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Climate-fishery interactions in coastal ecosystems

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

in

Marine Biology with a Specialization in Interdisciplinary Environmental Research

by

Erica M. Ferrer

Committee in charge:

Professor Octavio Aburto-Oropeza, Chair
Professor Jennifer Burney
Professor Kristy J. Kroeker
Professor James J. Leichter
Professor Lisa A. Levin
Professor Brice X. Semmens

2023

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University of California San Diego

2023

DEDICATION

I dedicate this work to the family members, friends, mentors, and animal companions who have helped me on this fabulous journey. When I look outward for inspiration, or inward for motivation, I look to you!

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Chapter five, in full, is a reprint of the material printed in *Frontiers in Marine Science*, and appears as: Ferrer, E. M., Giron-Nava, A., Aburto-Oropeza, O. Overfishing increases the carbon footprint of seafood production from small-scale fisheries. *Frontiers in Marine Science*. (2022). The dissertation author was the primary investigator and author of this paper.

Appendix A, in full, is a reprint of the material printed in *Frontiers in Marine Science*, and appears as: Martin, A. H., Ferrer, E. M., Hunt, C. A., Bleeker, K., and Villasante, S. *Frontiers in Marine Science*. (2022). The dissertation author was the secondary investigator and co-author of this paper.

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- Ferrer, E. M., Giron-Nava, J. A., and Aburto-Oropeza, O. (2022). Overfishing increases in the carbon footprint of seafood production from small-scale fisheries. *Frontiers in Marine Science*, 9(768784), 1-10. doi: 10.3389/fmars.2022.768784
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FIELDS OF STUDY

Major Field: Marine Biology
Studies in Fisheries Oceanography
Studies in Global Change Biology
Studies in Marine Policy

ABSTRACT OF THE DISSERTATION

Climate-fishery interactions in coastal ecosystems

by

Erica M. Ferrer

Doctor of Philosophy in Marine Biology with a Specialization in Interdisciplinary Environmental
Research

University of California San Diego, 2023

Professor Octavio Aburto-Oropeza, Chair

Coastal ecosystems and fisheries are complex in terms of the abiotic and biotic processes that host them, and the peoples and policies that steward them. This complexity is likely to increase under climate change, and our efforts to characterize climate-fishery interactions will be of critical

importance for ensuring the long-term “sustainability” of marine ecosystems and ecosystem services. To this end, I have oriented my chapters along two major axes: understanding the biology and oceanography of coastal ecosystems under climate change; and developing applied science for sustainable seafood harvest and fisheries management.

First, I discuss changes in deoxygenation and its effects on marine organisms within the context of the Planetary Boundary Framework¹. I propose that deoxygenation be added to the framework, discussing five possible “control variables” and the various interactions that exist between deoxygenation and other climate change processes.

With these processes in mind, I explore the effects of “press-pulse” climate stress on *Mano de León* scallops, a commercially-important species traditionally fished throughout Northwest Mexico. I find that, while the effects of press-pulse climate stress are generally negative, these animals may be more resilient to change than expected.

In the second portion of my dissertation, I explore which fisheries and fishery species can be considered most “climate-friendly” from a carbon perspective. I estimate the carbon footprint of several seafood products produced by small-scale fisheries in Northwest Mexico, demonstrating how certain types of seafood have a remarkably low carbon footprint. Subsequently, I demonstrate how overfishing very likely increases the carbon footprint of seafood and fisheries.

Looking forward, I hope to use this body of research to expand the intellectual toolkit we use for understanding climate-fishery interactions.

¹ Rockström, J., Steffen, W., Noone, K., Persson, A., Chapin III, F.S., Lambin, E.F., Lenton, T.M., Scheffer, M., Folke, C., Joachim Schellnhuber, H., Nykvist, B., De Wit, C.A., Hughes, T., van der Leeuw, S., Henning, R., Sverker, S., Snyder, P.K., Costanza, R., Svedin, U., Falkenmark, M., Karlberg, L., Corell, R.W., Fabry, V.J., Hansen, J., Walker, B., Liverman, D., Richardson, K., Crutzen, P., Foley, J.A., 2009. A safe operating space for humanity. *Nature* 461, 472–475.

CHAPTER 1

INTRODUCTION

We live on a rich and dynamic planet that is rapidly changing due to a series of anthropogenic stressors (Duarte et al., 2020). To protect our planet, our networks, and ourselves, we must understand how these stressors manifest in the marine environment, and what opportunities exist for mitigation and adaptation. Across the global ocean, a general list of major stressors might include overfishing, warming and extreme weather, deoxygenation, and ocean acidification, among others. Many refer to these stressors either by name, grouped, or nested within a more general reference to “climate change.” In this dissertation, I focus on climate change, in a general sense, and its interactions with marine life and fisheries.

In the second chapter of my dissertation, I synthesize the impacts of deoxygenation in various aquatic habitats. I provide evidence and advance the argument that deoxygenation should be considered a 10th “Planetary Boundary,” much like the nine others described in the popular Planetary Boundary Framework (Rockström et al., 2009). I identify key deoxygenation thresholds for scientists and managers to be aware of, and, subsequently, I synthesize known interactions between deoxygenation and six other stressors: climate change, loss of biodiversity, biogeochemical flows, land-system change, ocean acidification, and aerosol loading. Recognizing the difficulty of a managers’ job, I explore how each of these thresholds could be applied in practice and used to help managers mitigate and adapt to the consequences of declining oxygen in their local environment. Although it is primarily intended as an interdisciplinary and science-policy piece, this chapter serves as a helpful summary of the physical, chemical, and biological changes that are co-occurring in the marine environment and will no doubt alter fisheries (IUCN, 2019).

We know that in Northwest Mexico — where the bulk of my Ph.D. research has focused — fisheries are undergoing massive changes associated with climate. For instance, the Gulf of California has experienced a prolonged period of warming and decreased primary productivity over the last decade, following a highly disruptive El Niño event in 2015 (Frawley et al., 2019). This has led to profound ecological changes in the region (e.g., Velarde et al., 2015), and documented losses of once-profitable fisheries (e.g. Jumbo Squid fishery, Frawley et al., 2019). While it remains difficult to ascribe a long-term secular trend, experts are concerned that the ocean conditions of the 2010’s may be a harbinger of what’s to come in a warmer world. With increasing ocean warming, normal patterns in “ocean weather” will be affected, and we are likely to see more stressful norms combined with more frequent and extreme events (IPCC - SROCC Report, 2019). For example, in Northwest Mexico, there have been at least three major marine heatwaves since 1981 (Holbrook et al., 2019).

In my third chapter, I wanted to test the effects of locally-relevant climate stress on a commercially-important species found in Northwest Mexico. Specifically, my colleagues and I decided to test the effects of a simulated El Niño and / or a marine heatwave on the survival and physiology of *Mano de León* scallops (*Nodipecten subnodosus*). I report evidence derived from a six-week multiple-stressors experiment conducted at the Universidad Autónoma de Baja California (in Ensenada, Mexico). This research was designed to strengthen our understanding of organisms under press versus pulse climate stress, and in particular our understanding of commercially-important bivalves in a changing ocean (see Krufft Welton et al., 2023). Ideally, this research will contribute to the management and restoration efforts of *N. subnodosus* in the highly-productive fisheries region of Baja California, Mexico.

It is hard to overstate the importance of fisheries in this region (Cisneros-Mata, 2010), and in my fourth chapter (Ferrer et al., 2021), I demonstrate how many local small-scale fisheries in Mexico provide low-carbon seafood products. Animal taxa such as bivalves, large pelagic fishes, and non-resident demersal fishes represent low-carbon fishery options, and many are fished using non-invasive gear types. In contrast, some seafood taxa (like shrimp), possess a very high carbon footprint and are often fished in ways that are harmful to the environment (e.g., bottom trawling; SOFIA Report, 2018). We find that, in many cases, the disparity in carbon footprint between these types of seafood can be explained by the type of gear used to fish them. However, there are many other factors (both social and ecological) known to underlie “sustainable” seafood and fisheries (see SOFIA Report, 2018; Sumaila & Tai, 2020).

In my fifth chapter (Ferrer et al., 2022), which focuses on the same fisheries highlighted in Chapter four, I establish that seafood generated by stocks that are fished sustainably (at or below “Maximum Sustainable Yield”) has a significantly lower carbon footprint than seafood derived from stocks that are overfished. This relationship suggests that an end to overfishing would likely lower the carbon footprint of all seafood; and, as a corollary, suggests that if we rebuild fishery stocks, fuel intensity of fishing will decline (Sumaila & Tai, 2020). Colleagues and I were presented with a unique opportunity to test this hypothesis when we looked into the curious recovery North Atlantic Hake (*Merluccius merluccius*), described in Appendix A (Martin, Ferrer, et al., 2022). Between the years of 2008 and 2018, hake stock in northern Europe increased by nearly 6-fold, and we were able to demonstrate that as stock biomass increased, fuel intensity decreased across all gear types during this period. Cumulatively, this research (Chapter five & Appendix A) suggests that, not only is ending overfishing desirable for biological, economic, and social reasons (SOFIA Report, 2018), it is also desirable from an emissions and climate-change perspective.

Throughout the chapters of my dissertation, I seek to articulate the points of nexus where knowledge developed in the multi-disciplinary arenas of climate change science, marine ecology, and fisheries oceanography can be used to support healthy ecosystems and thriving coastal communities of people. Specifically, the research presented herein describes a wide diversity of climate-fishery interactions, from those that exist as co-occurring stressors and feedbacks, to those that might constitute types of “solutions” or opportunities for improvement. I hope to use this research to help improve management and conservation outcomes for fisheries and coastal ecosystems in a warming world.

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<https://doi.org/10.1126/sciadv.1400210>

CHAPTER 2

DEOXYGENATION WITHIN THE PLANETARY BOUNDARY FRAMEWORK: CONTROL VARIABLES, INTERACTIONS, AND APPLICATIONS

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ABSTRACT

The Planetary Boundary (PB) Framework, originally proposed by Rockström et al. in 2009, outlines nine manifestations of, and limitations on, anthropogenic pressure to our biosphere. The framework, which is intended to describe the “safe” conditions required for maintaining an ecologically-familiar and stable Earth System, has proven impactful across a number of applied-science, management, and policy arenas over the last decade. As it currently stands, the PB framework includes limits like climate change, land-use change, and ocean acidification, but overlooks deoxygenation, a critically-important manifestation of anthropogenic stress in our biosphere. Deoxygenation — that is, the contemporary and precipitous loss of dissolved oxygen across essentially all of Earth’s aquatic habitats — is a global issue that has progressed rapidly over the last 50 years. Given the threat of global deoxygenation and the myriad of interactions oxygen has with other PBs, scientists have proposed that deoxygenation be added as a 10th PB to the already-existing framework. To fully realize this recommendation, it is necessary to discuss

real-world “control variables” that can be used to monitor deoxygenation and its extent, relative to known biological, chemical, and physical thresholds most would consider “unsafe.” Here, we propose five “control variables” that can be used to monitor deoxygenation and our approach towards various oxygen / deoxygenation thresholds *in situ*: a hypoxia threshold; percent oxygen saturation; the presence, absence, and behavior of sentinel species; the ratio of oxygen supply-to-demand (The Metabolic Index, Φ); and “velocity” of the Metabolic Index (CV_Φ). We discuss real-world scenarios where each control variable could be used to monitor and curtail deoxygenation and its effects, identifying obstacles that exist in practice. We then highlight key interactions that exist between dissolved oxygen and climate change, biodiversity, land-system change, ocean acidification, and aerosol loading, all of which are relevant to maintaining climate and ecological stability. We conclude with a discussion about how and when deoxygenation control variables can be useful for policy-making and management at various scales.

1. INTRODUCTION

The Planetary Boundary Framework, originally proposed by Rockström et al. (2009) and subsequently updated by others (Steffen et al., 2015; Nash et al., 2017), outlines nine manifestations of, and limitations on, anthropogenic pressure to our biosphere. These manifestations and limitations, referred to simply as “planetary boundaries” (PBs) delineate what Rockström et al. (2009) describe as a “safe operating space for humanity.” Notably, climate change and biosphere integrity (i.e., the biodiversity of genes and functional groups) are cited as “core boundaries,” with interacting effects across all other Earth-System processes (Rockström et al., 2009; Steffen et al., 2015). Increasingly so, climate change and biodiversity loss are understood as directly connected, and in similar states of crisis (e.g., Pörtner et al., 2021; Pörtner et al., 2023). It is thus worth noting how both of these boundaries are directly mediated by levels of dissolved

oxygen in our atmosphere, terrestrial soils, freshwater ecosystems, and marine environment — the latter of which we focus on here.

The framework proposes that if any one of Earth’s PBs is surpassed, our climate system as we know it will be in jeopardy of change. This helps to paint a fairly intuitive picture of Earth as a *system of systems*, where our contemporary social-ecological “balance” is borne from the interaction and stability of multiple “spheres” (UCAR, n.d.). The PB Framework is not entirely prescriptive about how human societies should develop in response to these boundaries, however, many suggest that operationalizing them may be useful for identifying ‘safe and just corridors [of action] for people and the planet’ (Rockstrom et al., 2021). Over the last decade, the PB Framework has been applied in a number of research, business, and policy relevant contexts (e.g., O’Neill et al. 2018; World Business Council for Sustainable Development – Vision 2050²; Pörtner et al., 2021; Pörtner et al., 2023), having served as a useful reference for those interested in invoking several interconnected stressors at once.

Among the many anthropogenic stressors evolving on our planet is the rapid loss of dissolved oxygen felt across Earth’s hydrosphere. This process is known as “deoxygenation,” and presents a serious threat to ecological and climate stability. In popular science media, deoxygenation has been described as our oceans, lakes, and other bodies of water “losing their breath” (e.g., GO2NE Report, 2018; Poppick, 2019) — an apt analogy given that most aquatic animals, and many microorganisms, need oxygen to survive. In less than a century, and in some cases just over a decade, the concentration of dissolved oxygen (DO) across the world’s open ocean, coastal habitats, and freshwater ecosystems has declined precipitously (GO2NE Report,

² <https://www.youtube.com/watch?v=ajxqpHslf2w>

2018; Levin, 2018; Jane et al., 2021). Yet, deoxygenation is notably absent from previous iterations of the PB Framework (Rockström et al., 2009; Steffen et al., 2015; Nash et al. 2017).

We argue that deoxygenation should be considered a planetary boundary all its own, with one or more “control variables” designed to monitor deoxygenation and prevent us from surpassing the “safe” zone in terms of climate-ecosystem stability (Rockström et al., 2009; Steffen et al., 2015; see also Rose et al., submitted). Here, we begin with a discussion of five relevant control variables that can be used to monitor the extent of global deoxygenation (and we summarize its *current* state in the ***Supplementary Materials*** section of this text). Subsequently, we discuss key interactions that exist between oxygen and established planetary boundaries (PBs), providing readers with a novel synthesis of deoxygenation’s effects across the entire Earth System (see also IUCN Report, 2019). We go on to include important takeaways for those who work in the realm of climate and biodiversity conservation and management, and end with a discussion about how this information can be used to create better strategies for the protection of aquatic organisms and ecosystems at various scales.

2. DEOXYGENATION “CONTROL VARIABLES” AND REFERENCE POINTS

The first step in defining a new planetary boundary, or augmenting one that already exists, is articulating the relevant process of Earth-System change, in this case, deoxygenation. Next, one must identify one or more “response variables” that reflect the state of that process. So, in the case of deoxygenation, we anticipate that most people would find the widespread loss of organisms, and the loss of normal chemical and ecological function, to be among the most relevant of response variables. With this in mind, we must next attempt to define one or more “control variable(s)” for that process — that is, some measure used to determine how close that process is to exceeding “safe operating conditions.” In the case of climate change, for instance, many consider the

atmospheric concentration of carbon dioxide (parts per million), or the amount of energy imbalance present at the top of our atmosphere (watts / m²) as useful control variables (Rockström et al., 2009; Steffen et al., 2015). Finally, when defining a PB, it's important to summarize the current state of that process relative to the theoretical operating conditions most would consider “safe.”

Ideally, a boundary's control variable should be universally applicable for all subsystems linked to that boundary, and should function as a robust indicator of process change at scale (Steffen et al., 2015). There should also be enough available and reliable data to apply that control variable in a meaningful way (Steffen et al., 2015). In the case of deoxygenation, experts from across disciplines consider different oxygen thresholds most salient or significant, where all are but proxies for Earth's complex web of aerobic interactions. Even amongst ourselves, as authors, we were unable to reach a consensus about which single oxygen control variable or threshold matters “most” when it comes to maintaining Earth's biodiversity and climate. With this in mind, we posit that deoxygenation should have more than one control variable, i.e., a set of multiple reference points used to monitor the speed and extent of oxygen-related changes. We describe five potentially-useful options below (**Table 2.1**).

