed as of importance by the authors of the NDC.

Seychelles (MFF = 15.415)

The Seychelles is an island nation in the Indian Ocean and submitted a long (18 page NDC) with a high marine focus. The NDC states that as a Small Island Developing State (SIDS), priority concern is given to adaptation, which is estimated to cost at least USD 295 million to implement the adaptation contributions for 2030. The short mitigation section does recognize the carbon sequestration capacity of ocean biomass and marine ecosystems (blue carbon) but excludes this from calculations. However, the potential of additional carbon sinks in the form of marine ecosystems is recognized in the NDC and included in the Seychelles Strategic Plan 2040. Marine climate impacts receive a lot of focus in this NDC, including sea level rise and impacts to coastal and marine resources and coastal tourism. The main climate change threats include increases in sea temperature, changes in acidity and damage to marine ecosystems, increases in storms and storm surges, and sea level rise, and these threats are expected to significantly impact fisheries and tourism. The NDC states that a lot of human activity is concentrated in the low-lying coastal areas which are at highest risk of flooding from heavy rainfall, storm surges, and sea level rise. Coastal tourism, human health in high-density coastal areas, waste in coastal locations, food security (fisheries), and coastal and marine resources are considered vulnerabilities. The NDC highlights the need to support local and sustainable climate-smart fisheries efforts and the Seychelles have developed a Blue Economy national policy. A Sustainable Development Strategy includes climate adaptation in the sectors of tourism, biodiversity, and fisheries. A Biodiversity Strategy and Action Plan includes cross-sectoral projects with climate change adaptation implications in areas of sustainable tourism, watershed management, and sustainable fisheries. Seychelles has also established a Blue Economy Research Institute which will aim to function as a hub for climate change related research. The NDC also lists current supported projects for addressing climate change adaptation, which include: "three ecosystem-based adaptation projects funded by the GEF Climate Change Adaptation Fund, UNEP and the Government of China. The projects focus on management of coastal ecosystems, protection of mangroves, and sustainable watershed management collectively," and a fisheries project, "The Ministry of Agriculture and Fisheries and its associated parastatals (Seychelles Agriculture Agency and the Seychelles Fishing Authority) have been receiving support from donors including the African Development Bank, the International Fund for Agriculture Development, the Japanese Government and others to help work towards more sustainable agriculture and fisheries and contribute to improving food and nutrition security." The "blue economy" is an important component of the NDC and Seychelles is developing a Marine Spatial Planning project that will coordinate different interest in the blue economy while including climate change adaptation. One of the specific adaptation contributions is to set up a proper marine resource management institution, which is estimated to require USD 15 million. The NDC calls for more research to understand changes in ocean and air currents, the interplay between climate change and other climate phenomena such as El Nino, and on climate change impacts for industrial and artisanal fisheries, and in general highlights shortfalls in terms of capacity building and research. The very high MFF (15.415) received by this NDC accurately reflects the thorough and detailed inclusion of marine topics within the national climate plans of the Seychelles and the high integration of marine climate adaptation across many national ministries and policies under the philosophy of the blue economy. The summary only presents a sampling of marine topics that are found in the NDC, and more details can be found in the NDC itself.

Mauritius (MFF = 15.323)

Mauritius is an island nation in the South West Indian Ocean and submitted a short NDC (6 pages). The NDC specifies that it was the result of a participatory multi-stakeholder and cross-sectoral consultative process involving all relevant partners. This may explain part of the reason why it had such a thorough marine focus, as reflected by the very high MFF. The NDC specifies the area of the Exclusive Economic Zone, indicating that the marine territory is being considered in the creation of the NDC. The NDC lists the many ways in which Mauritius is vulnerable to climate impacts, several of which include the ocean/marine areas, "The country is highly vulnerable to the impacts of climate change, manifesting itself in several ways, including among others, intense cyclones, abnormal tidal surges, prolonged droughts, flash floods and increase of sea surface temperature." Further vulnerabilities are also specified: "the ecosystem and natural habitat of fish and other marine species are being rapidly eroded due to adverse impacts of climate change, with some coral reefs under the threat of extinction." The NDC also specifies that the coastal zone is important because it is used to cater to the tourism industry: "natural assets, such as beaches, which are vital to the tourism industry may deteriorate, posing threat to some $50 million in value from the sector by 2050." Coral bleaching, sea level rise, and beach erosion impacts are noted multiple times in the NDC, and coastal zone management is one of the country's adaptation priorities. A small desalination project is also included as an adaptation component in the NDC. Additional adaptation priorities/plans include: climate smart fisheries ("Development and implementation of sustainable fishing management plans, strengthening of institutional capacity and adaptation of infrastructure (quay) to climate change (sea level rise)") and improvement of marine and terrestrial biodiversity resilience ("Improvement of the management of marine and terrestrial protected areas and expansion of protected area network including rehabilitation of wetlands, sea-grass, mangrove plantation, increase in tree coverage areas and coral reef rehabilitation/farming"). Marine topics are also included in the country's mitigation contribution because "smart use of marine resources" is one of the listed mitigation activities, however no additional policy information is provided. The very high MFF (15.323) reflects the abundant references to marine or coastal ecosystems and related economic activities in the otherwise relatively short NDC and the diversity of different categories considered by the NDC (12 categories - Coastline Impacts/Adaptation; Ocean Warming Impacts; Tourism Impacts/Adaptation; Fisheries Impacts/Adaptation; Protecting Marine Biodiversity; Creation of Marine Protected Areas; Conservation and Ecosystem Based Management; Marine Ecosystem Impacts; Mangrove Restoration/Management for Adaptation; Coral Reef Impacts; Fisheries Management for Mitigation; Coral Bleaching).