Our recommendation for each control variable is premised on a balance of: (i) long-standing and cutting-edge deoxygenation research; (ii) data availability; (iii) the utility of defining said control variable for scientists and practitioners; and, (iv) the potential for that deoxygenation reference point / control variable to assist in monitoring, mitigation, and adaptation. Throughout this section, we describe data limitations as well as the infrastructure that does or does not exist for using certain control variables in the present day.

2.1. A HYPOXIA CUTOFF

One coarse but potentially useful oxygen threshold and control variable for people to be aware of is “hypoxia” — that is, “low oxygen,” or the oxygen level at which organisms begin to show negative symptoms of deprivation. Depending on the source / discipline, hypoxia is generally defined by an assortment of SI and non-SI units used to communicate the *concentration* of dissolved oxygen. The term “hypoxia” is frequently referenced throughout the scientific literature but tends to be a little vague in terms of any precise point value or definition. In much of the biological literature, hypoxia is cited as a dissolved oxygen concentration of $\leq 2 \text{ mg O}_2 / \text{L}$ ($\sim 60 \mu\text{mol} / \text{kg}$), however, this cutoff can mean different things for different species, at various life stages, under various temperatures, and so on. We recognize how the hypoxia cutoff of $2 \text{ mg O}_2 / \text{L}$ may be too liberal of an estimate when trying to conserve a particular species, or when exercising the principles of precautionary management. Indeed, it is estimated that $> 50\%$ of all marine benthic organisms experience lethal effects before this cutoff (Vaquer-Sunyer & Duarte, 2008). It is worth noting, however, that organisms who live in *naturally-low* oxygen environments (e.g., the deep sea) can tolerate fairly low-oxygen conditions below $2 \text{ mg O}_2 / \text{L}$ (Breitburg et al., 2018; Gallo et al., 2019; IUCN Report, 2019). Additionally, emerging evidence suggests that organisms exposed to high-oxygen or supersaturated conditions (e.g., animals in areas with high primary productivity) may be able to compensate for low-oxygen conditions that are short-lived (Giomi et al., 2019).

In their seminal paper, Vaquer-Sunyer & Duarte (2008) suggest that a more conservative cutoff of $4.6 \text{ mg O}_2 / \text{L}$ may be most appropriate when defining hypoxia in the marine environment. This value (of $4.6 \text{ mg O}_2 / \text{L}$) represents the point of oxygen availability at which an estimated 90% of all marine benthic species would avoid lethal consequences related to oxygen supply and

demand; specifically, this value is associated with the 90th percentile of the distribution of means generated by the authors' meta-analysis of lethal concentration values reported for 206 benthic species, across 872 published articles (Vaquer-Sunyer & Duarte, 2008). With this in mind, we recommend defining a hypoxia “zone of uncertainty” between 2 and 4.6 mg O₂ / L for most *coastal* environments, and refer to 2 mg O₂ / L as a boundary or reference point when discussing hypoxia across marine ecosystems in a very general way.

For reference, “suboxia,” which is also mentioned throughout the deoxygenation literature, refers to a far lower DO threshold of ~0.16 mg O₂ / L (5 μmol O₂ / kg) (Vaquer-Sunyer & Duarte, 2008; Breitburg et al., 2018; IUCN Report, 2019). Meanwhile, “anoxia” refers to the complete absence of oxygen, be it in the water column, in the sediment, in one's body tissues, etc. Suboxia or anoxia *in situ* is usually obvious given its profound effects on animal life, and since only a few select animals can survive without oxygen (Danovaro et al., 2010; Yahalomi et al., 2020). When systems go suboxic or anoxic, animals that can escape, do, and the ones that can't, perish (e.g., fish kills). The presence of suboxic or anoxic conditions has additional implications for the processes of remineralization and outgassing of greenhouse gases, as discussed further in **Section 3**. Although these states of low oxygenation are associated with fundamentally different and indeed fascinating kinds of biology and biogeochemistry, we argue that these reference points are not particularly useful within the PB context because they are so extreme. Meanwhile, at “hypoxic” levels of DO, numerous macrofauna can still be found along benthos and within the water column.

2.2. PERCENT OXYGEN SATURATION (% DO)

Another measure that we can use to monitor oxygen and identify deoxygenation thresholds is the measure of percent oxygen saturation (% DO). This metric is calculated as the concentration of DO *in situ* divided by the maximum concentration of DO that could exist in solution (at that

temperature, salinity, and barometric pressure). As a measure, % DO is essentially the same as the measure of oxygen's partial pressure in water, with a multiplicative factor, and reported in a different unit. Percent saturation (%) tends to be a little bit easier for people to interpret compared to measures of concentration (discussed above), or partial pressure, which is measured in units like Pascals (Pa) or milligrams of mercury (mmHG). It is fairly easy, however, to convert between units of DO concentration, partial pressure, and percent. The immediate benefits of referring to % DO as a control variable is that — in addition to taking temperature and salinity into account — it's fairly easy to interpret, cheap to measure, and the appropriate data have been collected at certain sites for decades (Gregoire et al., 2021). Information about oxygen saturation and % DO can also be reconstructed using proxies (e.g., Kranner et al., 2022; Limburg & Casini et al., 2018).

People who are not familiar with aquatic chemistry data can still get a relatively good feel for what environmental managers might consider “acceptable” versus “unacceptable” levels of % DO, a lot like a letter grade in school. For most coastal organisms that breathe oxygen, levels of % DO between 80% and 110% (at 25°C, 30 PSU, and pressure at sea-level) are considered normal and saturated (author pers. comm.). Somewhere between 30% and 60% DO is where many coastal macrofauna begin to show signs of duress (see Vaquer-Sunyer & Duarte, 2008), and under 30% DO saturation is generally considered “hypoxic” for most benthic organisms. In areas with naturally-occurring Oxygen Minimum Zones (OMZs), percent saturation values are usually measured below 5% ($< 20 \mu\text{mol O}_2 / \text{L}$) (Breitburg et al., 2018). Similarly, in areas with strong upwelling or highly variable oxygen conditions, % DO values can vary substantially throughout the day and by season; for example, in a study conducted by Kroeker et al. (2023) across six coastal California sites, lower- and upper-quartile values for % DO ranged anywhere from approximately 41–85% DO (estimated).

Thus, we suggest a % DO boundary around 30% to avoid the bulk of lethal effects on small- and larger-bodied organisms found outside of OMZs (see Vaquer-Sunyer & Duarte, 2008).

2.3. PRESENCE, ABSENCE, AND BEHAVIOR OF SENTINEL SPECIES

For situations where chemical data may not exist or are spotty, it might make sense to look to certain *species* as indicators of the approximate value and / or unexpected changes in DO. In many cases, the presence or absence of “sentinel species” can be used as a flag or rough approximation for low-oxygen conditions, where certain guilds and functional groups are frequently associated with high levels of oxygen. Similarly, changes in behavior can signal changes in oxygen, and the use of sentinel species as indicators may be particularly at the local level when traditional or local ecological knowledge is high. In circumstances where chemical data *are* available, monitoring population and behavioral changes among sentinel species can serve as an additionally helpful tool for understanding oxygen-related changes in ecology, fisheries, tourism, *etc.*

An obvious prerequisite for looking to sentinel species as the control variable or indicator of choice, is that we must understand which species are most sensitive to low oxygen and oxygen variability. We know, for example, that many species of marine predatory fish are vulnerable to even small losses in DO, with deleterious effects that are most pronounced among large fish at high temperatures and small fish at cool temperatures (Verberk et al., 2022). When DO drops below about 5 mg O₂ / L, most species of large-bodied marine fish (including sharks, tunas, billfishes, groupers, and snappers) will either evacuate the area, or will begin to behave in abnormal ways (Stramma et al., 2012; IUCN Report, 2019; Vedor et al., 2021). Where deoxygenation is indicated by the *absence* of large-bodied fishes, it might also be indicated by the *presence* of other, more resistant taxa, such as jellies and bacterial mats. Jellies need oxygen to survive, however,

special adaptations allow some species to store oxygen in their tissues for prolonged periods of time. This particular adaptation makes them well suited to dominate when their predators evacuate an area (Purcell et al., 2001; Ohman, 2019), and unexpected jellyfish blooms may signal local deoxygenation events (Purcell et al., 2001; IUCN Report, 2019). Likewise, low-oxygen conditions might also be signaled by the presence of certain bacterial mats that do not need a lot of oxygen to survive; a notable example of such includes those mats made from bacteria in the genus *Beggiatoa*, which grow like patterns of white cotton carpeting along the benthos, of varying size and texture (IUCN Report, 2019).

The dynamics surrounding sentinel species in freshwater environments are slightly different compared to those in marine environments, with a few important similarities. Compared to their marine counterparts, freshwater and brackish fish seem better equipped to handle short-term changes in oxygen — a trait that has most likely evolved from their history in turbid rivers, lakes, and streams (Verberk et al., 2022). Fewer fish species can survive *prolonged* periods of low oxygen, however — and popular fishery species, such as sturgeon, bass, and perch appear particularly sensitive to low DO (e.g., Stoklosa et al., 2018). Likewise, the presence of armored invertebrates, such as crabs and clams, as well as fish and invertebrate eggs, may serve as an indication of moderately high DO (Stoklosa et al., 2018). In contrast, soft-bodied invertebrates, such as slugs and worms, tend to be fairly resistant to low oxygen levels and may not prove particularly helpful as indicator species (Vaquer-Sunyer & Duarte, 2008; Stoklosa et al., 2018). At the far end of the DO spectrum, the presence of thick cyanobacteria at the surface of the water may signal *low* oxygen further down the water column, as cyanobacterial mats block light (and therefore photosynthesis) from above (e.g., Kosten et al., 2012).

Some environmental managers are already looking to sentinel species for information about local deoxygenation and hypoxia. For instance, in the City of San Diego, scientists and managers are piloting a project which looks at the behavior of oysters, and specifically their gape, as an indicator of hypoxia in the local estuary (NCOOS³), among other types of data. In a similar vein, fishers and observers can often identify when ocean weather events are occurring or likely to occur, based on their observations of animal behavior (e.g., evacuation), catch, and mortality (e.g., Cavole et al., 2020). Video footage⁴ shared by the Oregon Department of Fish and Wildlife (ODFW), for example, demonstrates what we might expect to see in terms of deoxygenation-induced mortality among popular fishery species. In the ODFW video³, we see a trap full of live crabs from the local Dungeness crab fishery immersed in mostly clear water to begin with. We watch as the water quality changes over the course of about two weeks, and within the span of a few days, the crabs inside the trap go from eating and seemingly healthy to deceased. Scientists with the ODFW have linked this period of poor water quality with low oxygen, and so the video apparently captures the consequences of hypoxia in nearly real-time, and on film.

In all cases where one might look to sentinel species as indicators of deoxygenation events or “safe” levels of oxygen, the importance of local ecological knowledge (LEK), and LEK experts who can apply what they know about species and natural history, cannot be understated.

2.4. THE METABOLIC INDEX: THE RATIO OF O₂ SUPPLY-TO-DEMAND (Φ)

Many of the physiological dynamics that drive the presence or absence of sentinel species under deoxygenation conditions can be summarized by “the Metabolic Index” (Deutsch et al., 2015), that is, the temperature-dependent ratio of O₂ supply-to-demand. For an environment to be

³ <https://coastalscience.noaa.gov/news/student-developed-sensor-used-to-measure-impacts-of-hypoxia-on-oysters/>

⁴ <https://oregonmarinereserves.com/2017/09/06/hypoxia-central-coast/>

considered ecologically habitable, the Metabolic Index (Φ) must exceed some critical value (Φ_{crit}), and is ultimately a measure of aerobic scope in an inherently oxygen-limited environment (Deutsch et al., 2015). We know that oxygen demands differ across species and ecosystems, where Φ_{crit} values for marine organisms vary from ~ 1.3 to 6.5 (Deutsch et al., 2015; Deutsch et al., 2020; Penn & Deutsch, 2022). As an organism's demand for oxygen increases (at a certain temperature and partial pressure of O_2), their Φ_{crit} shrinks and falls towards 1. Vice versa, when organisms require less oxygen, their Φ_{crit} value increases. When Φ falls *below* 1 in an environment, organisms will perish, suppress activity, or switch to anaerobic metabolism.

One of the outstanding problems for applying the Metabolic Index to management situations in the present day is that we currently lack metabolic demand data for all phyla, let alone all species (Deutsch et al., 2020), and models for oxygen supply are not always accurate. Thus, the Metabolic Index would probably be most useful as a control variable in situations where physiological data are plentiful and spatial oxygen models are accurate. This metric is likely to become more accessible going forward, as we continue to make progress in the field of experimental respirometry, and as access to *in situ* oxygen data grows.

2.5. CHANGE IN “VELOCITY” OF THE METABOLIC INDEX (CV_Φ)

The final metric by which we recommend (possibly) monitoring the status of deoxygenation is the change in velocity of organisms' Metabolic Index — that is, the change in *viable* aerobic habitat over a period of time and at a specific spatial scale, given organisms' physiological demands in that context. This proposal applies the idea of “climate velocities” (Loarie et al., 2009) to the already-mentioned Metabolic Index (Deutsch et al., 2015), and can provide us with a few key insights about the risks of deoxygenation in three-dimensional space (Parouffe et al., 2023). “Climate velocity” (CV) is a measure that has traditionally been used to

summarize the speed of temperature change over time ($^{\circ}\text{C} / \text{time}$), versus the change in temperature gradient of the local geography ($^{\circ}\text{C} / \text{area}$). A CV value tells us the speed and direction that a particular species will need to move to remain within its climatic niche (Loarie et al., 2009). For example, to maintain one's ideal thermal environment in response to rising temperatures, one animal might move a short distance up a seamount, whereas another might have to travel a long distance across the open ocean (Brito-Morales et al., 2018). In order to escape climate-induced extinction, organisms in areas with low CV values will need to move faster (and in the right direction) compared to those organisms with high CV values.

Analogously, the velocity of the Metabolic Index — what Parouffe et al. (2023) refer to as the “climate velocity of Φ ,” or CV_{Φ} — can be used to summarize the speed of change in aerobic habitat *versus* the change in aerobic habitat across the local oxygen gradient. In this respect, CV_{Φ} values account for deoxygenation extinction risks in both time and three-dimensional space, whereas the Metabolic Index is mostly two-dimensional. For example, two similar populations of fish, one living nearshore and another living offshore, might have similar Φ_{crit} and Φ values today but be differentially exposed to the risks of deoxygenation tomorrow if one has easier access to a well-oxygenated area nearby.

Parouffe et al. (2023) apply this concept of CV_{Φ} to explore changes in the metabolic habitat of organisms living in the Peru / Humboldt Current OMZ. Individuals with a $\text{CV}_{\Phi} < 0$ are at high risk of deoxygenation-induced extinction, whereas individuals with a $\text{CV}_{\Phi} > 0$ are at lower risk. Through a series of sensitivity analyses, they demonstrate that CV_{Φ} is only weakly dependent on the physiological traits of the model organism (Parouffe et al., 2023), suggesting that values for CV_{Φ} could be informative even in the absence of strong physiological priors. Ultimately, this

control variable might prove most useful in very specific geographic contexts, where downscaled oxygen models and habitat data are available.

Table 2.1. Summary information about each proposed control variable.

Deoxygenation Control Variable	Response Variable(s)	Boundary (safe operating conditions)
Hypoxia cutoff (oxygen concentration)	Increased animal die offs and ecosystem simplification.	Oxygen concentration > 2 mg / L, as this is an approximate physiological minimum for <i>many</i> species.
Percent (%) O₂ Saturation	Increased biogeochemical reactions associated with low oxygen, including those reactions which impact climate change.	A percent saturation > 30% reflects an approximate physiological minimum for many species.
Presence, absence, and behaviors of Sentinel Species	Increased animal die offs and ecosystem simplification.	The presence or absence of key indicator species, as deemed important by local peoples.
The Metabolic Index (Φ)	Increased information about extirpation and extinctions.	$\Phi = 2-5$ (ideal) $\Phi > 1$ (physiological minimum)
The “ velocity ” of the Metabolic Index (CV_{Φ})	Spatial distribution and species habitat change.	$CV_{\Phi} > 0$ (lower risk of extinction) $CV_{\Phi} < 0$ (higher risk of extinction)

3. OXYGEN’S INTERACTIONS WITH OTHER PLANETARY BOUNDARIES

The connections that exist between global deoxygenation and the other nine PBs are numerous, but for the purposes of this article, we explore those connections that are relatively well-known (**Table 2.2**) and immediately relevant to our determination of deoxygenation control variables presented in the previous section. For a comprehensive review of known interactions between oxygen and other multiple stressors, we strongly recommend readers also refer to the synthesis reports by scientists with the Global Ocean Oxygen Network (GO2NE Report, 2018) and the International Union for the Conservation of Nature (IUCN Report, 2019).

Table 2.2. Summary of key interactions between (marine) deoxygenation and other planetary boundaries.

Other Planetary Boundary	Key Interactions with Oxygen
Climate change (<i>Section 3.1</i>)	Warming caused by climate change leads to oxygen loss via changes in solubility, respiration, and ventilation (stratification). Conversely, deoxygenation may impact climate via changes to biogeochemical cycling, including perturbations to the N cycle and the production of Nitrous Oxide (a powerful greenhouse gas), or even changes to Blue Carbon (explained in <i>Section 3.5</i>).
Biogeochemical flows (<i>Section 3.2</i>)	Heavy N and P loading into aquatic environments has led to eutrophication and oxygen loss across Earth's hydrosphere. Conversely, deoxygenation reduces the availability of fixed N and increases the productivity of Nitrous Oxide through denitrification, while internal loading of P can lead to the resuspension of P and further decreases in oxygen.
Biosphere integrity (<i>Section 3.3</i>)	Deoxygenation can lead to physiological impairments among a wide assortment of organisms, loss of biodiversity and alterations in ecosystem function; there are numerous examples of this (already) happening, from the micro to macroscopic.
Ocean acidification (<i>Section 3.4</i>)	Increased respiration or eutrophication processes can drive local ocean acidification (OA). OA and deoxygenation often co-occur together, with high nutrients.
Land-system change (<i>Section 3.5</i>)	Increased nutrient runoff / turbidity near coastlines frequently leads to deoxygenation, with possible feedback effects to climate regulation via changes in the Biological Pump and Blue Carbon stocks.
Aerosol loading (<i>Section 3.6</i>)	Increased aerosol pollutant deposition of iron can lead to accelerated oxygen loss via enhancing surface production and consumption at depth. Meanwhile, the cooling effects of aerosols lessens the severity of deoxygenation via reducing warming and stratification.

3.1. CLIMATE CHANGE (AND CLIMATE REGULATION)

As a general rule, the solubility of oxygen in water decreases as temperature rises. In fact, about 50% of contemporary oxygen losses in the upper ocean ($\leq 1000\text{m}$) can be attributed to temperature changes in oxygen solubility (Schmidtke et al., 2017). Thus, a well-known feature of

climate model projections is that, at least in the upper ocean, the extent to which deoxygenation will progress in our lifetimes depends directly on our ability to limit greenhouse gas emissions and warming (Bopp et al., 2013; Keeling et al 2010; Kwiatkowski et al 2020). Under the most “liberal” warming scenarios generated by the UN’s Intergovernmental Panel on Climate Change (that is, a worst case scenario of RCP 8.5), Earth’s average air temperature is expected to warm an additional $\sim 3.7^{\circ}\text{C}$ by 2100 (relative to the 1986–2005 period), while average sea surface temperature is expected to increase by $\sim 2.6^{\circ}\text{C}$ (IPCC - SROCC Report, 2019). Concomitantly, the rate of deoxygenation in the subsurface ocean (100–600m) is projected to increase by approximately three-fold (13.3 mmol/m^3 ; Kwiatkowski et al., 2020). In contrast, under the most stringent or optimistic climate scenario (RCP 2.6), deoxygenation continues at a much slow rate and average ΔDO in the subsurface ocean will potentially stabilize at a rate of loss somewhat similar to that of today, 6.4 mmol/m^3 (versus current rate = $\sim 4.5 \text{ mmol/m}^3$; Kwiatkowski et al., 2020). Meanwhile, in the deep ocean, the long-term prognosis changes, with legacy effects of contemporary warming projected to play out over millennia. Even if we were to stop emitting CO_2 *today*, deep-sea deoxygenation will continue for many centuries (Keeling et al., 2010; Battaglia and Joos, 2018; Oschlies, 2021). These figures serve as an important reminder of the thermal inertia that already exists within Earth’s climate system, and why it is of the utmost importance that we curb our carbon footprint *quickly*.

While change in oxygen solubility remains one of the clearest links between climate change and global deoxygenation, it is imprecise, and frequently inaccurate, to assume that the severity of DO losses will be exactly proportional to changes in temperature. There exist a myriad of physical, biogeochemical, and ecological processes (many of which are directly affected by climate change) that differentially partition heat throughout the world’s hydrosphere (GO2NE Report, 2018; IUCN

Report, 2019). These processes give rise to heterogeneous changes in DO, as evidenced by deoxygenation hotspots with unequal rates of loss (Breitburg et al., 2018; Levin, 2018; Kwiatkowski et al., 2020). Oxygen stratification, in both freshwater and marine systems, is a huge driver of oxygen loss and deoxygenation trends. Under climate change, stratification is likely to increase, limiting oxygen exchange between water masses (Oschlies et al., 2018). Simultaneously, climate-induced changes in upwelling and deep-water movement may lead to OMZ expansions or changes in distribution (Oschlies et al., 2018; Busecke et al., 2022).

Conversely, there exist pathways through which deoxygenation may alter ecosystems' ability to *regulate* climate (**Table 2.2**). For instance, deoxygenation is likely to affect Earth's climate via changes in the Nitrogen cycle, where declining $[O_2]$ is associated with increased denitrification and the production of Nitrous Oxide (N_2O) (Battaglia and Joos, 2017; Schmidt et al., 2017). Nitrous Oxide is produced by microbes during nitrification and denitrification, and is a potent greenhouse gas and ozone depletor. The production of N_2O is strongly sensitive to oxygen levels within the OMZ, and in fact, low-oxygen regions account for the large majority of N_2O produced by the world's oceans (Bange et al., 2010). Thus, any expansion of OMZs may increase the production and emissions of N_2O into the atmosphere, which, in turn, would exacerbate global warming and a loss of ozone.⁵ This represents a distinct biogeochemical feedback between deoxygenation and climate regulation to be aware of, although the magnitude of this shift in N_2O equilibrium is still poorly understood, and the time horizon for resulting changes is likely to be relatively long (Bange et al., 2010; Battaglia and Joos, 2017; Limburg et al., 2017; Busecke et al., 2022).

⁵ In fact, N_2O production is currently recognized as the top contributor to stratospheric ozone depletion, another planetary boundary to be aware of (Portmann et al., 2012).

To a lesser-known extent, but within an emerging area of research, we expect increasing deoxygenation to also be associated with changes in carbon sequestration and aquatic “Blue Carbon” stocks. We explain this idea further in **Section 3.5**, as it has to do with the loss of habitat and biodiversity as well as climate.

3.2. BIOGEOCHEMICAL FLOWS: NITROGEN & PHOSPHORUS LOADING

While deoxygenation is closely tied to a number of Earth’s biogeochemical flows, including Iron, Silicon, and Sulfur, we will focus here on the interactions between deoxygenation and Nitrogen (N), and deoxygenation and Phosphorus (P). Since the invention and widespread commercial use of synthetic fertilizers over the last two hundred years, flows of N and P have been *significantly* altered by human activities. Considering that the chemical composition of the ocean has been fairly stable over the last hundreds of millions of years, even small perturbations to the N and P cycles can have significant effects on Earth’s overall biogeochemistry (Watson et al., 2017; IUCN Report, 2019). In all likelihood, N and P loading probably surpassed any “safe” threshold over a decade ago (Rockström et al., 2009; Steffen et al., 2015).

In coastal waters, deoxygenation is closely tied to nutrient-loading of N and P via terrestrial runoff, through a process known as “eutrophication.” Eutrophication is the cycle by which excess nutrients lead to hyperactive primary production, followed by the mass mortality of primary producers (i.e., algae blooms and busts). Subsequent consumption and respiration of this primary productivity (i.e., phytoplankton consumed by microbes), depletes the surrounding waters of oxygen and produces carbon dioxide (CO₂). Eutrophication is often ephemeral, ebbing and flowing with the occasional nutrient injection, such as when it rains and fertilizers are swept off of the land and into the sea, or in conjunction with seasonal warming (IUCN Report, 2019). On some occasions, however, low-oxygen conditions can persist for months to years, particularly in bodies

of water with restricted turnover (Carpenter, 2005). In areas where nutrient injections are effectively constant, as is the case for many river deltas and wetlands, low-oxygen conditions can be observed year-round (e.g., the Gulf of Mexico, Rabalais et al., 2002).

Deoxygenation affects nutrient cycling in aquatic ecosystems by altering the chemical conditions under which fundamental biological processes play out. These feedbacks can be quite complex and it is not entirely clear how the chemical equilibrium of Earth's hydrosphere will adjust in response to the widespread loss of DO (Battaglia and Joos, 2017; Busecke et al., 2022). For example, the breakdown of organic matter into its simplest inorganic forms — a process known as “remineralization” — can take place through various chemical pathways (as referenced above) *and* is temperature-dependent. At low oxygen levels, the process of remineralization typically occurs through the pathway of *denitrification*, where organic matter reacts with nitric acid (HNO_3) to form carbon dioxide (CO_2), water (H_2O), phosphoric acid (H_3PO_4), elemental nitrogen (N_2), and Nitrous Oxide (N_2O). This represents a loss of *fixed* nitrogen, which has distinct consequences for the growth and survival of primary producers who use fixed nitrogen to build their amino acids (Bianchi et al., 2012; IUCN Report, 2019).

At the same time, it seems as though excess P, both organic and inorganic, can drive the release of more P from anoxic sediments (Watson et al., 2017). It has been predicted that as phosphoric acid and its derivatives (e.g., H_3PO_4 and H_2PO_4^-) work their way up the water column, they will *stimulate* primary productivity and N fixation, along with bacterial respiration (Niemeyer et al., 2017; Oschlies et al., 2018). On net, this may counteract some of the fixed-N losses from denitrification but could also exacerbate local eutrophication and drive a reinforcing (positive) feedback loop for additional deoxygenation to occur (Niemeyer et al., 2017; Oschlies et al., 2018).

Indeed, physical evidence suggests a close link between P release from sediments and major anoxic events of the past, linked to mass extinctions (Watson, 2016; Watson et al., 2017).

3.3. BIOSPHERE INTEGRITY: LOSS OF BIODIVERSITY

Severe deoxygenation in the form of hypoxia and anoxia poses an immediate risk of asphyxiation to all organisms that “breathe” underwater. Occasionally, we are confronted with the profoundly lethal effects of deoxygenation in the form of, for example, mass “fish kills” or coastal “dead zones” (Rabalais et al., 2002). But even minor decreases in dissolved O₂ can have negative consequences for biodiversity, limiting organisms’ aerobic scope(s) and imparting significant physiological stress. To give just a few examples, sub-lethal oxygen levels have been shown to have (negative) effects on the growth, survival, and abundance of organisms at virtually every level of the food web (Vaquer-Sunyer & Duarte, 2008), from zooplankton (e.g., Roman et al., 1993), to bivalves (e.g., Gobler et al., 2014), cephalopods (e.g., Navarro et al., 2018), crustaceans (e.g., Gravinese et al., 2020), corals (e.g., Pezner et al., 2023), pelagic fishes, and benthic fishes (e.g., Domenici et al., 2007; Stramma et al., 2012; Vedor et al., 2021). Likewise, hypoxic conditions have been shown to alter animals’ reproductive fitness (Thomas et al., 2007), their susceptibility to disease (Lehmann et al., 2016), feeding patterns (Bernatis et al., 2007), ability to orient, and even their ability to see (McCormick et al., 2019).

No doubt the threat of global deoxygenation scales up from individual organisms to entire ecosystems, however, the full extent of ecosystem-level losses we might expect to see in our lifetimes remains largely uncertain (IUCN Report, 2019). Evidence derived from paleo records, and corroborated by survey data from contemporary OMZs, suggests that DO is directly related to biodiversity: as DO declines, so too does species diversity and evenness (e.g., Sperling et al., 2016; Gallo et al., 2020). At least two of Earth’s previous mass extinction events have been linked

directly with periods of low ocean oxygen or high DO variability (Keeling et al., 2010; Stockey et al., 2021; Kozik et al., 2022). Meanwhile, based on our exploration of modern-day OMZs, it seems as though just a few oxygen-resistant species reign supreme when DO is scarce, including some species of worms, molluscs, jellyfishes, ctenophores, and specially-adapted fishes (IUCN Report, 2019; Gallo et al., 2020). These various lines of evidence suggest that modern-day deoxygenation is likely to accelerate our current biodiversity crisis and what some consider Earth’s “Sixth Mass Extinction” (Barnoski et al., 2011).

Within the PB Framework, the boundary of “Biosphere Integrity” rests on two sub-boundaries: (a) genetic and (b) functional diversity (Rockström et al., 2009; Steffen et al., 2015). “Genetic diversity” refers to the composition and abundance of *genes* contained within a population or populations, while “functional diversity” refers to the composition and abundance of *traits* represented by organisms in an ecosystem. (Examples of functional traits include omnivory, the ability to calcify, burrow, break down waste, and so on.) Respectively, the sub-boundaries for Biosphere Integrity are defined by the interim control variables of (a) “extinction rate” and (b) “Biodiversity Intactness Index (BII).” *Extinction rate* refers to exactly what you might expect, the number of species that go extinct in a certain amount of time, while *BII* refers to the number of ecological guilds that remain represented in an ecosystem. With respect to genetic diversity and extinction, deoxygenation is expected to induce widespread extirpation of organisms throughout the tropics and subtropics (Penn & Deutsch, 2022). We expect the same with respect to functional diversity as well, where, as discussed, DO losses threaten communities of organisms in various lake, estuarine, shelf, and open-ocean habitats (IUCN Report, 2019).

3.4. OCEAN ACIDIFICATION AND THE COVARIANCE OF AQUATIC PARAMETERS

The relationship between deoxygenation and ocean acidification (OA) is notable in that these two processes tend to covary with one another, driven by different-but-interlocking mechanisms. OA refers to the increasing acidification / declining pH of seawater borne from the increased dissolution of anthropogenic carbon dioxide (CO₂) at the ocean's surface. Occasionally, OA will also be used as a shorthand for other processes that produce CO₂ in the water column or to describe similar chemistry observed in freshwater systems. The dissolution of CO₂ in water leads to an increase in the concentration of dissolved hydrogen ions (H⁺), lowering the pH of the surrounding seawater. Typically, we observe that as pH in the water column declines, so does oxygen availability — a relationship that is primarily mediated by photosynthesis and respiration. Powered by solar energy (light), primary producers use CO₂ molecules, along with water and nutrients, as the chemical building blocks for photosynthesis; this process generates sugar and oxygen (DO) as end products. As part of normal aerobic consumption, organisms respire DO from their surrounding environment, producing energy and releasing CO₂. OA is, therefore, directly tied to the ocean's carbon cycle, which is indirectly connected to oxygen cycle through photosynthesis and respiration.

Scientists who study the effects of multiple stressors on organisms and ecosystems, be it in the lab or in the field, are working to elucidate the antagonistic, additive, and / or synergistic effects that arise in the presence of low DO and low pH (Kroeker et al., 2017; Gobbler & Baumann, 2016). For example, the combination of low oxygen and low pH has been shown to have negative effects on the early life stages of numerous larval organisms (e.g., Gobbler et al., 2014), and for some adult organisms as well (Gobbler & Baumann, 2016; Krufft Welton et al., 2023). Likewise, there

exist theoretical (modeling) interactions between the effects of increasing OA and deoxygenation that are associated with negative changes in primary productivity that are mediated, largely, by changes in temperature (e.g., Kwiatkowski et al., 2020).

Because nutrients, such as N and P, tend to be “limiting” reagents for photosynthesis, the occasional nutrient injection (from, say, coastal runoff or upwelling) is most often associated with an uptick in primary productivity and an increase in respiration. In many real-world examples, low-pH and low-oxygen conditions co-occur with high nutrient availability (e.g., Kroeker et al., 2023). This is usually the case for inland and coastal bodies of water, where terrestrial nutrient runoff is high. This is also the case for areas of wind-driven upwelling, where winds move water offshore, only to be replaced by cool, nutrient-rich waters from the deep.

The frequent covariance of low DO, low pH, and high nutrient availability observed *in situ* can make disentangling the impacts of each by itself fairly difficult. It seems that context very much matters and that temperature as a fourth co-variate may ultimately determine whether or not the biological outcomes of local OA, deoxygenation, and nutrient-loading will be positive or negative. For inland and coastal bodies of water where terrestrial nutrient inputs are high, DO is low, and pH is low, organisms can be readily pushed beyond their physiological limits come summertime (e.g., Rabalais et al., 2002); in scenarios like this, we often observe intense seasonal eutrophication and die offs associated with temperature spikes. In areas of coastal upwelling on the other hand, where (typically) nutrients are high, DO and pH are low, but temperatures are cool, we observe non-uniform and occasionally positive physiological outcomes among organisms and ecosystems (e.g., Navarro et al., 2018; Donham et al., 2023).