Eritrea (MFF = 10.674)
Eritrea is a coastal nation, bordering the Red Sea, and submitted an intermediate length NDC (14 pages). The NDC explicitly includes marine resources as one of the country's vulnerable sectors to climate change impacts. The NDC states that the diverse ecogeograpic zones of the country provide unique habitat for the marine and terrestrial fauna and flora, and that both marine and terrestrial ecosystems have been negatively affected by climate change. Specifically, the following impacts are listed: "Over the past 60 years temperature has risen by approximately 1.7°C with tremendous impact on biodiversity losses, sea level rise and coral bleaching due to increase in sea water temperature, decline in food production, loss of biodiversity and overall loss of resilience of the ecosystem." Food insecurity is an important vulnerability, with artisanal fisheries constituting a main economic activity for the population. The NDC included a specific section on marine resource development as an adaptation component: "As Eritrea is coastal state, climate change has direct impact on the development of marine resources. In the major cities, efforts are underway to monitor the sea level rise, increase sea water temperature and acidity. In this regard, the state has introduced and plans to promote an Integrated Coastal Marine and Islands Resources Management System through enforcement of policy measures and legal frameworks. Promote sustainable fishing techniques through training and, equipping with boats and fishing gear. This will ensure adequate protection and sustainable exploitation of Eritrea's coastal, marine and island resources and the development of the fisheries sector." The NDC also lists several marine focused adaptation goals for 2030 which include, "the development of marine and terrestrial protected areas over 1.5 million ha" and "desalination of seawater for domestic and economic sectors in 15 coastal towns and villages and 7 islands." The NDC specifies that 167 million ($US) will be needed in international support to meet the marine sector adaptation measures for 2030. The NDC also includes a section on the need for additional research and development, including time series data and scientific research, for all sectors (includes the marine sector). In contrast to some other NDCs from developing countries, Eritrea's NDC was well developed and listed many specific programs and policies, as well as existing national policy documents. The high MFF (10.674) reflects the range of different marine adaptation components included in the NDC (8 categories - Coastline Impacts/Adaptation; Fisheries Impacts/Adaptation; Marine Ecosystem Impacts; Ocean Warming Impacts; Ocean Acidification Impacts; Coral Bleaching; Creation of Marine Protected Areas; Seawater Desalination) as well as the addition of a section on additional marine research needs. However, the NDC did not include marine ecosystems in the mitigation section.

Indonesia (MFF = 9.802)
Indonesia submitted an intermediate length NDC (11 pages) with a high marine focus. It states that it is located in a pivotal geographic position in the global ocean conveyor belt, and relates this to the role Indonesia must play in combatting climate change, but it is unclear what is meant by this. Indonesia recognizes the vulnerability of low-lying areas in the archipelago and "views integrated land- and ocean-based climate change adaptation and mitigation efforts as a critical strategic consideration in achieving climate resilience in food, water, and energy." Sea level rise is an adaptation concern, and the NDC states that "the poorest and most marginalized populations tend to live in high-risk areas that are prone to flooding, landslides, sea level rise, and water shortages due to drought." Reducing risks to all development sectors, including maritime and fisheries, is Indonesia's medium-term climate change adaptation strategy goal.

Indonesia is also developing additional legal instruments for coastal and small islands management. The NDC specifies that various stakeholders, including academia the private sector, and civil society organizations, were consulted in the preparation of this NDC, and notes that the NDC preparation takes into account the 2015 SDGs, including conservation and sustainable use of the oceans, seas, and marine resources. This NDC employs a landscape approach, covering terrestrial, coastal and marine ecosystems, and promotes climate resilience in food, water and energy by improving its management of natural resources by protecting and restoring key terrestrial, coastal and marine ecosystems. Improving fisheries productivity is included in the unconditional mitigation section. Further adaptation actions include integrating watershed management. The MFF (9.802) reflects that marine topics receive a fair amount of focus in this NDC, but that in contrast to NDCs that received a higher MFF, specific policies and funding mechanisms are lacking.

Solomon Islands (MFF = 9.281)
The Solomon Islands submitted an intermediate length NDC (14 pages) that has a high focus on marine topics. The NDC begins by introducing the coastal geography of the Solomon Islands, stating that it is an island nation comprised of an archipelago of 994 islands with many islands being low-lying coral atolls. Its coastline is the second largest in the Pacific and it has an Exclusive Economic Zone (EEZ) that is tuna-rich and potentially mineral-rich. Coastal areas are surrounded by fringing reefs and lagoons and 80% of the national population live in low lying coastal areas. Fisheries is an important economic sector. The NDC acknowledges carbon storage in the ocean ecosystem in the mitigation section. Sea transport is also included in the mitigation section as a source of greenhouse gas emissions that could be reduced. The NDC specifies that adaptation is not an option, but rather a matter of survival, with sea level rise being one of the key issues. The NDC cites results from the Pacific Climate Change Scientific Programme which projects that sea surface temperature will increase around the Solomon Islands. King tides and sea level rise are listed as vulnerabilities, and unusual king tides are cited to have caused coastal erosion, considerable damage to coral reefs, coastal inundation, pollution of water sources and damage to coastal infrastructures. Fisheries and marine resources and coastal protection are also included as sectors in the National Programme of Action. Tsunami impacts are also included in the NDC but are not counted for the MFF, since they are not related to climate change. Interestingly, some of the detail in the NDC suggests that ocean scientists may have contributed to developing this NDC: "The interannual climate of Solomon Islands is basically driven by natural drivers such as the Inter-Tropical Convergence Zone (ITCZ), the South Pacific Convergence Zone (SPCZ), the West Monsoon and the El Nino Southern Oscillation (ENSO)" and "During an El Nino ocean surface waters over the western Pacific (including Solomon Islands) are usually cooler than normal and warmer than normal from central to eastern of the Pacific…The divergence results in nutrient rich waters rising to the ocean surface in the eastern Pacific causing outbreaks in plankton growth which is followed by tuna stocks." The MFF (9.281) reflects the high amount of focus on marine topics, but the NDC tends to include more descriptions of impacts than detailed policy objectives, showing that a high MFF does not always indicate a thorough policy approach.