3.5. LAND-SYSTEM CHANGE: HABITAT LOSS & CLIMATE REGULATION

Steffen et al. (2015) define “land-system change” as, “the area of forested land as a percent of original forest cover.” Among other examples (such as desertification, urbanization, *etc.*), they cite agricultural development as a major contributor to contemporary land-system change (Steffen et al., 2015). In 2017, Nash et al. expanded this definition of land-system change, renaming the boundary “earth surface change,” to account for alterations in marine habitat that “impact climate regulation.” They cite the deforestation of mangroves and the disturbance of seafloor sediments as two notable examples of changes in the marine environment that have impacts on climate and carbon cycling (Nash et al., 2017).

Earth surface change, such as the development of agricultural land, certainly has effects on DO through increased nutrient runoff and eutrophication (as discussed). But, when we consider the effects of declining oxygen availability on habitat fragmentation and carbon cycling, deoxygenation might be considered a type of land-system change all its own. DO changes in the water column have quickly altered habitat availability for pelagic and semi-pelagic organisms (see IUCN Report, 2019), particularly those who traverse or spend time near the OMZ. As just one example, large predatory fishes, such as billfishes, blue sharks, and tuna must consume a large amount of oxygen while hunting. Thus, deoxygenation lessens the availability of foraging habitat for these taxa, and in response, their behaviors and aggregations are shifting (Stramma et al., 2012; IUCN Report, 2019; Vedor et al., 2021). It appears as though deoxygenation may lead fish and invertebrates to congregate nearer to the surface of the ocean, or closer to shore (e.g., Craig, 2012; Stramma et al., 2012; Vedor et al., 2021). Habitat loss and degradation of this nature may increase the vulnerability of these species to other anthropogenic stressors, such as overfishing (Stramma et al., 2012; Vedor et al., 2021), while also threatening critical ecosystem services.

As areas of low oxygen expand, we are likely to see changes in aquatic Blue Carbon stocks, associated with changes in ecology and biogeochemical cycling (see Mariani et al., 2020; Bianchi et al., 2021). While the methods for quantifying Blue Carbon stocks and flux are still fairly new (Geraldi et al., 2019; Macreadie et al., 2022), recent theoretical evidence suggests that deoxygenation is likely to *decrease* the ability of the ocean to regulate climate via the loss of large predators, fish biomass, and disruptions to the “Biological Pump” (ideas shared at the OBP *Fish, Fisheries, and Carbon Workshop*, March, 2023⁶). This is a rapidly growing area of research, where as of now, a few relevant theoretical feedback loops have already been proposed. For instance, the ocean helps to sequester a massive amount of anthropogenic carbon dioxide long-term through mixing of inorganic carbon (CO₂) and the fixation of CO₂ into organic detritus that *sinks*. A portion of all carbon present in the ocean’s upper layers sinks into the deep sea via passive and active mixing, where it can be stored for millennia. As deoxygenation alters patterns of life and biogeochemical cycling throughout the ocean, we expect to see fewer and smaller organisms sinking into the deep sea (i.e., less deadfall) (see Mariani et al., 2020; Bianchi et al., 2021; Martin et al., 2022). If this expectation holds true, then deoxygenation is a lot like a forest shrinking with respect to habitat loss and the loss of climate-regulating services.

3.6. AEROSOL LOADING (AND CLIMATE REGULATION)

A lesser-known but exciting area of research has focused on the effects of atmospheric aerosol loading and deposition on climate and ocean deoxygenation. Aerosols such as sulfate and black carbon (soot) can have pronounced effects on the climate and biogeochemistry of the Earth System. For example, volcanic aerosols can cool the land and ocean surface through their direct

⁶ <https://www.us-ocb.org/fish-fisheries-and-carbon/>

reflection of shortwave irradiance from the sun (LeGrande et al. 2016), thus increasing $[O_2]$ solubility and influencing upper ocean stratification (Frölicher et al. 2009; Eddebbar et al., 2019). In fact, while most of the changes in ocean oxygen content over the last century are due to anthropogenic warming (Schmidt et al., 2017), external forcing, such as volcanic eruptions, may have shielded our atmosphere from some heating and “added” oxygen into the ocean’s interior; this is supported by modeling evidence that contemporary deoxygenation has slowed down after major volcanic eruptions (Eddebbar et al., 2019; Fay et al., 2023).

Working in opposition to this pattern of aerosol-induced cooling, which may in fact increase DO, the *biogeochemical* effects of anthropogenic aerosols are expected to decrease DO and intensify ocean deoxygenation. Atmospheric aerosol deposition on the sea surface can increase the availability of key nutrients that promote primary productivity in the euphotic zone, with knock-on effects to oxygen availability down the water column. For instance, the accelerated loss of oxygen in the Pacific Ocean basin has been tied to an increase in iron deposition borne from aerosol pollutants. The extra iron in the water column intensifies surface primary productivity, organic carbon export, and enhanced microbial respiration at depth (Ito et al., 2016).

The effects aerosols on both ocean temperature and biogeochemistry raise numerous questions for those interested in the potential climate-regulating effects of the ocean, which is a natural carbon sink and also the subject of various proposals for “climate interventions.” Like many, we contend that all forms of climate interventions (i.e., geoengineering) should be considered with a high degree of skepticism and caution, particularly given their potential to harm aquatic life. Aerosols specifically have been considered for use in solar geoengineering projects, including “stratospheric aerosol cooling” and “cloud brightening,” while the atmospheric deposition of iron serves as a natural analog for the effects of widespread “iron fertilization” (see

NASEM Report, 2022). Similar to the effects of anthropogenic and volcanic aerosol emissions, geoengineering methods are likely to have unexpected but potentially pronounced effects on Earth and its oxygen cycles. We refer readers to work by Levin et al. (2023), who discuss the risks of marine geoengineering in greater detail.

4. WHEN TO USE WHICH CONTROL VARIABLE?

So far, we've highlighted the known and potential extent of deoxygenation, the control variables (proxies) we can use to measure it as a boundary all its own (**Table 2.1**), and its interactions with other PBs (**Table 2.2**). One of the practical considerations that we view as critical to the application of this research is an understanding of when and where it is most useful to reference one deoxygenation control variable over another. The utility of one boundary might only be realized at a certain spatial scale, for instance, or with access to a certain amount of data. We've discussed these considerations throughout the text, and summarize when it might be most useful to use each boundary in **Table 2.3**, here.

Table 2.3. A table of information describing when it is either most useful or most difficult to reference a certain control variable.

Control Variable	Most useful when...	Difficult to use when...
Hypoxia cutoff (oxygen concentration)	• In the absence of fine-scale data.	• Attempting to conserve / protect a wide array of species. • No chemical data is available.
Percent O₂ Saturation (% DO)	• In the absence of fine-scale data.	• No chemical data is available.
Presence, absence, and behavior of Sentinel Species	• In the absence of fine-scale data. • In the presence of robust local ecological knowledge.	• The natural history of the ecosystem is not well known.
The Metabolic Index (Φ): the measure of O ₂ demand versus supply	• There is an abundance of physiological data for the organisms in that ecosystem; there exists oxygen models for that ecosystem / sets of taxa.	• In the absence of <i>in situ</i> oxygen and temperature data. • In the absence of oxygen and temperature data models. • In the absence of organisms' physiological data.
The “ velocity ” of the Metabolic Index (CV_{Φ})	• Most useful in data rich scenarios. • When trying to prevent lethal effects.	• In the absence of <i>spatially-explicit</i> oxygen models.

5. CONCLUDING REMARKS

We have demonstrated the remarkable, complex, and far-reaching importance of oxygen and deoxygenation in linking Earth’s “core” planetary boundaries: climate change and biosphere integrity. We make recommendations for five deoxygenation control variables, and outline deoxygenation’s numerous interactions with the other PBs. We discuss when and where it might be most useful to reference one control variable over another, recognizing the importance of this research in practice. We hope that our breakdown of deoxygenation as a new planetary boundary might help to facilitate the integration of deoxygenation into future priorities for environmental

policy-making and management. In the words of scientists with the IUCN (2019), “[deoxygenation] will not be easy to reverse, but the costs of doing so clearly outweigh the costs of any inaction.” With this in mind, we hope that the ideas and information presented herein will contribute to deoxygenation mitigation and adaptation efforts, both new and underway.

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SUPPLEMENTARY MATERIALS

A. A BRIEF OVERVIEW OF DEOXYGENATION TERMS AND TRENDS

When we consider deoxygenation in a PB context, its current state probably rests somewhere in what Rockström et al. (2009) would refer to as the “zone of uncertainty.” This zone refers to states of increasing risk that threaten Earth’s climate-biological resilience (Steffen et al., 2015). Rapid declines in DO are borne from a multitude of drivers, including anthropogenic eutrophication, changes in mixing, and – primarily – global warming (Shepherd et al., 2017; Oschlies et al., 2018). Since the start of the Industrial Revolution, the ocean (along with other bodies of water) has absorbed greater than 90% of the total excess heat trapped in our atmosphere by anthropogenic greenhouse gases (IPCC - SROCC Report, 2019). As a result, the solubility and partial pressure of elemental oxygen (O_2) in water has declined across the globe (Oschlies et al., 2018; IPCC - SROCC Report, 2019).

The effects of deoxygenation on ecological and biogeochemical functioning can be wide-ranging and acute, however, the loss (and gain) of oxygen in both marine and freshwater environments is a *natural* process in the sense that such changes have always occurred. In some cases, the increase or decrease of DO over millennia has coincided with dramatically altered states of Earth’s climate and ecological networks, in that declines in DO have been linked to mass extinction events (e.g., Stockey et al., 2021; Kozik et al., 2022), and conversely, periods of elevated DO have been linked to evolutionary radiation (e.g., Dahl et al., 2010). Naturally-occurring “oxygen deficiencies” (i.e., low- O_2 acute events, cycles, and zones) generally arise from weak ventilation (low flow, low mixing) and microbial respiration (Sverdrup, 1938; Wyrтки, 1962; Karstensen et al., 2008). These deficiencies in DO go by various names in the scientific literature, depending on their size, location, root cause, and temporal extent. For example, a naturally-

occurring, low-oxygen area in the open ocean might be called an “oxygen minimum zone” (an OMZ), whereas a persistent low-O₂ water mass observed at the mouth of an estuary might be referred to “as a dead zone.”⁷ While it can be difficult to deconvolve natural and anthropogenic changes in DO — due, in part, to a lack of data, but also because these changes co-occur and vary substantially (Long et al., 2016) — we use the term “deoxygenation” here to refer to the modern-era and anthropogenic trend of rapid DO losses observed worldwide (Keeling et al., 2010).

On average, global ocean oxygen levels have declined by about 2% over the last 50 years (Schmidtko et al., 2017) with more pronounced rates of oxygen declines observed regionally (Levin, 2018), and oxygen losses in freshwater lakes globally have been even greater, about 5–6% (Jane et al., 2021). Scientists predict continued and, in some cases, even catastrophic DO declines in our lifetimes (Oschlies et al., 2018; IUCN Report, 2019). According to Schmidtko et al. (2017), the global oceanic dissolved oxygen content amounts to 227.4 Pmol (1 petamol = 10¹⁵ mol), with this oxygen inventory non-uniformly distributed throughout the world’s oceans. The area of highest loss has been flagged as the North and Equatorial Pacific, and in fact, oxygen losses in this region account for nearly 40% of all oxygen losses observed over the past half century (from 1960–2016) (Schmidtko et al., 2017). Today, the North and Equatorial Pacific regions have an estimated rate of oxygen loss of [30 mol / m² / decade], i.e., over 370 Tmol lost per decade (Schmidtko et al., 2017).

Deoxygenation “hotspots,” such as the North Pacific, have been identified in a number of freshwater, coastal, and open-ocean ecosystems, including >390 temperate lakes around the world (Jane et al., 2021), >200 coastal sites (Breitburg et al., 2018), large areas of the Northern and

⁷ Note that the term “deadzone” is a bit of a misnomer in that it implies all living things die or cannot survive in an affected area. This is not the case. However, “dead zones” do show low biodiversity.

Equatorial Pacific (as stated), areas surrounding the poles, the Southeast Atlantic, and Indian Ocean (Levin, 2018).

While the signal for deoxygenation has been accruing since at least the 1960s (e.g., Sarmiento et al., 1998; Ito et al., 2017), only about 25 years have passed since the first reports of deoxygenation as a global threat were only published (e.g., Sarmiento et al., 1998). Anecdotal evidence suggests that the realization of deoxygenation as a cosmopolitan issue has been slow but exponential. As a result, many questions about deoxygenation feedbacks, effects, and trajectories remain unanswered. The fate of the tropical oxygen minimum zones, for instance, remains highly uncertain, with climate models currently disagreeing on the sign and magnitude of future changes in this region (Bopp et al 2013; Kwiatkowski et al 2020). The research presented herein reminds us of the many fascinating connections that exist between deoxygenation and the other nine planetary boundaries.

CHAPTER 3

TESTING THE EFFECTS OF PRESS VERSUS PULSE CLIMATE STRESS ON A VULNERABLE AND COMMERCIALY-IMPORTANT SPECIES OF SCALLOP, *NODIPECTEN SUBNODOSUS*

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ABSTRACT

Climate change, including global warming and the rise in frequency of extreme events, is and will continue to have profound effects on species, populations, and ecosystems. A helpful framework for understanding the risks to organismal populations brought on by these various changes is the “press-pulse” framework, where “press” refers to a chronic stress imposed on a population over time, and a “pulse” refers to an acute stress. In the eastern tropical / subtropical Pacific, climate change is responsible for a variety of press-pulse changes in “ocean weather,” such as exaggerations in the ENSO cycle (El Niño Southern Oscillation) and increased exposure to marine heatwaves (MHWs). This complex and changing oceanographic landscape exists as the backdrop for species distributed along the temperate and tropical west coast of North and South America, including the Pacific Lion’s Paw scallop, *Nodipecten subnodosus*. *N. subnodosus* is one

of the largest pectinid species in the world (growing > 20cm), whose distribution ranges from Northwest Mexico to Peru, with a fascinating history as a target of small-scale fisheries in the region of Baja California. For the purposes of understanding the effects of locally-relevant climate stress on *N. subnodosus*, I conducted a six-week multiple-stressor experiment in the lab, designed to mimic local temperature and food stress associated with an El Niño “press” and / or a MHW “pulse.” I distributed 125 young- / sub-adult scallops across 18 tanks and six experimental treatments, where each treatment is defined by a set of three factors: food availability (high or low), background temperature (high or low), and the presence or absence of a MHW. I found that all three factors had a negative effect on the scallops’ survival, with mixed positive effects on their routine metabolism, growth, resistance to lethal temperatures, and gonad size (relative to adductor). I find evidence to suggest that scallops may upregulate their metabolism and grow faster under warm-water conditions, while down-regulating their metabolism and growth when food availability is low. Notably, the presence or absence of a MHW had no effect on growth, but did affect the animals’ Lethal Temperature Maxima and (most likely) their gonad size. In contrast, neither gonad size nor Lethal Temperature Maxima appear to be affected by background conditions nor food availability. I discuss results from this experiment in the wider context of *N. subnodosus*’ biology, and summarize takeaways for those interested in this species of scallop as a target for fisheries and aquaculture. Ideally, this work will contribute to the management and potential restoration efforts of *N. subnodosus* in Mexico, and serve as a helpful reference material for those interested in understanding similar species in an ever-evolving ocean environment.

1. INTRODUCTION

The ocean sequesters a massive amount of heat trapped on our planet by anthropogenic greenhouse gas emissions, having warmed by about 1°C (on average) since the start of the

Industrial Revolution (IPCC - SROCC Report, 2019). In particular, the upper layers of Earth's ocean, i.e., coastal and euphotic zones, attenuate a disproportionate amount of heat and are projected to warm an additional $\sim 0.5^{\circ}\text{C}$ by mid-century (IPCC - SROCC Report, 2019). Such warming already does and will continue to have profound effects on ocean climate and weather — from changes in short-term pulses, like Marine Heatwaves (MHWs), to the effects on longer-term and cyclic events, such as El Niño and La Niña. In turn, these patterns regulate ecological health and fisheries productivity in ways that we should be thinking about long-term in order to manage marine resources effectively and with precaution (Bates et al., 2018).

Ocean “climate” refers to the general behavior of the Earth's oceanographic system over a prolonged period of time, whereas “ocean weather” refers to changes in oceanography that take place on the order of minutes to weeks (Bates et al., 2018). The phrase “ocean weather” can also be used to refer to extreme events, including marine heatwaves, hurricanes, hypoxia episodes, destructive tidal flows (Bates et al., 2018). These events exist against the backdrop of a changing climate and a shifting “ecological baseline,” such that populations of marine flora and fauna are increasingly vulnerable to environmentally-induced extinction (Harris et al., 2018).

A helpful framework for understanding the risks to organismal populations brought on by our changing (and naturally-variable) climate is the “press-pulse” framework (Harris et al., 2018). Using this framework, a “press” stress refers to a chronic stress imposed on a population over an extended period of time (e.g., a gradual increase in temperature). “Pulse,” on the other hand, refers to a relatively short-but-acute stress (e.g., a MHW). Increasing average temperatures (i.e., global warming) superimposed with the increasing frequency of acutely-stressful events, gives rise to an increasingly harsh real-world climate, where individuals and populations are more likely to be stressed beyond their physiological limits. Indeed, a number of marine organisms already face

population collapse and / or local extirpation associated with changes in climate and weather, including notable crashes documented among sea birds (e.g., Piatt et al., 2020), fishes (e.g., Pershing et al., 2015), macroalgae (e.g., Harris et al., 2018; Beas-Luna et al., 2020), and invertebrates (e.g., Kluger et al., 2019; Tomasetti et al., 2023). This is not to say that all climate-related mortality events are borne from press-pulse interactions, nor that the effects of such interactions are always deadly — but rather, that by using the press-pulse framework to inform our scientific research, we can better identify how chronic and acute stress *interact* to alter population outcomes over time. Equipped with this information, we may be able to make better recommendations for biological conservation and fisheries management in response to future climate projections and periodicities (Bates et al., 2018; Harris et al., 2018; IPCC - SROCC Report, 2019).

Along the west coast of Central and South America, anthropogenic changes in oceanic climate and weather have been associated with negative effects on marine organisms, ecosystem services, and people (IPCC - SROCC Report, 2019; Muelbert et al., 2021). For example, as a consequence of anthropogenic warming, El Niño events (that is, the warm-water phase of the El Niño Southern Oscillation) are becoming more severe (Grothe et al., 2019), and are projected to occur more frequently in our lifetimes (Cai et al., 2014). El Niño is associated with the warm-water lip that develops every four to nine years across the eastern equatorial Pacific, occasionally contrasted by the La Niña cool phase of the ENSO cycle. Along with warmer sea surface temperatures (from Chile to California), El Niño events are usually associated with heavy rains in Central and South America (flooding), decreased precipitation across the Indian Ocean basin (drought), decreased upwelling, lower primary productivity, increased animal vagrancies, and numerous disruptions to coastal agriculture and fisheries (Cai et al., 2014; Grothe et al., 2019;

IPCC - SROCC Report, 2019). Along America’s coastal shelf, El Niño can bring varying oxygen and pH conditions to the North or South (Arntz et al., 2006), but almost always brings higher ocean temperatures and lower primary productivity.

In addition to the “typical” abiotic and biotic stress brought on by an El Niño alone, a troubling pattern is beginning to take shape, where the end of an El Niño event is followed by a period of *extreme* heat (Heidemann & Ribbe, 2019; Cheung et al., 2021). While this observed pattern is still relatively new, it seems as though marine heatwaves (MHWs)⁸ of various forms may ride on the warm-water inertia of El Niño (Heidemann & Ribbe, 2019; Cheung et al., 2021; Amaya et al., 2023). MHW’s have been known to kill both habitat-forming and non-habitat forming species, while also jeopardizing human-use and ecosystem services (Frölicher & Laufkötter, 2018; IPCC - SROCC Report, 2019; Cheung et al., 2021). MHWs, be them alone or in combination with El Niño, reflect great cause for concern — in some cases, profoundly altering marine ecosystems. Scientists generally agree that MHWs are becoming more frequent and more severe as a direct result of global warming (Frölicher & Laufkötter, 2018; IPCC - SROCC Report, 2019). In the waters off Baja California, for example (where our study was based), there have been at least three MHWs documented since 1981 (Holbrook et al., 2019).

In an effort to test the press-pulse framework in a way that is both ecologically- and socially-meaningful, we applied the framework to a species of scallop that is likely already vulnerable to climate change and is of commercial interest in Northwest Mexico (Ruiz-Verdugo et al., 2016). Specifically, we tested the effects of El Niño and MHW stress on Pacific Mano de León scallops, *Nodipecten subnodosus*, a species with an interesting history as a fishery target in the waters off Baja California. *Almeja Mano de Leon*, or Lion's Paw scallops as they are often

⁸ Marine heatwaves are defined by Hobday et al. (2016) as a period of five or more days with “anomalously-warm” seawater temperatures.

referred to in English, are found along the Pacific coast of Mexico, down to Peru, with a patchy distribution across Ecuador (Ruiz-Verdugo et al., 2016; Instituto Nacional de Pesca, 2021). They are one of the largest species of swimming scallops in the world (family: Pectinidae), growing up to 23 cm in height, over an estimated four to five years (Instituto Nacional de Pesca, 2021). Given their impressive size and beautiful orange-pink shell, Mano de León are a valued commodity amongst fishers, sellers, and shell collectors.

In Baja California, *N. subnodosus* has been the target of small-scale fisheries for generations. In recent years, however, the fishery has struggled to stay open (and is currently closed) due to a series of poorly-understood population busts. By the late 1960s, wild populations of Mano de León in Northwest Mexico were beginning to show signs of over-exploitation, and in 1970, Mexican fishing authorities imposed a 20-year moratorium on the animals' harvest (Barrios-Ruiz et al., 2003). In 1990, the fishery was reopened, and catch trends suggest that wild populations had begun to recover (Barrios-Ruiz et al., 2003). The fishery peaked in 1999 at 157 metric tonnes of scallop (meat), only to mysteriously collapse again circa 2010 (Barrios-Ruiz et al., 2003; Ruiz-Verdugo et al., 2016).

The circumstances that led to this second collapse of Mano de León are not entirely clear (Ruiz-Verdugo et al., 2016). Was it overfishing? A handful of years with poor recruitment? A bout of parasitism? Or, perhaps, a regional outbreak of disease? Climate change, which is generally considered a type of “press” or chronic stress, has also been cited as one of the many possible culprits (or co-culprits) for this unexpected collapse (Ruiz-Verdugo et al., 2016). Whatever the underlying cause(s), fisheries managers, fishers, and scientists share an interest in understanding what exactly happened to Mano de León in this region (Ruiz-Verdugo et al., 2016).

This unique interest in Mano de León specifically, as well as a desire to understand the effects of press versus pulse climate stress on bivalves more generally (Carrier-Belleau et al., 2021; Krufft Welton et al., 2023), helped to orient this study. Results from previous analyses suggest there would be negative effects of both press and pulse stress on Mano de León, and perhaps *synergistically* negative, depending on the combination of stressors and measured outcomes (Carrier-Belleau et al., 2021; Krufft Welton et al., 2023). We tested the effects of food availability and various press-versus-pulse temperature regimes on the survivorship and physiological response of young- and sub-adult Mano de León (ranging in height from 4.8–9.3cm), using an experimental design of six treatments over six weeks.

Each experimental treatment was designed to resemble a locally-relevant and real-world climate scenario that has either already occurred or is likely to play out in the region of Northwest Mexico. The six treatments used in this experiment (**Figure 3.2**) are defined by three interacting factors: food availability (factor 1: *Food* is low or high); background temperature (factor 2: *Background* temperature conditions are cool or warm); and heatwave (factor 3: *Heatwave* is or is not in effect). The real-world analogue for each treatment is as follows: (1A) cool “control” conditions (21°C), (2A) warm-water conditions (25°C), (3A) warm-water and low-food conditions, (1B) cool conditions followed by a severe MHW (28°C), (2B) warm conditions followed by a moderate MHW (28°C), and (3B) warm conditions with low food followed by a moderate MHW (28°C). Note that the warm-water and low-food factors were designed to mimic the oceanographic stress associated with El Niño events.

We hypothesized that there would be either additive or synergistic negative effects of press and pulse stress on the survivorship, growth, and physiology of these organisms (as opposed to antagonist or dampening effects). We report changes and discrepancies in the scallops’

survivorship and physiology, derived from a number of observations and physiological assays designed to estimate scallops' survivorship, growth, resting metabolism, resistance to lethal temperatures, gonad size, and gonad development as a function of food availability, background temperature conditions, and exposure to MHWs. We use our results to discuss the prognosis for this species in terms of a natural fisheries recovery or intentional efforts to cultivate them through aquaculture (Ruiz-Verdugo et al., 2016; Instituto Nacional de Pesca, 2021). We anticipate that the suite of results gained from this experiment will serve as a helpful reference material for those interested in cultivating *N. subnodosus* in the lab or at sea, testing the effects of press versus pulse stress on similar species, and / or integrating the effects of “ocean weather” into projections for marine biodiversity and fisheries stability.

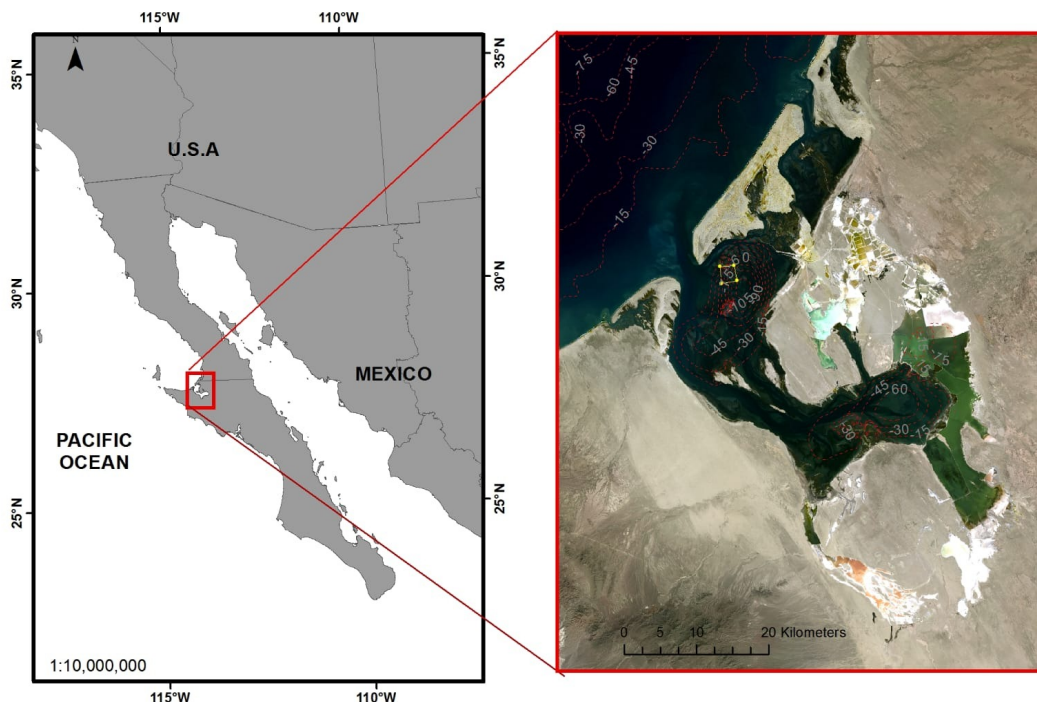


Figure 3.1. Map of Guerrero Negro, in Baja California Sur, where we collected the scallops.

2. METHODS

The lab experiment underlying this study was conducted during the summer of 2021 in the Mollusc Biotechnology Lab at Universidad Autónoma de Baja California (UABC) in Ensenada, Mexico. The experiment lasted approximately six weeks (39–44 days, depending on the tank), and during this time, we collected a number of physiological data points from the scallops. Subsequent analyses associated with this research were conducted from October, 2021, to present at UABC, Scripps Institution of Oceanography (San Diego, California), and the University of California, Santa Barbara. All of the statistical analyses and figures presented herein were generated using Microsoft Excel, R (R Core Team, 2023), Python (Python Software Foundation, 2021), or HOBOWare⁹.

2.1. EXPERIMENTAL DESIGN FROM A BIRD’S EYE VIEW

As explained, the primary motivation for this experiment was to understand the health and resistance of *N. subnodosus* to locally-relevant press and pulse climate stress, and we therefore designed our treatments to resemble the conditions we might see during an El Niño year, or during a MHW. In this sense, our experimental design can be described as a “phenomenological” one, meaning it was inspired by real-world observations and phenomena that are known to occur throughout the Baja California region. We distributed scallops into one of six treatments: Treatments 1A, 1B, 2A, 2B, 3A, or 3B. As described previously, our six treatments can be summarized as the combination of the following three factors, with two levels each: (1) background food availability (HIGH or LOW), (2) background temperature (HIGH or LOW), and

⁹ HOBOWare is available for free download at: <https://www.onsetcomp.com/products/software/hoboware#overview>

(3) the presence or absence of a MHW towards the end of the experiment (heatwave ON / heatwave OFF). See **Table 3.1** and **Figure 3.2** for a complete breakdown of each treatment.

During an El Niño year, net primary productivity is typically reduced by 5–10%, compared to the *average* of primary productivity across the region (Racault et al., 2017). Thus, we designed two feeding regimens that we felt would be consistent with a reduction in primary productivity during an “El Niño-like” year. Here, “high food availability” refers to a daily food ration ranging in size from $1.80\text{--}2.35 \times 10^{10}$ cells per scallop per day (where cell counts are normalized to the cell size of *Isochrysis* phytoplankton; Retailleau et al., 2023). In contrast, “low food availability” refers to ~70% of that high food ration. In terms of selecting relevant background temperatures, we determined that normal Spring / Summer conditions for these animals living in Baja California lagoons range from 14°C–26°C, on average¹⁰; we therefore selected 21°C and 25°C as our two realistic Summer background temperatures. Finally, the presence or absence of a heatwave (heatwave ON or OFF) refers to the acute temperature increase that occurred in half of all tanks during the final two weeks of the experiment (the final 13–16 days, depending on the treatment and date of sacrifice). Under MHW conditions, animals were exposed to 28°C heatwave, regardless of previous thermal history, at a rate of +2–3°C / day.

One hundred and twenty five (125) individual scallops were placed into one of 18 tanks, allowing for an average sample size of seven scallops per tank. Under this design, the tanks themselves are our independent units of replication, where $n_{\text{replicates per treatment}} = 3$, $n_{\text{treatments}} = 6$, $n_{\text{individuals per replicate}}$ is 6 or 7, and $N_{\text{total scallops}} = 125$. Individuals were assigned to a tank based on which collection period they came from (collection described below in **Section 2.2**) and their relative wet weight at the beginning of the experiment. We did our best to assign scallops from

¹⁰ Sea-surface temperatures reported at: <https://seatemperatures.net/north-america/mexico/guerrero-negro/>

Collection Day 1 and *Collection Day 2* evenly across treatments, and to distribute small versus large individuals across tanks. Basic summary statistics for our sample population, along with a statistical snapshot of each treatment, are presented in **Table 3.2**.

Of immediate relevance to readers is a brief introduction to the YSI meter and HOBO loggers referenced throughout this *Methods* section. The YSI meter is a handheld device used to take instantaneous point measurements of temperature, barometric pressure, pH, dissolved oxygen, and salinity — while the HOBO loggers were used to record *in situ* measurements of temperature over time, continuously. Additional information about these *in situ* measurements, and records of seawater conditions for each tank, can be found in the *Supplementary Materials* section of this text (**Figure 3.S1**).

Finally, it is worth mentioning that because this experiment ultimately involved the sacrifice of these animals, we strived to adhere to the “4R” rule of “Replace, Reduce, Refine, and Recognize” (Erren et al., 2017). This rule recommends that if animals must be sacrificed for a given research experiment, we, as researchers, should try to ascertain as much information as possible from as few individuals as necessary. Here, we report on the scallops’ growth, resting metabolic rates, resistance to Lethal Temperatures, their gonadal mass, and gonad differentiation.

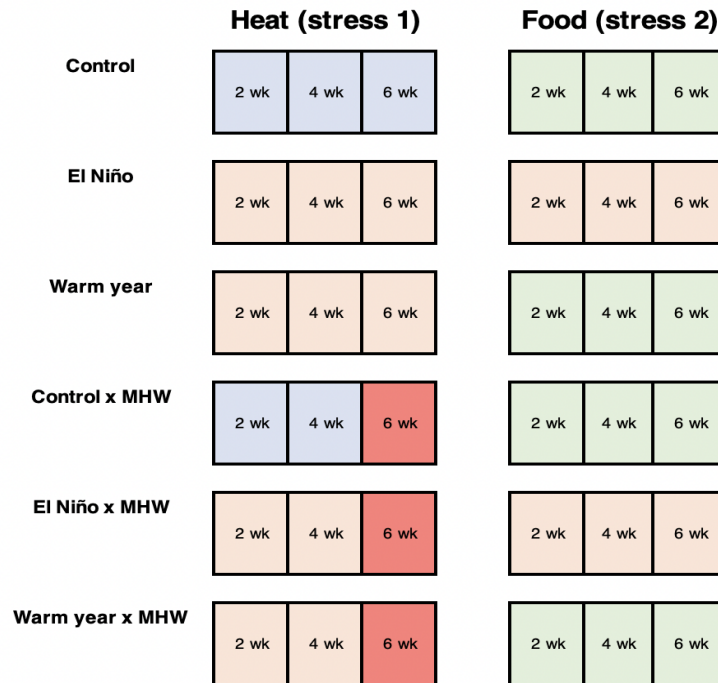


Figure 3.2. Experimental Design from a bird's eye view.