Djibouti (MFF = 8.778)
The Republic of Djibouti is a coastal nation, bordering the Red Sea and Gulf of Aden. It submitted an intermediate-long length NDC (15 pages) that had a high ocean focus and this is

reflected by its high calculated MFF (8.778). The NDC provides a detailed mitigation component, and mitigation plans include a marine component. The NDC includes plans for a tidal power plant in Goubet that would utilize tidal turbines as a renewable energy source, but these plans are conditional on the provision of additional finance and are not a priority component of the NDC. The NDC also contains a high focus on adaptation, which is likely a result of the country identifying itself as highly vulnerable to climate change and in great need of investment from the international community for adaptation measures. In the NDC, "protection against rising sea levels" and "protection of biodiversity" are listed as priority adaptation objectives (biodiversity includes mangrove biodiversity - specified later in the NDC). Coastal impacts from climate change are a priority concern for the country and are included several times in the NDC and are also listed as included in the country's National Adaptation Programme of Action. The NDC also specifies disappearing coral cover as a climate impact to the country's marine ecosystems. The adaptation plans listed are not just theoretical, but include some that are already funded adaptation measures. For example, the "PRAREV-PECHE" is funded through the International Fund for Agriculture Development and includes sustainable co-management of marine resources, mangrove rehabilitation for coastal protection, restoration of coral reefs, and the development of ecotourism activities. Other funded projects listed in the NDC include 2 desalination plant projects and a project to strength resilience of two rural coastal communities, with plans including ecosystem rehabilitation. In summary, the NDC included a variety of ways that marine ecosystems were included as adaptation components (8 categories - Coastline Impacts/Adaptation; Fisheries Impacts/Adaptation; Mangrove Restoration/Management for Adaptation; Tourism Impacts/Adaptation; Marine Ecosystem Impacts; Coral Reef Impacts; Ocean Warming Impacts; Seawater Desalination) and one way marine ecosystems were included as mitigation components (1 category - Ocean Renewable Energy). The high MFF (8.778) reflects the high inclusion of marine adaptation categories with some policy details, and the more minimal inclusion of marine ecosystems as mitigation components.

Sudan (MFF = 8.265)
Sudan borders the Red Sea and submitted a long NDC (18 pages). Adaptation is the first and overriding priority of Sudan’s climate actions and hence constitutes a major part of Sudan’s NDC. The coastal zone is one of the sectors focused on in the adaptation component of the NDC, and the NDC specifies: “Sudan’s coastal zone faces several major climate-related hazards, namely sea level rise, increase of seawater temperature and salinity changes in addition to storm surge intensification.” These impacts have given rise to the following vulnerabilities: coral reef bleaching, loss of mangrove areas, decline fish production, loss of other marine resources, and inundation of coastal resources and infrastructure. Sudan’s adaptation contributions for the coastal zone sector include: “1) New information systems: Enhancing monitoring programs in natural and urban settings to detect biological, physical, and chemical changes and responses due to direct and indirect effects of climate change; 2) Implement integrated coastal zone management: an integrated approach to land use planning, creation of ecological buffer zones, establishing protected inland zones to accommodate salt marsh, mangrove and sea grass; 3) Building awareness: This involves enhancing the awareness of coastal developers through national and international activities, technical assistance, and capacity-building.” The relatively high MFF (8.265) reflects the inclusion of diverse marine topics as well as a greater level of specificity of marine impacts and adaptation contributions.

Vietnam (MFF = 8.087)

Vietnam submitted an intermediate length NDC (11 pages) that included substantial inclusion of marine topics, with coastal vulnerability and management, sea level rise, and mangrove activities receiving a large amount of focus. Wetlands are included in the land use, land use change and forestry (LULUCF) section and enhancing carbon sinks for the LULUCF section is one of the specified mitigation targets. Reducing greenhouse gas emissions from fisheries is also a mitigation goal. Adaptation is an important focus of the NDC and marine topics receive the most attention in this section. The NDC states that sea levels have already risen by about 20 cm and the Mekong Delta is one of the world's most susceptible and vulnerable delta regions to sea level rise. The NDC includes projections for how much land area and the percentage of the population that will be impacted if sea levels rise by 100cm. Saltwater intrusion and storm surges are also a threat. Marine-specific climate change adaptation priority actions include: 1) developing an assessment and monitoring system for sea level rise, 2) protecting, restoring, planting, and improving the quality of coastal forests, including mangroves, especially in coastal estuaries and the Mekong and Red River deltas, and 3) responding to sea level rise and urban inundation through implementing integrated coastal zone management, using sea level rise scenarios for planning for infrastructure and resettlement, implementing anti-inundation measures for large coastal cities, upgrading and completing sea dykes, and controlling saltwater intrusion. The NDC also calls for additional capacity building for technology to protect the coastline and for sustainable aquaculture production. The NDC also has several marine-specific key indicators that will be used for evaluating climate change adaptation activities, which include: the construction of piers and boat storm shelters and installation of sufficient communication equipment on offshore fishing boats, as well as increasing the area of protected forest in coastal areas to 380,000 hectares, including 20,000 to 50,000ha of additional mangrove planting. The relatively high MFF (8.087) reflects the relatively in-depth plans proposed for managing risks in the coastal sector, but is lower than the MFF received by some other NDCs because most of the focus is on coastal impacts.