Table 3.1. All six experimental treatments and their resemblance to real-world phenomena.

Treatment ID	Treatment Code	Treatment Description:	“press” or “pulse” stress?	Real-World Analogue
1A	S-C-nH	Satiated-Cold-nonHeatwave: 21°C with 100% food availability for the entire experiment (6 weeks).	NA, “control” treatment	A normal year
1B	S-C-H	Satiated-Cold-Heatwave: 21°C with 100% food availability for four weeks with a +7°C increase (28°C) for the remainder of the experiment.	pulse	A severe MHW during a normal year
2A	S-W-nH	Satiated-Warm-nonHeatwave: 25°C with 100% food availability for the entire experiment (6 weeks).	press	A warm year
2B	S-W-H	Satiated-Warm-Heatwave: 25°C with 100% food availability for four weeks, with a +3°C increase (28°C) for the remainder of the experiment.	press x pulse	A MHW during an already-warm year
3A	U-W-nH	Unsatiated-Warm-nonHeatwave: 25°C with 70% food availability for the entire experiment (6 weeks).	press x press	A warm year with low primary productivity
3B	U-W-H	Unsatiated-Warm-Heatwave: 25°C with 70% food availability for four weeks, with a +3°C increase (28°C) for the remainder of the experiment.	(press x press) x pulse	A MHW during an El-Niño year

Table 3.2. A basic statistical summary of our sample population, and sample per treatment (generated at the beginning of the experiment).

Basic Summary Statistics			
	Number of individuals at the beginning of the experiment	Average mass (& standard deviation) at the beginning of the experiment	Median mass at the beginning of the experiment
Entire experiment	125	82.2	62.4
Treatment 1A S-C-nH	21	87.1	53.0
Treatment 1B S-C-H	20	84.1	71.7
Treatment 2A S-W-nH	21	80.7	66.0
Treatment 2B S-W-H	21	80.4	62.4
Treatment 3A U-W-nH	21	80.7	51.1
Treatment 3B U-W-H	21	80.7	59.2

2.2. SCALLOP COLLECTION, ACCLIMATION PERIOD, AND TAGGING

Scallops, ranging in size from 4.8–9.3cm, were collected in collaboration with local fishers (under permit PPF/DGOPA-025/21) from the lagoon ecosystem of Guerrero Negro (**Figure 3.1**), over the course of two collection days in July, 2021 (Collection Day 1: July 2nd and Collection Day 2: July 22nd). Guerrero Negro is located on the Pacific side of Baja California Sur, Mexico, where temperatures range from approximately 14°C–26°C in the summer months.¹¹ Scallops were transferred from the lagoon to the lab using Styrofoam coolers filled with seawater, at a stocking density of ~25 scallops per cooler. Using these coolers, the scallops were transported to UABC

¹¹ Sea-surface temperatures reported at: <https://seatemperatures.net/north-america/mexico/guerrero-negro/>

(Ensenada) over the course of approximately 10 hours. Throughout transport, the temperature of the seawater in the coolers was maintained between 19°C–22°C and oxygen saturation was kept above 80% using a supplementary oxygen tank.

Upon arrival at UABC, scallops were placed in a large 500-L fiberglass “quarantine” tank (equipped with recirculating seawater) for two days. Temperature, pH, dissolved oxygen, and ammonia were monitored periodically (using the YSI device and ammonia test described below), and kept mostly constant. No mortalities occurred during this initial holding period. On the second day of quarantine, the scallops were scrubbed free of epibionts and subsequently transferred to a large 800-L holding tank, where the temperature was maintained at 19.8°C–23.4°C (during the week leading up to the experiment).

After the scallops were transferred into the holding tank, the quarantine tank was sterilized and cleaned for future use. Like those collected before them, scallops collected during the second trip (on July 22nd) were held in quarantine for two days, cleaned, tagged, and subsequently introduced to the holding tank on July 24th. All scallops were kept in the holding tank until the experiment began on August 3rd, 2021.

While in the holding tank, scallops were fed daily using primarily Shellfish Diet 1800, a highly-concentrated and nutritious mix of five phytoplankton species that is manufactured by Reed Mariculture in Santa Barbara, California.¹² This feed is generally considered an industry standard and has been used in a number of other experiments involving shellfish (e.g., Carrier-Belleau et al., 2021). However, in an effort to encourage the best possible growth over the course of the experiment, we endeavored to feed our scallops a diet of freshly-cultivated phytoplankton, supplemented with Shellfish Diet, whenever possible. We began feeding the scallops this mix of

¹² See the Reed Mariculture – Shellfish Diet 1800 product description at: <https://reedmariculture.com/products/shellfish-diet>

shelf-stable and fresh phytoplankton shortly before the experiment began (see **Section 2.3** for details).

Notably, on July 11th, 2021, before the experiment began and between the first and second collection dates, we observed a die-off of scallops in the holding tank, most likely attributed to iron nutrient poisoning from the fresh phytoplankton diet (see **Supplementary Materials - Section C** for details). After closely investigating possible causes of this mortality event, and correcting for them, no additional mortalities were observed prior to the experiment starting on August 2nd, 2021. As a result of this early die-off, we were careful to implement additional redundancies and fail-safe measures when testing the quality of seawater and fresh food, before and during the experiment. Not only did we test more frequently for excess ammonia (*API* $\text{NH}_3/\text{NH}_4^+$ test kit), but in the case of detecting excess nitrates (a proxy for iron), we used more than one type of test (*API* NO_3^- and *NYOS REEFER* brand test kits).

Scallops were assigned a unique ID number and tagged by threading a fine piece of fishing line, with a plastic label, through a very small hole on the scallop's anterior wing (made using an extremely small-bit drill). These plastic ID tags allowed us to monitor individuals over time, and helped us to ensure that scallops from the first and second collection dates were evenly distributed across treatments and tanks once the experiment began.

2.3. EXPERIMENTAL SETUP & CONTROL OVER SEAWATER CONDITIONS

Hardware & Sensors

With respect to experimental set up, we utilized a diversity of hardware and infrastructure that was either designed or augmented to support saltwater aquaria. We organized the 18 experimental tanks (50-gallon plastic tubs) along three two-tiered racks. Each tank was equipped

with: one 200-watt heater, one HOBO logger, one plastic apparatus designed to recirculate and re-oxygenate the water (constructed using PVC pipe), one basket to hold the scallops, and two biological filters to consume ammonia and excess waste.

Temperature Control

We controlled temperature in the experimental tanks using 200-watt *Aquatop* heaters, which were able to maintain temperatures near their designed setpoint¹³ of 21°C (mean= 21.2°C ± s.d.= 0.4), 25°C (mean= 24.9°C ± s.d.= 0.3), and 28°C (mean= 27.9 °C ± s.d.= 0.2). See **Figure 3.S1** which shows temperatures recorded in each tank, over time.

When transferring the individual scallops from the principal holding tank to their experimental tanks, all treatments / tanks began at a setpoint of 21°C. For the treatments where background temperature was assigned “HIGH,” we increased the temperature in their tanks at a rate of ~1°C per day, until tanks reached 25°C on *Day 4* of the experiment. We made sure to increase the temperature slowly during this initial period of acclimation, so as not to impose a rapid thermal shock on the animals. Later on, when exposing animals in treatments 1B, 2B, and 3B to a MHW, we increased the temperature at a higher rate of 2–3°C per day, to mimic the more stressful rate of warming typically associated with a MHW. *In situ* temperature profiles for each experimental tank are shown in **Figure 3.S1**.

Control of food

Scallops were fed a mixed solution of fresh phytoplankton and Shellfish Diet 1800 three times a day – morning (~10am), afternoon (~2pm), and evening (~7pm) – unless otherwise stated.

¹³ Note that the heater controls came pre-programmed by the manufacturer and were coded in Fahrenheit as opposed to degrees Celsius. Still, we were able to readily manipulate temperature and many of our °C setpoints have a reasonable analogue in °F. Specifically, 70°F is roughly equivalent to 21°C, 77°F is exactly equivalent to 25°C, and 82°F is roughly equivalent to 28°C.

Fresh phytoplankton, *T-isochrysis galbana* and *Chaetoceros muelleri*, were cultivated in a greenhouse space, adjacent to the experimental aquarium. We used a submersible pump to transfer the desired volume of fresh phytoplankton from the greenhouse to several large (500-L) holding tanks inside the experimental aquarium facility. Phytoplankton coming out on the receiving end of the pump were passed through a 20 μm sieve and stirred to ensure that the phytoplankton slurry inside the holding tanks was more-or-less homogeneous before feeding. Scallops in “Satiated” tanks were fed ~10% of their estimated dry weight every day, based on phytoplankton cell counts taken every 2–3 days. Scallops’ diet consisted of fresh *T-isochrysis* and *Chaetoceros*, except when the density of these fresh phytoplankters was too low, in which case, we compensated with Shellfish Diet. Our goal was to supply the scallops in the “Satiated” treatments with enough phytoplankton to promote growth, without overfeeding them, while still providing the scallops in the “Unsatiated” treatments enough food to avoid starvation. Note that, while the exact cell counts fed to the scallops each day varied, depending on the density of live phytoplankton, the “low food” ration given to the scallops in “Unsatiated” tanks was always equal to 70% of the normal / “high food” ration given to scallops in “Satiated” tanks. In other words, scallops in treatments 3A and 3B were fed ~70% of the food ration fed to scallops in “Satiated” treatments 1A, 1B, 2A, and 2B. As stated previously, the amount of food fed to scallops in “Satiated” treatments ranged from ~1.80–2.35 $\times 10^{10}$ cells per scallop per day, whereas scallops in “Unsatiated” tanks received ~1.26–1.65 $\times 10^{10}$ cells per scallop per day.

2.4. RECORDING MORTALITIES & ESTIMATING LIKELIHOOD OF SURVIVAL

In general, mortalities were easy to spot, particularly since authors EMF, VH, and ER tended to the tanks for several hours a day (feeding the animals, taking water measurements, siphoning and cleaning the tanks, etc.); moreover, all animals were *intentionally* inspected at least

once per day. Scallops that were dead or moribund were usually found with their shells gapping open and were promptly removed from their tank. We recorded the date of mortality for all animals who died prematurely and used these data to generate percent estimates of mortality and a model for the likelihood of scallop survival based on the factors we tested. Specifically, to generate our model for likelihood of survival, we estimated the fixed effects of each factor (Food Availability, Background Temperature, and Heatwave), and their interactions, on the binomial likelihood of a scallop being alive (1) or dead (0). We applied the following mixed-effects linear model to our data, where “Scallop ID” is plotted as a random effect:

$$\text{Eq. 1) Survival (YES or NO) = Food (HIGH or LOW) * Background (HIGH or LOW) * Heatwave (ON or OFF) + random effects (Scallop ID)}$$

We constructed this model using the “lme4” package (Bates et al., 2015) in R, and provide summary statistics for our model parameters as appropriate.

2.5. GROWTH: COLLECTING MASS DATA OVER TIME AND EVALUATING DAILY GROWTH RATES

The height, width, and wet weight of each individual scallop was measured by the same person, author ZG, at the start of the experiment (*Week 1*: August, 2nd); at the end of every week, beginning in *Week 3* (*Week 3*: August 20th, *Week 4*: August 27th, *Week 5*: September 3rd); and before the animals were sacrificed (*Week 6*: September 12th–16th, depending on tank number). We measured the height and width of each scallop using vernier digital calipers, after which, we weighed the scallop on a digital scale. When weighing the scallops, we were sure to let the water drip off the animals before placing them on the scale, however, in an effort to reduce stress on the

organisms while weighing, we were careful not to shake them dry. We tried to avoid agitating them as much as possible, despite the fact that scallops are known to hold some amount of water inside their shells while shut.

We used these mass data for a variety of purposes, including estimating scallops' growth over time. Daily growth rates were calculated using the following equation (**Equation 2**):

Eq. 2) Daily growth rate (g / day) = (mass at T₂ - mass at T₁) / number of days between T₂ and T₁.

We estimated the fixed effects of each experimental factor (Food, Background Conditions, and Heatwave), plus their interactions, on the daily growth rate of scallops by applying the following mixed effects (linear) model to our data:

Eq. 3) Growth Rate ~ Food (HIGH or LOW) * Background (HIGH or LOW) * Heatwave (ON or OFF) + random effects (Scallop ID, nested within Tank)

We constructed this model (**Equation 3**) using the “lme4” package (Bates et al., 2015) in R, and provide summary statistics for our model parameters as appropriate.

2.6. ROUTINE METABOLISM: MEASURING AND EVALUATING ROUTINE METABOLIC RATE (RMR)

We measured routine metabolism (i.e., an organism's oxygen uptake during normal, “routine” activities) at the individual level for 68 scallops, over a week-long period, at the end of the experiment. Prior to beginning the respirometry trials, scallops were fasted for 24 hours at the

tank level. After fasting, we selected 2–4 scallops per tank (of roughly equal size), and transferred them to one of four respirometry chambers set up in the adjacent lab space. (We resumed a normal feeding schedule thereafter.) Scallops were selected by authors EH and EMF based on their size — small enough to fit in the chamber, but big enough for us to detect a metabolic signal.

The respirometry chambers (1.505 L by volume) were equipped with Pyroscience oxygen sensors embedded in the outflow tube of each chamber. Scallops were placed in one of the four respirometry chambers for a total of three hours, during which time, the animals were left undisturbed. To avoid calculating scallops' elevated metabolism while still recovering from handling stress, we evaluated scallops Routine Metabolic Rate (RMR) based on measurement cycles recorded in only the last half of the trial (i.e., we kept only the observations from the last 1.5 hours of each 3-hour run). Each measurement cycle lasted 10 minutes, with a 2 minute flush, unless otherwise noted.

All but one individual was kept above 80% oxygen saturation throughout the entire duration of the trials (that one individual had a minimum oxygen percent saturation of 71% for one measurement cycle, with a mean of 90% saturation). We generated our RMR estimates using methods designed for intermittent flow-through respirometry and provide additional details regarding our experimental setup and analytical assumptions made in the *Supplementary Materials* section of this text.

Metabolic rate measurements were computed using the `AnalyzeResp_0` package in R (developed by Kraskura, 2022; see also Chabot et al, 2016; Little et al., 2020). This package computes metabolic rates by applying a series of quality-control filters and computational functions to oxygen data collected by the Pyroscience sensors embedded inside the respirometry chamber. Ultimately, we used this package to calculate the RMR for our 68 individuals, out of

which 63 individuals were associated with usable data; runs from the 5 other scallops were not usable due to equipment failure and unexpected spawning during the trial.

With these RMR estimates in hand, we tested for the effects of (i) test temperature (i.e., the temperature at time of trial) and (ii) food availability on the final RMR of scallops using two models: a linear model with fixed effects of temperature and food across treatments, and a two-way ANOVA across the paired satiated-and-unsatiated treatments (treatments 2A and 3A, 2B and 3B). Our fixed-effects linear model is coded such that RMR is predicted by the test temperature conditions as a factor with three levels (21°C, 25°C, or 28°C), “background” temperature conditions as a factor with two levels (21°C and 25°C), and food availability as a factor with two levels (HIGH food, LOW food) (**Equation 4**); we constructed this linear model using the “lme4” package in R (Bates et al., 2015). The second, and much simpler model we employ, is a two-way ANOVA (**Equation 5**), which is essentially a simplified linear model that tests for the effects of HIGH food availability and LOW food availability at only two temperature conditions (25°C and 28°C). Respectively, we constructed these two models using the “lm” and “aov” function in base R; we provide summary statistics for our model parameters as appropriate.

Eq. 4) $\text{RMR} \sim \text{Temperature Conditions (21°C, 25°C, or 28°C)} + \text{Food (HIGH or LOW)} * \text{Background (T/F)} + (\text{random effect of tank})$

Eq. 5) $\text{RMR} \sim \text{aov}(\text{Temperature Conditions (25°C, or 28°C)} + \text{Food (HIGH or LOW)})$

2.7. LETHAL TEMPERATURE MAXIMA: TESTING AND EVALUATING SCALLOPS' RESISTANCE TO LETHAL TEMPERATURE STRESS

At the end of the experiment, the scallops were sacrificed as part of a Lethal Temperature Maxima (LTM) assay. The purpose of this assay was to determine if there were treatment effects on the average thermal maximum of *N.subnodosus*, defined as the point at which these animals stopped responding to stimuli and could no longer survive (i.e., were dead or obviously moribund).

Organisms were subjected to this assay at the same time as their tank mates, at a rate of 2–3 tanks per day, one calendar day after individuals from those same tanks were used to assess RMR (as described above). Notably, scallops were starved for 24 hours, at the tank-level, before those respirometry trials began, and subsequently the fed the night after, as per usual. This suggests that organisms were at least partially satiated before they were subjected to the following Lethal Temperature test: (1) animals were removed from their tanks, weighed, and transferred (along with their biological filters) to one of three LTM tanks set up in the lab. These tanks resembled the experimental tanks in virtually all manner (same type of tank, water source, recirculation mechanism, and biological filters), with the one exception that these LTM tanks were equipped with larger, 500-watt heaters, as well as highly-precise digital temperature controllers.