Marshall Islands (MFF = 5.490)

The Marshall Islands is an island nation of 24 low-lying coral atolls in the North Pacific. It submitted an intermediate length NDC (10 pages) with an intermediate marine focus. The NDC includes marine ecosystems as both mitigation and adaptation components of the NDC. For the mitigation component, the NDC references the use of transformational technologies, including Ocean Thermal Energy Conversion (OTEC), as a source of renewable energy that will allow the country to meet mitigation goals. Sea transport is also included in the NDC as a sector of anthropogenic GHG emissions. The NDC also includes mangrove rehabilitation as an example of a marine focus that would have both mitigation and adaptation benefits by enhancing carbon sinks and protecting water resources. The NDC states that communities and infrastructure face major impacts from: "sea- level rise, sea surges, typhoons and rainfall intensity; water and food security issues from changing rainfall patterns and ocean acidification; health issues from rising temperatures and prolonged drought periods, as well as the potential for increasing peak wind speeds and changes to ocean circulation patterns", however, additional adaptation plans for these are laid out in the National Climate Change Policy Framework (NCCPF) national policy document. The NDC also points out that the country has created two additional national documents that set out adaptation actions: the Joint National Action Plan (JNAP) and the Climate Change Adaptation and Disaster Risk Management National Action Plan (DRM NAP). While the NDC received an intermediate MFF (5.490) which reflects its inclusion of marine ecosystems as both mitigation and adaptation components, the MFF may be underrepresenting how the Marshall Islands is considering marine ecosystems in its climate change mitigation and adaptation plans because more specific adaptation plans are likely present in their other national policy documents. This is an inherent weakness of this type of analysis, but analyzing additional national policy documents is outside of the scope of this analysis and would also not allow for a standardized comparison across countries (which analyzing the NDCs allows for).

Georgia (MFF = 4.556)
Georgia is a coastal nation, bordering the Black Sea, and submitted a short-intermediate length NDC (8 pages). The NDC specifies sea level rise and other factors in the Black Sea as a negative consequence of climate change, and includes a more detailed section on coastal impacts: "Sea level rise impacts are projected to induce multiple negative consequences in coastal zone of Georgia. It is imperative to assess and implement adaptation measures in order to minimize economic losses. Combination of various coastal zone protection technologies are recommended by the second "Technology Needs Assessment" report of Georgia to prevent the significant damage caused by the Black Sea level rise. According to the National communications of Georgia to the UNFCCC costs of the coastline adaptation program is estimated about 600 million USD. In absence of adaptation measures the estimated losses only in the tourism sector will reach about 2 billion USD by 2030. Due to very high social costs involved, priority will be given to the integrated coastal planning and management instruments, rather than investments in coastal erosion abatement only." While the NDC includes a section on coastal impacts, the intermediate MFF (4.556) for the NDC reflects the low diversity of topics covered (4 categories - Coastline Impacts/Adaptation; Tourism Impacts/Adaptation; Additional Research Requirements; Ocean Warming Impacts) and no inclusion of marine ecosystems as mitigation components.

Tonga (MFF = 4.079)
Tonga is an island nation in the Central South Pacific. It submitted an intermediate-long length NDC (15 pages) that has a considerable focus on marine topics. The NDC states that Tonga is one of the most vulnerable countries to sea level rise, and vulnerabilities to coastal impacts are high (with 30% of mobilized development assistance over the last six years having been directed to address extensive coastal erosion). Seawall building is part of their resilience building response capacity. The NDC cites a recent report from the Pacific-Australian Climate Chance Science and Adaptation Planning Program (PACCSAP) and includes that ocean acidification, risk of coral bleaching, and sea level rise are all predicted to increase in the future with very high confidence. Degradation of marine resources is listed as a concern and the NDC lists that the current national fisheries policies need to be reviewed from a climate perspective to ensure they support a Resilient Tonga. One of Tonga's mitigation contributions to climate action is to double the 2015 number of Marine Protected Areas by 2030 (though it is unclear how this would lower greenhouse gas emission). The NDC also includes impacts from tsunamis, storm surges, and tropical cyclones but these were not included in the keyword search since these are not direct climate change impacts, and therefore are not reflected in the MFF for Tonga. The importance of trees for protection of coastal areas is identified and there is a substantial section on forest protection for adaptation and mitigation benefits. Given that this is an island nation, some of these forests may be mangroves, however we do not make this assumption given that this is not

specified in the NDC. The MFF score (4.079) reflects that while marine topics do receive a fair amount of focus in this NDC, few specific policies or details are provided for the marine topics.

Morocco (MFF = 3.624)
Morocco is a coastal nation bordering the Mediterranean Sea to the north and the Atlantic Ocean to the west. It submitted an intermediate-long length NDC (15 pages) that includes marine ecosystems both within the mitigation and adaptation section but focuses exclusively on marine topics as they pertain to economic uses (fisheries) and human population vulnerabilities (i.e. coastal impacts and sea level rise). Fisheries are included in the energy sector under the laid out mitigation strategy, though this sector makes up a very minor component of the country's energy use. Fisheries, aquaculture, and coastal ecosystems are also listed in the NDC as highly vulnerable to climate change impacts, and the NDC says that Morocco prioritizes minimizing risks of climate changes impacts (adaptation) than reducing greenhouse gas emissions (mitigation), with 64% of climate-related spending going to adaptation. Sea level rise is also stated to be a vulnerability. The adaptation plans target specific sectors, with the coast being one of the sectors, since coastal zones are considered to be one of the most vulnerable areas for the Moroccan population. A National Strategy for Integrated Coastal Management is also already in place, which includes climate change adaptation. Risk management approaches for these vulnerable areas are reliant on observation and research systems to better understand current and future climate risks, and the NDC calls for additional technical and institutional capacity building, particularly regarding the creation of data and knowledge sharing. One of the objectives of Morocco's adaptation component is also to protect fishery resources through an ecosystem-based adaptation approach. Morocco also includes desalination plans in its NDC (desalination of 285 million m^3/year of drinking water supply by 2030). Erosion control in priority watersheds is also an adaptation goal. The relatively low MFF (3.624) reflects the inclusion of marine topics that pertain to direct human-use but the lack of a marine conservation focus in the NDC and a lack of detailed plans relating to marine topics (as opposed to a more thorough focus on plans relating to freshwater sources).