Prior to beginning the assay, the LTM tanks were preheated to match the temperature of the corresponding experimental tanks. Animals were quickly transferred out of their experimental tank, weighed, and placed into the corresponding LTM tank nearby. The scallops were given about 30 minutes to acclimate to their new environment, and after this initial acclimation period, the temperature in the tank(s) was increased at a rate of 0.5°C every half hour. Scallops were monitored throughout the test, with continuous visual assessment of the animals' appearance and overall

condition. YSI checks were conducted every 15 minutes to ensure that our temperature control was accurate and that oxygen saturation never dropped below 80%.

To determine when each scallop was no longer responsive or had perished, we ran a small plastic baton along the edge of the animal's mantle whenever mortality seemed likely. In all cases, scallops began to gape open over the course of the assay, and their mantles drooped, signaling poor health and a gradual loss of motor control. Towards the end of the assay, once the scallops began to perish, visual inspection was effectively constant, but we tried to avoid picking up the animals and excessive touching. If, upon being touched or poked, the animal did not move and its mantle, seemed unresponsive or flaccid, we considered the animal deceased and recorded the time and temperature at death.

We estimated the effect of each factor, and their interactions, on scallops' Lethal Temperature maximum by applying a fixed-effects linear mixed model to all of our data (i.e., across all treatments), adhering to the linear relationship described in **Equation 6**. As before, we constructed this model using the "lme4" package (Bates et al., 2015) in R, and provide summary statistics as appropriate.

Eq. 6) Lethal Temperature Maximum (°C) ~ Food (HIGH or LOW) * Background Temperature (HIGH or LOW) * Heatwave (ON or OFF)

Subsequently, we applied a Tukey *post-hoc* test to ascertain how values for mean LTM are or are not statically-similar between treatments.

2.8. REPRODUCTION: DISSECTIONS AND EVALUATING TREATMENT EFFECTS ON GONAD SIZE AND DEVELOPMENT

Upon Time of Death (ToD) — that is, when an animal was pronounced deceased at the end of the LTM assay — scallops were dissected by author VH or ER. When conducting dissections, we adhered to a standardized protocol of dissection (conducted by order of ToD), weighing, and storing. Summarily, we collected blot wet weights for each of the scallop's viscera and major organs, including their adductor muscle, ingestion gland, mantle, foot, gill, and gonad. In cases where the individual's gonad was identifiable (n= 104 out of 125), the person dissecting the organism would separate it from the remaining viscera, weigh and record its mass, place the animal's gonad atop a standard waterproof paper quadrat (12.7 cm x 12.7 cm) and take a picture of it using a camera affixed to a tripod.

Using the gonad photographs taken at the time of dissection, we estimated scallops' total gonad area using Vidana software version 1.0.¹⁴ This software estimates surface area given a known reference length (e.g., a picture scale bar). Author ER hand-traced the gonad's dimensions using a digital tablet, and gonad area was calculated using the Vidana software by applying a 10,000-point density quadrat to the photograph itself. To ensure that this method of estimation was sound, we performed a repeated-measurements test and found a standard deviation between measurements of $\pm 0.01\text{cm}^2$, compared to an average gonad area of 5.45cm^2 . We were also able to estimate the likelihood of gonad differentiation / expression based on scallops' size. Differentiated gonad tissue was distinguished based on color — orange for ovary tissue, white for testis tissue — again, by author ER. Gonads were visually categorized as differentiated (i.e., male, female) versus

¹⁴ <http://www.ex.ac.uk/msel/vidana>

undifferentiated (i.e., not yet reproductive) (**Figure 3.3**), and all data was recorded in a larger spreadsheet. This dataset was compiled and curated in Microsoft Excel, and analyzed using R.

Measurements of scallops' width, length, and mass were taken throughout various stages of this experiment, as described previously. Thus, paired with dissection data, we can use these estimates of mass to generate a ratio of gonad-to-adductor tissue mass ($GM:AM$) for each scallop. This ratio, in theory, can give us some idea about whether or not scallops spend more energy on reproduction versus overall tissue growth. Thus, we estimated the fixed effect of each experimental factor (and their interactions) on the animals' $GM:AM$ by applying a linear mixed effects model to our data (**Equation 7**). Like many of our other analyses, we constructed this model using the “lme4” package (Bates et al., 2015) in R, and provide summary statistics for our model parameters as appropriate.

$$\text{Eq. 7) Gonad:Adductor Ratio (GM:AM) } \sim \text{Wet Weight} + \text{Food (HIGH or LOW)} * \\ \text{Background (HIGH or LOW)} * \text{Heatwave (ON or OFF)}$$

Subsequently, we applied a simplified two-way ANOVA to a portion of our data, ignoring the effects of Food Availability by restricting our analysis to only those scallops found in *Satiated* treatments (treatments 1A, 1B, 2A, and 2B). That is to say, we ran a two-way ANOVA, using the “aov” function in base R, to test whether or not there were statistically-significant effects of Background Temperature and Heatwave on the mean value for $GM:AM$, independent of food.

Finally, we calculated a binomial logistic growth model for this species, predicting the likelihood of gonad differentiation based on shell height (mm). We plot that curve and report notable values as appropriate.

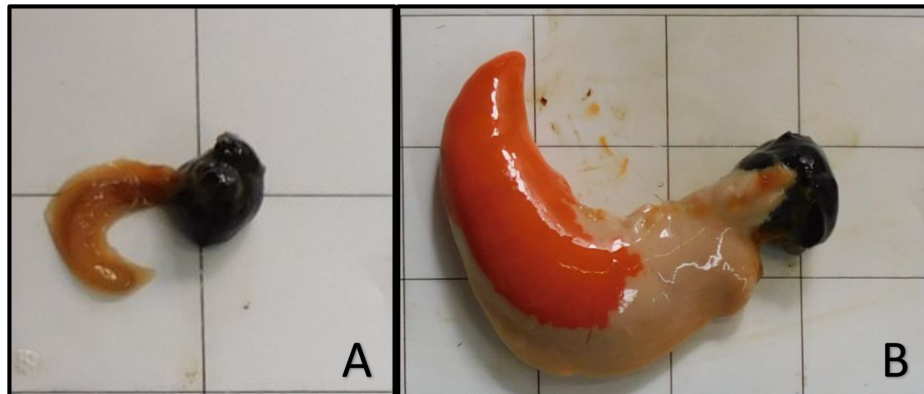


Figure 3.3. Images of (A) undifferentiated versus (B) differentiated gonad taken from two separate individuals of *N. subnodosus*. In the undifferentiated gonad (A) we can see a pale color for the gonadal mass and the intestine, which looks like a black stripe on the leftmost side. Conversely, the differentiated gonad (B) shows the presence of ovaries in bright orange and testes in cream white. The dark mass, attached to the gonad in both figures, is the individual's ingestion gland.

3. RESULTS

3.1. MORTALITY / SURVIVAL

We recorded the date of mortality for all scallops who perished prematurely and used these data to generate survival curves (**Figure 3.4**). In total, 18 individuals died before the end of the experiment, with the majority of those mortalities having occurred in warm-water tanks (see **Table 3.3**). Notably, there was a moderate spate of mortalities that occurred from August 21st–22nd, during which an entire tank-full of scallops perished (*Tank 7B: Satiated-Warm*), along with three other scallops from *Tank 6C (Satiated-Warm)*. While we cannot ascribe the cause of death with certainty, we hypothesize that this event was most likely the result of acute (but fleeting) hypoxia that occurred in both tanks following an unexpected spawning event. After spawning, the scallops didn't clear the food in their tank, and YSI measurements for $[O_2]$ taken after we noticed the scallops poor condition was lower than usual (around 80%). Mortalities subsided after we conducted a full water change in the tank, but animals from *Tank 7B* could not be saved. We

discuss this event in greater detail in the **Discussion** section of this text. If we ignore this event (*), the majority of mortalities still stem from treatments with either higher Background Temperature (*Satiated-Warm-nonHeatwave*, n= 1* and *Unsatiated-Warm-nonHeatwave*, n= 3), or experiencing a Heatwave (*Satiated-Cold-Heatwave*, n= 3; *Unsatiated-Warm-Heatwave*, n= 1). Remarkably, no premature deaths were recorded in any of the tanks when at 21°C (**Table 3.3**).

Results from our assessment of scallop's predicted likelihood of survival indicate a statistically-significant and negative effect of Food Availability, Background Temperature, and Heatwave, plus the positive interaction between Background Temperature x Heatwave (all p-values < 0.05) (**Table 3.4**). Note that while the negative effect of Food Availability is significant, the effect size for this factor on predicted survival is incredibly small, nearly 23- and 26-times smaller than the negative effects of Background Temperature or Heatwave, respectively (**Table 3.4**).

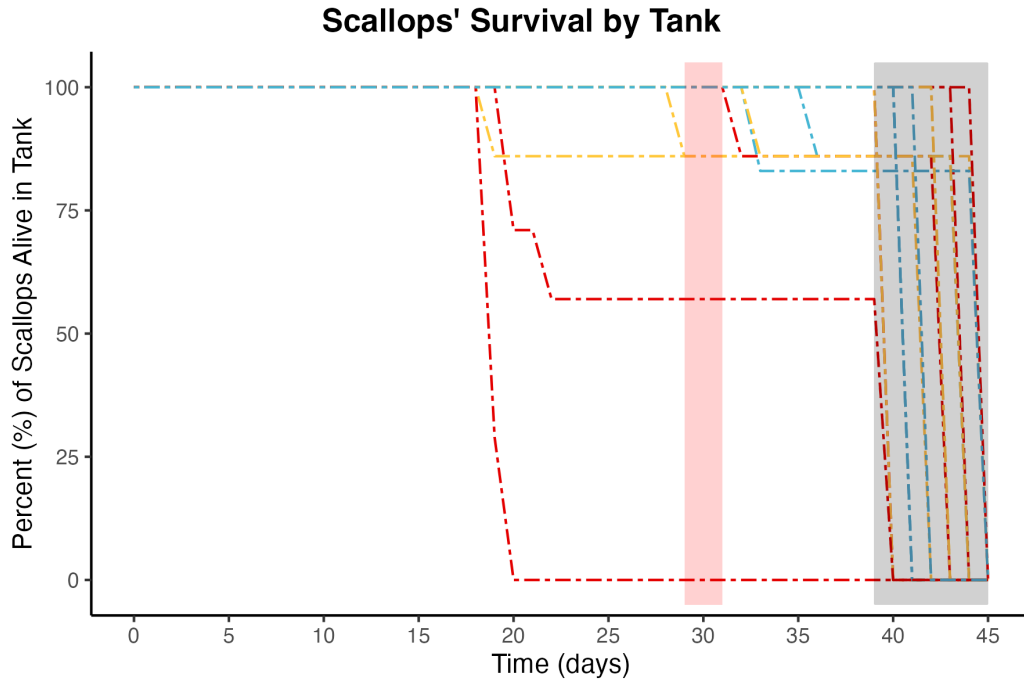


Figure 3.4. Survival curves for all experimental tanks / treatments, where each line signifies the percent of animals living in a single tank over time. On the x axis is time, reported as in days into the experiment, which lasted a maximum of 45 days. On the y axis is percent (%) of animals still living in the tank. (Notice how lines all overlap towards the beginning of the time series since all of the scallops, in all tanks, were still alive at this point.) The color of each line indicates the Food Availability and Background Temperature conditions of the tank prior to heatwave onset in *Days 29–31* of the experiment. The period of time from *Days 29–31*, highlighted by the transparent red block, is when the MHW onset, after which point, 8 of the 17 tanks still ‘online’ were exposed to a 28°C heatwave. The gray rectangle at the end of the plot denotes the final week of the experiment, where we began to take tanks ‘offline’ for use of the scallops in Lethal Temperature assays and dissections.

Table 3.3. Mortalities reported by treatment.

Treatment			Number of Mortalities	% of Treatment	% of Total
Treatment Code (n, sample size)	Background conditions	Heatwave (or no heatwave)			
1A (n= 21)	<i>Satiated</i> x <i>Cold</i>	<i>nonHeatwave</i> (21°C)	n = 0	(0.0%)	(0%)
1B (n= 20)		<i>Heatwave</i> (28°C)	n = 3	(15.0%)	(2.4%)
2A (n= 21)	<i>Satiated</i> x <i>Warm</i>	<i>nonHeatwave</i> (25°C)	n = 11*	(52.4%)	(8.8%)
*10 scallops died during a single mortality event on August 21st: 7 from Tank 7B and 3 from Tank 6C.					
2B (n= 21)		<i>Heatwave</i> (28°C)	n = 0	(0.0%)	(0%)
3A (n= 21)	<i>Unsatiated</i> x <i>Warm</i>	<i>nonHeatwave</i> (25°C)	n = 3	(14.3%)	(2.4%)
3B (n= 21)		<i>Heatwave</i> (28°C)	n = 1	(4.8%)	(0.08%)

Table 3.4. Estimated effect size of Food Availability, Background Temperature, the presence / absence of a Heatwave, and their interactive effects on likelihood of survival (described by **Equation 1**). Here, two asterisks (**) denote an effect that is statistically significant to the 0.01-level, whereas one asterisk (*) denotes an effect that is statistically significant to at least the 0.4-level; effects with no asterisk are not statistically significant. “N/A” means not applicable, as in the model did not report an interaction term, most likely due to collinearity

Factor:	Food	Background temperature	Heatwave	Food × Background	Food × Heatwave	Background × Heatwave
Factor effect size	-7.2**	-173.4**	-205.3**	N/A	31.7	197.3
p-value	0.017**	< 0.001**	< 0.001**	N/A	0.36	< 0.001**

3.2. ROUTINE METABOLISM

To ascertain the effects of Food Availability, Background Temperature, and the presence / absence of a Heatwave on RMR, we analyzed the results of two complementary statistical models, as described above (*Section 2.6*). Results from our fixed-effects linear model (**Table 3.5**), where we considered all treatments, indicate a statistically-significant effect of Food Availability ($p = 0.0542$) and Test Temperature ($p < 0.05$) on RMR (**Figure 3.5**). Meanwhile, results from the simple two-way ANOVA (where our analysis was restricted to only four treatments: S-W-nH, U-W-nH, S-W-H, U-W-H) support the positive effect of Food Availability on RMR ($p = 0.0795$), but do not support the effect of Test Temperature on RMR ($p = 0.9097$) (**Figure 3.5**). In other words, when we consider the effects of temperature on RMR across a wide range of test temperature conditions (21–28°C), there is a noticeable effect of increasing metabolism, but that effect disappears between higher temperatures (25°–28°C). We found that RMR was highest among animals tested at 28°C, followed by animals at 25°C, and 21°C.

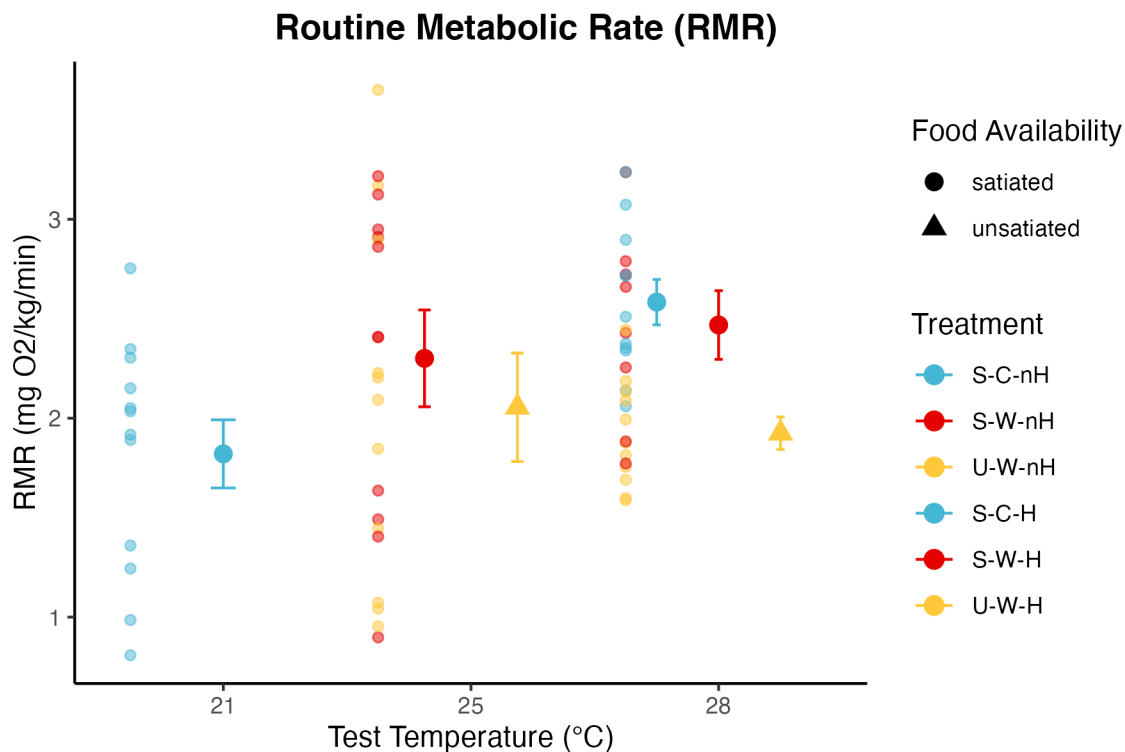


Figure 3.5. Graphs for Routine Metabolic Rate (RMR) across all six treatments, organized by Test Temperature (i.e., the temperature that scallops were tested at: 21°C, 25°C, or 28°C), color-coded by treatment, and shape-coded by Food Availability. Here, S-C-nH: *Satiated-Cold-nonHeatwave*, S-C-H: *Satiated-Cold-Heatwave*, S-W-nH: *Satiated-Warm-nonHeatwave*, S-W-H: *Satiated-Warm-Heatwave*, U-W-nH: *Unsatiated-Warm-nonHeatwave*, and U-W-H: *Unsatiated-Warm-Heatwave*. Each data point on the graph is color-coded and shape-coded, representing the estimated RMR for one individual scallop, with 8–11 scallops per treatment.