Ecuador (MFF = 2.687)
Despite being a coastal nation on South America's Pacific coast, Ecuador's NDC received a relatively low MFF (2.687). It submitted an intermediate length NDC (13 pages) that includes marine ecosystems rarely and mostly superficially. Marine ecosystems are only included as adaptation components in this NDC in 4 categories (Protecting Marine Biodiversity; Marine Ecosystem Impacts; Management of Watersheds for Adaptation; Coastline Impacts/Adaptation). Marine topics are considered in the greatest detail in the ecosystem sector of the NDC: "This will foster biologic terrestrial and marine and coastal biodiversity conservation. Furthermore, climate change criterion will be incorporated and implemented in the management plans for protected areas as well as in studies on the dynamics of terrestrial and marine and coastal ecosystems, their population and their relations with fulfilling human necessities, particularly in light of possible climate change scenarios." No specific plans are given in the NDC for marine adaptation or management. The NDC makes several mentions of increasing the amount of clean energy coming from hydroelectric plants, but since most hydroelectric plants utilize freshwater systems, these are not included in calculating the MFF. The low MFF (2.687) reflects the lack of concrete marine-focused adaptation plans and the lack of any marine-focused mitigation components.

Myanmar (MFF = 2.487)
Myanmar is a coastal nation, bordering the Bay of Bengal and Andaman Sea, and submitted a long NDC (18 pages) that contained a minor marine focus (MFF = 2.487). The development of the NDC is stated to have been a nationally led process, with the Ministry of Environmental Conservation and Forestry (MOECAF) acting as the focal point for NDC development. Unsurprisingly, the NDC is very focused on the forestry sector for mitigation and adaptation components. The NDC states that Myanmar is one of the most highly vulnerable countries in the world to the adverse impacts of climate change, and specifies sea level rise as one of these vulnerabilities. The NDC specifies that adaptation to the "devastating effects of climate change" is the national priority. Hydroelectrical power is important for the energy sector of this NDC, but is assumed to utilize freshwater sources, and therefore not considered in MFF calculations. Increasing the resilience of mangroves and coastal communities which are at risk of flooding is included in the forest management component of the NDC within the mitigation section of the NDC. The NDC also specifies that Myanmar is implementing a project for Mangrove Rehabilitation Plan to the Enhancement of Disaster Prevention in Coastal and Delta Area. A National Watershed Management Policy is also drafted. Fisheries are specified as being important in supporting the population. Even though Myanmar provided a thorough, detailed NDC and has a long coastline, the NDC is very limited in consideration of marine mitigation or adaptation issues, with most of the marine adaptation components being focused only on coastal impacts of sea-level rise, and receiving less focus than other topics in the NDC. Coastal zone protection is only considered as a third priority level sector. No consideration is given to marine ecosystem consequences of climate change. The low MFF (2.487) accurately reflects the limited focus on marine issues in this lengthy NDC.

Iceland (MFF = 2.195)
Iceland is a coastal nation in the northern Atlantic, and submitted a short NDC (3 pages). Marine ecosystems are included very minimally in the NDC but they are included in the following context. Iceland specifies that wetland restoration will be included in the country's goal of meeting mitigation target. The NDC also mentions that Iceland will look at the fisheries sector as a sector for mitigation options, but no additional details are provided. The NDC only includes mitigation components, and no section on adaptation is included. The low MFF (2.195) accurately reflects the minimal focus on marine ecosystems in the NDC.

Armenia (MFF = 0.655)
Even though Armenia is a landlocked country, its NDC recognizes oceans as one of Earth's ecosystems that absorb greenhouse gas emissions by explicitly stating this in their applied definition for GHG neutral emissions volume: "the total annual volume of GHG emissions, which can be fully absorbed by the earth's ecosystems (ocean, land vegetation, soil) and be irreversibly accumulated in the ecosystems (around 11 Gt/year) carbon dioxide equivalent." As a result, the mitigation value of the ocean is recognized in this NDC, even though there is no direct policy proposed regarding marine ecosystems since Armenia does not have any national marine territory. In terms of the adaptation component included in the NDC, Armenia prioritizes aquatic natural ecosystems and agriculture (including fisheries) as most vulnerable sectors to climate change, however, these references were not included in calculating the MFF because these are assumed to pertain to freshwater aquatic systems and fisheries (since Armenia has no marine

territory). The calculated MFF is very low (0.655), reflecting that oceans are included in the NDC but in a very limited context.

Australia (MFF = 0)
Australia's NDC is short (3 pages long) and is focused almost exclusively on mitigation. Sectors covered by the NDC include "energy; industrial processes and product use; agriculture; land-use; land-use change and forestry; waste." There is no explicit mention of anything pertaining to oceans or marine ecosystems, or use of marine ecosystems (such as aquaculture or fisheries). While it is possible that these are implicit under some of the sectors listed, we felt that using explicit mentions of marine-related topics to calculate the MFF introduced less subjective bias during the data collection and thereby increased reproducibility of the results. As a result, Australia's NDC received a MFF of 0 for having no explicit mention of coastal, marine or ocean ecosystems or any inclusion of any sectors or components that are ocean or marine inclusive.

USA (MFF = 0)
The US submitted a short NDC (5 pages) which contained no explicit mention of ocean or marine topics in either mitigation or adaptation plans. This is reflected by the low MFF of 0. The NDC is focused exclusively on mitigation measures, which include fuel standards for vehicles, building sector emissions, and policies under the Clean Air Act. It should be noted that the NDC specifies that the US target covers all IPCC sectors, which theoretically includes the wetland supplement. However, since no policy actions are specified and wetlands are not explicitly covered by the NDC, while other sectors are explicitly covered, we do not include this in the MFF calculation.

Belarus (MFF = 0)
Belarus is a landlocked country with no marine territory. It submitted an NDC of intermediate length (8 pages) that is focused largely on mitigation, and includes land-use change components to its mitigation strategy (including increasing sustainable forest management, restoring peatlands, preserving wetlands that are important waterfowl habitat, and further conserving natural ecosystems and protected areas). The keyword search identified "wetlands" in the NDC, but these were not counted in calculating the MFF since they were assumed to be freshwater wetlands, since Belarus has no marine territory. Since Belarus has no explicit mention of ocean or marine ecosystems, it received an MFF of 0.

Nepal (MFF = 0)
Nepal is a land-locked country and possessed no marine territory. It submitted an intermediate length NDC (12 pages) that was prepared through a broad-based stakeholder consultation process. Nepal's NDC focuses on both mitigation and adaptation components and includes watershed and forest conservation, as well as forest management as a carbon storage mechanism (including implementing REDD+ policies). Watersheds are assumed to be freshwater given the lack of marine territory. Hydroelectric power is also included in the NDC, but this is also assumed to be from freshwater sources. Interestingly, conservation and management of forest and freshwater aquatic systems are treated in this NDC in a manner similar to how mangrove, marine, and coastal systems are treated in NDCs from coastal nations that received high MFFs. The low MFF of 0, accurately reflects the lack of marine inclusion in this NDC.

Chapter 7, in full, is a reprint of the material as it appears in **Gallo, ND,** Victor, DG, and Levin, LA (2017) Ocean commitments under the Paris Agreement. *Nature Climate Change* 7, 833-838. The dissertation author was the primary investigator and author of this material.

CHAPTER 8

Conclusions

Natalya D. Gallo

8.1 Key findings of the dissertation

To predict how demersal fish communities on continental margins may be affected by ocean deoxygenation, we must first understand what conditions demersal fishes can live in, how low oxygen conditions currently influence attributes of community ecology in systems that have strong gradients in oxygen, and how natural variability of conditions experienced by seafloor communities compares to the magnitude of change expected under climate projections. This dissertation focuses on demersal fish communities in areas with oxygen minimum zones (OMZs) to answer these questions.

Studying the Rule-Breakers

Throughout the course of this dissertation, I frequently encountered the misassumption that demersal fishes were excluded from OMZs because, in general, fish show greater sensitivity to hypoxia compared to most invertebrates (Vaquer-Sunyer and Duarte 2008) and fish kills frequently accompany hypoxic events in shallow systems (Grantham et al. 2004), which affects our intuition. However, demersal fishes living in OMZs around the world are clearly unaware of their presumed intolerance to hypoxia (Fig. 1 A). In reviewing studies, I found that demersal fish have been documented in every OMZ system for which data were available (Chapter 2). In several cases, demersal fishes were even present under oxygen conditions so low that invertebrate megafauna were excluded, such as on the Pakistan margin (Murty et al. 2009). Though OMZ studies often noted fish observations, authors seemed to be unsure what to make of these – observations were often caveated with the suggestion that fish were simply passing through and not residing under the conditions they were observed under, or otherwise briefly mentioned before re-focusing on invertebrate community trends and zonation.

Seventy-seven demersal fish species from 16 orders were identified in the comparative review as capable of living under OMZ conditions (Gallo and Levin 2016), and this list continues to expand (Chapter 3), showing that demersal fishes are important components of OMZ communities worldwide. No single demersal fish family or genus has exploited all OMZs globally (Gallo and Levin 2016), suggesting that extreme hypoxia tolerance has evolved multiple times in demersal fishes. This provides scientists with a rich comparative opportunity to study the mechanisms that underlie hypoxia tolerance across species, families, and orders (Fig. 1 B).

For Chapters 3 and 4, I focused on one of the most extreme OMZ systems in the world – the Gulf of California. Despite the extensive low oxygen conditions, high densities of demersal fishes were observed living where oxygen conditions were nearly anoxic (Chapter 3, 4), supporting the findings from Chapter 2. To show that demersal fishes were residing in these low oxygen habitats, and not simply passing through, we looked at the probability density of the distributions of two species, the cusk-eel *Cherublemma emmelas* and the catshark *Cephalurus cephalus*, in relation to oxygen conditions across multiple ROV dives. While these species were abundant under suboxic conditions ($[O_2] < 5$ μmol kg^{-1}), they were absent in better oxygenated environments in our study, suggesting a habitat preference for low-oxygen environments (Chapter 4).

Based on their oxygen niches, *C. emmelas* and *C. cephalus* may represent the most hypoxia tolerant fish species known to date. The peak distribution for both species was at oxygen levels of 1.5-2 μmol kg^{-1} ($pO_2 = 0.1\text{-}0.15$ kPa) (Chapter 4). Deutsch et al. (2015)

suggest that species distributions are limited by metabolic conditions that are 2-5 times their critical oxygen threshold (P_{crit}). Assuming the conservative value of 2, this suggests that the P_{crit} for *C. emmelas* and *C. cephalus* is ~0.05 kPa. For comparison, previous studies that combine data from marine and freshwater studies have reported the P_{crit} for fishes overall ranging from 1.02-16.2 kPa (Rogers et al. 2016), and the P_{crit} of specifically hypoxia-tolerant fishes ranging from 0.80-5.33 kPa (Nilsson 2010). The estimated P_{crit} for these species is therefore several times lower than for any previously reported fish species.

OMZs provide the perfect conditions for evolution of extreme hypoxia tolerance due to the chronic, extensive, severely hypoxic conditions that are present over millions of years, though the regional and vertical extent and severity of hypoxia can change through time (Moffitt et al. 2013, Moffitt et al. 2015). Since there was no term to describe animals that appear to be specialized to low-oxygen conditions, the term "ligooxyphile" has been proposed (Chapter 4), which should aid in comparing low-oxygen specialists across systems. From the perspective of ocean deoxygenation, marine ligooxyphiles may expand their ranges as low oxygen conditions expand with climate change, as shown recently for the OMZ-tolerant pink urchin (Sato et al. 2017). However, even ligooxyphiles may experience fitness trade-offs under the lower part of their oxygen range.

Shedding Light on Community Trends

Looking across oxygen gradients in a number of regions (Chapter 2, 3, 6), one trend is very clear: demersal fish diversity is positively correlated with environmental oxygen conditions, and this relationship is non-linear, with diversity decreasing rapidly below a specific oxygen threshold. The specific oxygen threshold differs across systems, but on upwelling margins, is typically at a lower oxygen concentration than that used to define the OMZ (22.5 μmol kg^{-1}). In the Gulf of California, oxygen concentration explained 52% of the variance in demersal fish community diversity, and the oxygen threshold below which diversity sharply decreased was found to be ~7 +/- 1 μmol kg^{-1} (Chapter 3). Similarly, Keller et al. (2017), found that for the US West Coast, 32% of the variance in demersal fish species richness could be explained as a function of near-bottom oxygen conditions. When this analysis was restricted to trawls within the OMZ, the explanatory power of oxygen conditions increased to 59% (Keller et al. 2017); similar to the results from the Gulf of California, which has widespread OMZ conditions (Chapter 3).

In contrast to diversity patterns, the relationship between oxygen concentration and demersal fish catch per unit effort (CPUE) or density is not clear. Food availability or productivity may be a more important driver of these patterns than oxygen. Similarly, in coastal systems and semi-enclosed seas, the relationship between demersal fish landings and near-bottom oxygen is complicated by the positive effects of nutrient enrichment on fish populations (Breitburg 2002). Further complications in interpreting observed patterns arise because low-oxygen events can give rise to habitat compression of intolerant species, leading to a local increase in densities (Craig 2012, Piontkovski and Al-Oufi 2014). In the comparative review, no clear relationship emerged between demersal fish density or CPUE and environmental oxygen conditions (Chapter 2). In the Gulf of California, the highest density fish communities were observed under suboxic conditions and near-bottom oxygen conditions were only able to explain 4% of the variance in demersal fish densities (Chapter 3). However, for the US West Coast, Keller et al. (2017) did find a significant positive relationship between demersal fish CPUE and near-bottom oxygen conditions.

When considering the impacts of deoxygenation on seafloor communities, it is important to recognize that due to warming, fishes could experience oxygen stress even if the oxygen conditions themselves do not change. Warming temperatures increase metabolic demand, therefore species that are living close to the lower limits of their oxygen niche may find that current oxygen conditions are no longer sufficient if temperatures warm. In this way, both warming and deoxygenation work to limit the habitat area that is metabolically suitable (Deutsch et al. 2015, Pörtner et al. 2017). This is especially worth considering for bodies of water in which extensive low oxygen conditions already occur, and in which significant warming at seafloor depths is predicted under climate change scenarios (Chapter 3).

Along with impacting fish communities directly through physiological mechanisms, ocean deoxygenation may also indirectly impact communities through changes to prey availability. Diel vertically migrating (DVM) organisms provide important food subsidies to deep-sea demersal fish communities on continental margins (Trueman et al. 2014). On margins with OMZs, this mechanism of bentho-pelagic coupling may be reduced because low-oxygen waters compress the daytime depth of the DVM community (Bianchi et al. 2013, Netburn and Koslow 2015, Klevjer et al. 2016), thus cutting the demersal fish community off from these resources. Consistent with this hypothesis, in the SCB, a transition occurs from a fish community dominated by pelagic feeders to a fish community dominated by benthic feeders, and this transition corresponds to the upper boundary of the OMZ (Chapter 6). Within the OMZ core, the trophic niche of the fish community also decreases (Chapter 6). Less than 1/4 of the seafloor in the SCB is at depths shallower than the upper boundary of the OMZ, therefore most demersal fish communities in the SCB must rely on benthic resources, which is a less efficient trophic pathway. OMZ expansion with climate change may further limit the ranges of pelagic-feeding species, such as rockfish (*Sebastes spp.*) through this additional, previously undescribed, indirect mechanism (Chapter 6).

By sampling fish communities across oxygen gradients in areas with OMZs, we can predict that deoxygenation will affect demersal fish communities on continental margins in the following ways. Expansion of low oxygen conditions will lead to a shift in community composition as intolerant species are excluded and hypoxia-tolerant species become competitive (Chapter 2, 3, 5, 6). As non-hypoxic areas become hypoxic, a shift from fish-dominance to invertebrate-dominance in the community may be observed (Chapter 5). Beyond a certain region-specific oxygen threshold, demersal fish community diversity will begin to decrease rapidly until only a few fish species with extreme hypoxia tolerance are left (Chapter 2, 3, 6). Demersal fish community density or CPUE may also be affected as oxygen levels decline, but this relationship is not consistent across regions, and likely has more to do with food availability (Chapter 2, 3, 6). Decreasing oxygen conditions may also alter trophic relationships, leading to a shift from reliance on pelagic resources to benthic resources and thus lengthening the food chain supporting the demersal fish community (Chapter 6).

Appreciating the Variance Around the Mean

When considering future deoxygenation predictions, or reporting losses in oxygen through time, it is the change to the mean conditions that is considered. However, existing modes of variability determine exposure histories of animals and likely influence sensitivity of communities to climate change (Chu et al. 2018, Frieder 2014). Communities that live in areas with high natural oxygen variability may be less vulnerable to deoxygenation because the high variance may provide temporary reprieve, and thus buffer some of the negative impacts of low mean oxygen conditions. For this reason, considering the range of conditions experienced to the mean may be informative in predicting climate impacts. We find that for the SCB, relative oxygen variability is high at both 200 and 400 m, but is lower at 300 m (Chapter 5). The largest relative decrease in oxygen has been observed at 300 m in the SCB (Bograd et al. 2008), suggesting seafloor communities may be particularly vulnerable at this depth zone. This depth zone seems to be associated with high sediment resuspension, potentially due to the meeting of two water masses, making observation of communities by landers or ROVs difficult (Chapter 5). Despite seafloor communities on the upper margin experiencing substantial natural variability of environmental conditions at short time scales (daily and weekly), no community responses were observed in relation to changes in environmental conditions (Chapter 5), suggesting that animals respond to variability at these time scales by coping through physiological adjustments.

Policy Considerations

While the international climate policy community is finally starting to recognize the role of oceans and marine ecosystems in climate policy, much improvement is still needed. Currently, most ocean-focused components of national climate plans relate to sea level rise and other coastline impacts (Chapter 7). Out of 161 submitted national climate pledges, only Mauritania recognized ocean deoxygenation as an issue to be considered in its climate action plan (Gallo et al. 2017).

The SCB is one of the best studied regions in the world, and the presence of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) long-term time series has provided an invaluable record of oxygen changes in this region since the 1950s. Other regions of the world that are experiencing deoxygenation do not have the same resources and historical data available. Due to their small size and ease of use with small boats, small landers such as *DOV BEEBE* (Chapter 5), can serve as a powerful tool for monitoring environmental variability on continental margins. By coupling the collection of environmental data with community data, they can help shed light on community vulnerabilities to climate driven environmental change. Through support of the international community, scientific institutions in developed countries can help developing countries establish the capacity to monitor and study these changes, since global datasets show that deoxygenation had already reduced oxygen levels in many parts of the world (Schmidtko et al. 2017).

Literature Cited

Bianchi, D., Galbraith, E.D., Carozza, D.A., Mislan, K.A.S., Stock, C.A. 2013. Intensification of open-ocean oxygen depletion by vertically migrating animals. Nature Geoscience 6: 545-548.

Bograd, S.J., Castro, C.G., Lorenzo, E.D., Palacios, D.M., Bailey, H., Gilly, W., Chavez, F.P. 2008. Oxygen declines and the shoaling of the hypoxic boundary in the California Current. Geophys. Res. Lett. 35, L12607.

Breitburg, D. 2002. Effects of hypoxia, and the balance between hypoxia and enrichment, on coastal fishes and fisheries. Estuaries 25(4b): 767-781.

Chu, J.W.F., Curkan, C., Tunnicliffe, V. 2018. Drivers of temporal beta diversity of a benthic community in a seasonally hypoxic fjord. R. Soc. Open sci. 5: 172284.

Craig, J.K., 2012. Aggregation on the edge: effects of hypoxia avoidance on the spatial distribution of brown shrimp and demersal fishes in the Northern Gulf of Mexico. Mar. Ecol. Prog. Ser. 445, 75–95.

Deutsch, C., Ferrel, A., Seibel, B., Pörtner, H.-O., Huey, R.B. (2015) Climate change tightens a metabolic constraint on marine habitats. Science 348: 1132–1136.

Frieder, C.A. 2013. Evaluating low oxygen and pH variation and its effects on invertebrate early life stages on upwelling margins. University of California, San Diego. 182 pgs.

Gallo, N.D., Levin, L.A. 2016. Fish ecology and evolution in the world's oxygen minimum zones and implications of ocean deoxygenation. Advances in Marine Biology 74: 117-198.

Gallo, N.D., Victor, D.G., Levin, L.A. 2017. Ocean commitments under the Paris Agreement. Nature Climate Change 7: 833-838.

Grantham, B.A., Chan, F., Nielsen, K.J., Fox, D.S., Barth, J.A., Huyer, A., Lubchenko, J., Menge, B.A. 2004. Upwelling-driven nearshore hypoxia signals ecosystem and oceanographic changes in the northeast Pacific. Nature 429, 749-754.

Keller AA, Ciannelli L, Wakefield WW, Simon V, Barth JA, Pierce S (2017) Species-specific responses of demersal fish to near-bottom oxygen levels within the California Current large marine ecosystems. Mar. Ecol. Prog. Ser. 568: 151-173.

Klevjer, T.A., Irigoien, X., Rostad, A., Fraile-Nuez, E., Benitez-Barrios, V.M., Kaartvedt, S. 2016. Large scale patterns in vertical distribution and behavior of mesopelagic scattering layers. Scientific Reports 6: 19873.

Murty, S.J., Bett, B.J., Gooday, A.J., 2009. Megafaunal responses to strong oxygen gradients on the Pakistan margin of the Arabian Sea. Deep-Sea Res. II 56, 472–487.

Netburn, A.N., Koslow, J.A. 2015. Dissolved oxygen as a constraint on daytime deep scattering layer depth in the southern California current ecosystem. Deep-Sea Res. I 104: 149-158.

Nilsson, G.E. 2010. Respiratory physiology of vertebrates: Life with and without oxygen. Cambridge University Press, New York, 334 pgs.

Piontkovski, S., Al-Oufi, H., 2014. Oxygen Minimum Zone and fish landings along the Omani Shelf. J. Fish. Aquat. Sci. 9, 294–310.

Pörtner H-O, Bock C, Mark KC (2017) Oxygen- and capacity-limited thermal tolerance: bridging ecology and physiology. J. Exp. Biol. 220: 2685-2696.

Rogers, N.J., Urbina, M.A., Reardon, E.E., McKenzie, D.J., Wilson, R.W. 2016. A new analysis of hypoxia tolerance in fishes using a database of critical oxygen level (P_{crit}). Conservation Physiology 4(1): 1-19.

Sato, K.N., Levin, L.A., Schiff, K. 2017. Habitat compression and expansion of sea urchins in response to changing climate conditions on the California continental shelf and slope (1994-2013). Deep-Sea Res. II 137: 377-389.

Schmidtko, S., Stramma, L., Visbeck, M. 2017. Decline in global oceanic oxygen content during the past five decades. Nature 542: 335-339.

Trueman, C.N., Johnston, G., O'Hea, B., MacKenzie, K.M. 2014. Trophic interactions of fish communities at midwater depths enhance long-term carbon storage and benthic production on continental slopes. Proc. R. Soc. B. 281, 20140669.

Vaquer-Sunyer, R., Duarte, C.M. 2008. Thresholds of hypoxia for marine biodiversity. Proc. Natl. Acad. Sci. USA 105, 15452–57.

Figures

Figure 8.1. There is a common misperception that demersal fish can't live in oxygen minimum zones (OMZs) due to the chronic severely hypoxic conditions; on the contrary, demersal fishes are known from every OMZ for which data are available (A). If deoxygenation trends continue and low oxygen zones in the ocean expand, these highly adapted OMZ-dwelling species may expand their ranges (B). These illustrations were drawn by Bas Kohler at the 4th International Symposium on the Effects of Climate Change and the World's Oceans, in response to data I presented from Chapters 3 and 4 at the conference.