Table 3.5. The effect sizes of Test Temperature (21°C, 25°C, or 28°C), Food Availability (HIGH or LOW), and Background Temperature (21°C or 25°C) on predicted routine metabolic rate (RMR). Here, two asterisks (**) denote that an effect is statistically significant to at least the 0.05-level, whereas one asterisk (*) denotes an effect that is near-statistically significant to the 0.1-level; effects with no asterisk are not statistically significant.

Treatment:	Test temp. 21°C	Test temp. 25°C	Test temp. 28°C	Food: HIGH	Background temperature: 25°C	Total effect size
1A (S-C-nH)	1.44**	0	0	0.38*	0	1.82* (1.82)
2A (S-W-nH)	0	2.20*	0	0.38*	-0.21	2.58* (2.37)
3A (U-W-nH)	0	2.20**	0	0	-0.21	2.20** (1.99)
1B (S-C-H)	0	0	2.20**	0.38*	0	2.58* (2.58)
2B (S-W-H)	0	0	2.20**	0.38*	-0.21	2.58* (2.37)
3B (U-W-H)	0	0	2.20**	0	-0.21	2.20* (1.99)

3.3. GROWTH

A visual assessment of daily growth rates over time (**Figure 3.6**) suggests that differences in growth rates, though statistically significant (**Table 3.6**), are small. Results from our mixed-effects linear model predicting daily growth rates (**Equation 2**) suggest that daily growth rate is significantly increased by Food Availability - HIGH (effect size= 0.30, $p > 0.05$) and Background Temperature - HIGH (effect size= 0.21, $p > 0.05$), and that the interaction between Food Availability x Background Temperature is large and negative (effect size= -0.25, $p > 0.05$), such that animals in *Satiated-Warm* conditions grew slightly slower than animals in *Satiated-Cold* conditions. Meanwhile, the presence / absence of a Heatwave was not a statistically-significant predictor of daily growth rates ($p = 0.375$, effect size= -0.11). The interactions between Food

Availability (HIGH) x Heatwave (ON), and Background Temperature (HIGH) x Heatwave (ON), were not statistically-significant ($p > 0.05$) and very small (effect sizes= 0.03 and 0.06, respectively). Daily growth rates were highest among scallops in the *Satiated-Cold* tanks (rate = 0.30 g / day), followed by scallops in the *Satiated-Warm* tanks (rate = 0.26 g / day), followed by scallops in the *Unsatiated-Warm* tanks (rate = 0.21 g / day) (**Table 3.7**). Note that these results were consistent between the simpler, alternative models we ran.

Table 3.6. Effect size of Food Availability, Background Temperature, presence / absence of a Heatwave, and their interactive effects on daily growth rates. Here, two asterisks (**) denote an effect that is statistically significant to at least the 0.05-level, whereas one asterisk (*) denotes an effect that is near-statistically significant to the 0.1-level; effects with no asterisk are not statistically significant.

Factor:	Food	Background temperature	Heatwave	Food × Background	Food × Heatwave	Background × Heatwave
Factor effect size (95% Confidence Interval)	0.30** (0.21, 0.38)	0.21** (0.13, 0.29)	-0.11 (-0.34, 0.13)	-0.25** (-0.40, -0.11)	0.03 (-0.16, 0.22)	0.06 (-0.13, 0.25)
p-value	< 0.001**	< 0.001**	0.375	0.001**	0.758	0.544

Table 3.7. Estimated daily growth rates (g / day) based on fixed and interactive effects of Food Availability, Background Temperature, Heatwave. Here, two asterisks (**) denote an effect that is statistically significant to at least the 0.05-level, whereas one asterisk (*) denotes an effect that is near-statistically significant to the 0.1-level; effects with no asterisk are not statistically significant. And, here, “n.a.” means that the effect of that factor was “not applicable” to that treatment.

Treatment:	Food	Background Temperature	Heatwave	Food × Background	Food × Heatwave	Background × Heatwave	Total effect size
1A (S-C-nH)	0.30**	n.a.	n.a.	n.a.	n.a.	n.a.	0.30** (0.30)
1B (S-C-H)	0.30**	n.a.	-0.11	n.a.	0.03	n.a.	0.30** (0.22)
2A (S-W-nH)	0.30**	0.21**	n.a.	-0.25**	n.a.	n.a.	0.26** (0.26)
2B (S-W-H)	0.30**	0.21**	-0.11	-0.25**	0.03	0.06	0.26** (0.24)
3A (U-W-nH)	n.a.	0.21**	n.a.	n.a.	n.a.	n.a.	0.21** (0.21)
3B (U-W-H)	n.a.	0.21**	-0.11	n.a.	n.a.	0.06	0.21** (0.16)

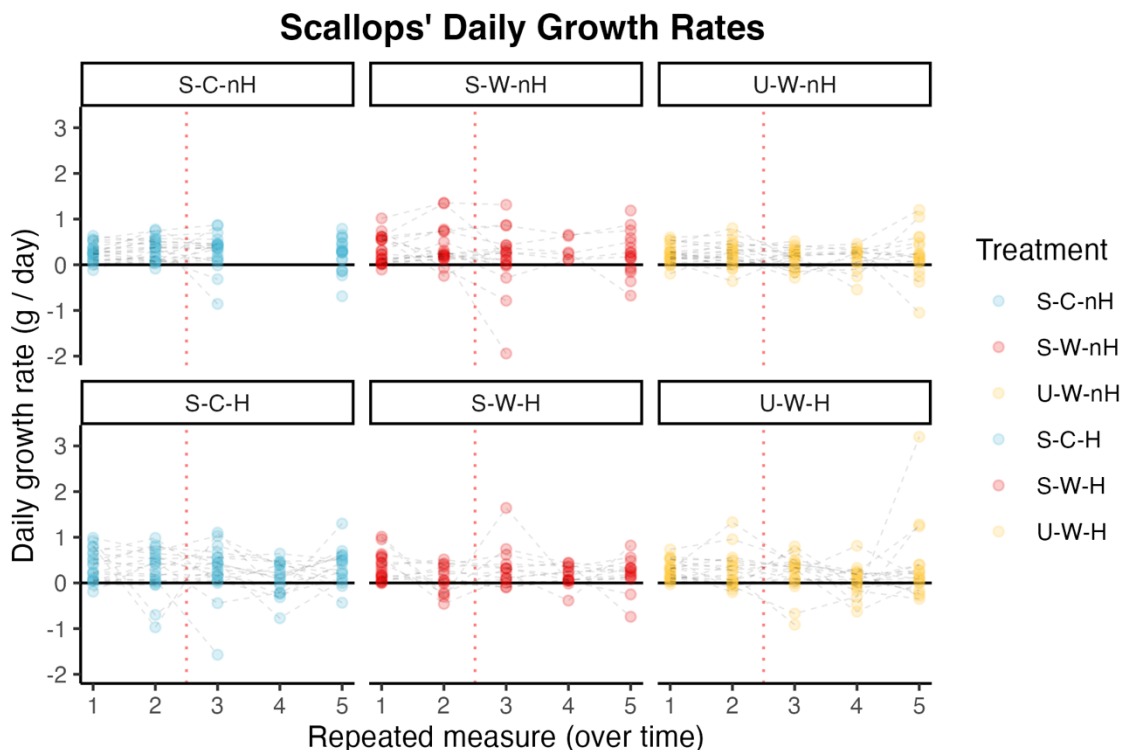


Figure 3.6. Individual daily growth rates across *repeated measures* (i.e., over time), shown by treatment. Here, S-C-nH: *Satiated-Cold-nonHeatwave*, S-C-H: *Satiated-Cold-Heatwave*, S-W-nH: *Satiated-Warm-nonHeatwave*, S-W-H: *Satiated-Warm-Heatwave*, U-W-nH: *Unsatiated-Warm-nonHeatwave*, U-W-H: *Unsatiated-Warm-Heatwave*. On the x axis are our repeated measures, indexed by time, where the time between each point is equal to approximately equal to one week. On the y axis, we have estimates for daily growth rate reported in grams per day (g / day). Measures for daily growth rates were calculated using **Equation 2** (for each individual scallop) at *Week 3*, *Week 4*, *Week 5*, *Week 6*, and at the *end of the experiment*, such that each data point shown here reflects an estimate for daily growth for one scallop at one point in time. Note that animals in the *Satiated-Cold-nonHeatwave* (S-C-nH) treatment had only four repeated measures for daily growth due to a scheduling conflict with RMR sampling (hence the missing data points at *repeated measure 4*). Tracks for daily growth over time are shown for each scallop, connected by the thin dashed lines between points. The red dotted line, shown between *repeated measures 2 and 3*, indicates the point in time after which treatments did or not experience a MHW.

3.4. LETHAL TEMPERATURE MAXIMA

According to results from our linear fixed-effects model, only Heatwave had a detectable effect on Lethal Temperature Maxima (effect size= 0.04, p value= 0.056) (**Table 3.8**). Indeed, the average Lethal Temperature among individuals from treatments experiencing a Heatwave was 0.7°C higher than those not experiencing a Heatwave (35.6°C versus 34.9°C). However, when

testing across treatments (as opposed to testing the effects of specific factors), Lethal Temperature Maxima (LTM) between a handful of treatments were revealed to be statistically-different from one another (**Figure 3.7**; results from Tukey post-hoc test). Specifically, four out of the six treatments had LTM means that were statistically indistinguishable from one another, while the *Satiated-Cold-nonHeatwave* treatment has a mean LTM that is statistically different, and lower, than all of the others except for the *Satiated-Warm-nonHeatwave* treatment (which is statistically-similar, though not identical). The final noteworthy result from this analysis is that the mean *Lethal Temperature maximum* for scallops reared under *Unsatiated-Warm-Heatwave* conditions is statistically different (and higher) from all the other means except for that of the *Satiated-Cold-Heatwave* tank. The average LTM observed across all six treatments was 35.6°C ($\pm$ SEM= 0.1°C), where individual means for each treatment are reported in **Figure 3.7** and effect sizes are reported in **Table 3.8**.

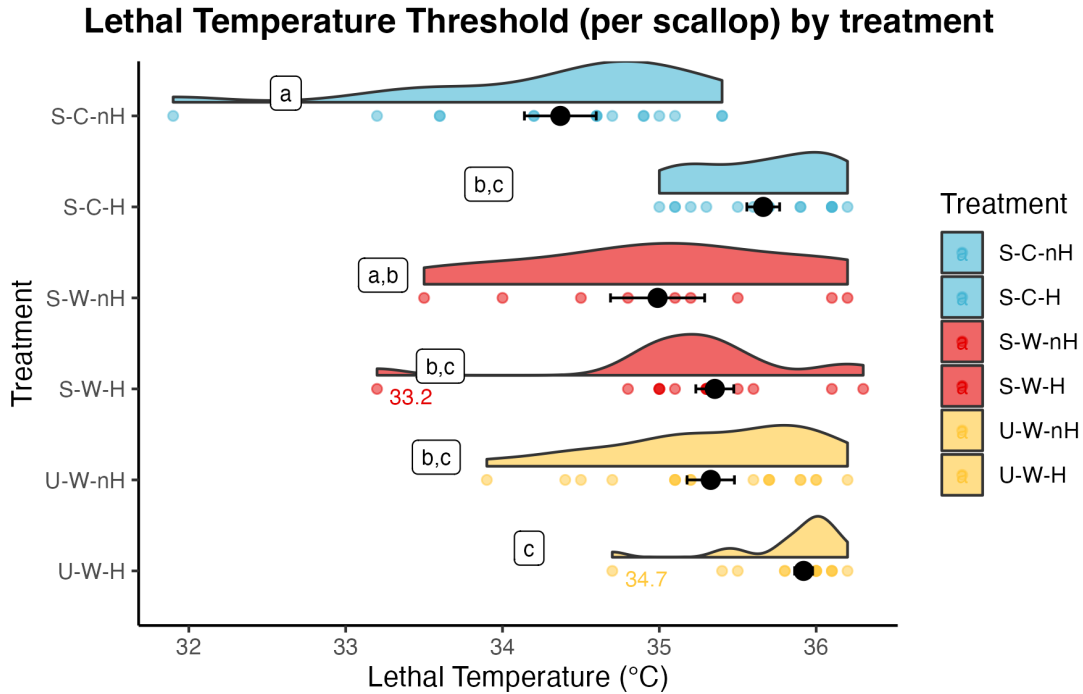


Figure 3.7. Results from our Lethal Temperature assay, where each data point represents the average Lethal Temperature Maximum recorded for an individual scallop, color-coded and grouped by treatment. On the x axis, we have Lethal Temperature reported in °C, and on the y axis, we have treatments listed (where S-C-nH: *Satiated-Cold-nonHeatwave*, S-C-H: *Satiated-Cold-Heatwave*, S-W-nH: *Satiated-Warm-nonHeatwave*, S-W-H: *Satiated-Warm-Heatwave*, U-W-nH: *Unsatiated-Warm-nonHeatwave*, U-W-H: *Unsatiated-Warm-Heatwave*). Across each set of points is a large black dot with whiskers, marking the mean and range in Standard Error of the mean (SEM) for that treatment. Two outlier points, in treatments S-W-H and U-W-H, are identified and labeled; these two outliers are shown here for transparency but were excluded from our calculation of mean and SEM. Above each set of points is the density distribution for those data, modeled using the `geom_flat_violin()` function available through R package “PupillometryR” (Forbes et al., 2020). Letter labels, shown to the lefthand side of each distribution, denote results from our Tukey posthoc test, where treatments with the same letter are statistically-similar to one another.

Table 3.8. Effects of Food Availability, Background Temperature, presence / absence of a Heatwave, and their interactive effects on Lethal Temperature Maxima, as derived from our linear fixed-effects model (**Equation 5**) and excluding extreme outliers ($n=2$). Here, the one value listed in bold and marked with an asterisk (*) is statistically significant to the 0.1-level, while the other effects are not statistically significant.

Factor:	Food	“Background” temperature	Heatwave	Food × Heatwave	Background × Heatwave
Factor effect size (95% Confidence Interval)	-0.02 (-0.04, -0.01)	0.01 (-0.01, 0.04)	0.04* (0.00, 0.08)	0.00 (-0.03, 0.03)	-0.02 (-0.05, 0.01)
p-value	0.183	0.263	0.056*	0.988	0.188

3.5. GONAD MASS AND DIFFERENTIATION

Results from our linear fixed-effects model predicting $GM:AM$ (**Equation 6**) indicate no effect on $GM:AM$ ratio from any of the experimental factors we tested, except for a statistically-significant interaction between Food Availability and Heatwave (**Table 3.9; Figure 3.8**). And, when we controlled for the effect of Food Availability by ignoring the data from the *Unsatiated* treatments and applying a two-way ANOVA to only the *Satiated* treatments, we see a potentially positive effect of heatwave on $GM:AM$ ratio with a p value of 0.11 (**Table 3.10**).

Regarding the *likelihood* of gonad differentiation, our binomial logistic regression (**Figure 3.9**) shows the relationship between shell height (mm) and predicted likelihood (1 - Yes differentiated, 0 - Not differentiated). The mean shell height for scallops with differentiated gonad was 66.1mm (n= 80), compared to a mean height of 58.8mm for the undifferentiated scallops (n= 24), and the average height of all scallops dissected= 64.4mm (n= 104). Interestingly, the smallest differentiated individual was also the smallest scallop we dissected at the end of the experiment, with a shell height of 47.7mm. Within our sample, there were no scallops over ~65mm in height whose gonad tissue remained undifferentiated, however, results from our logistic regression indicate that, any one scallop with a shell height of 65mm, has an 80% chance of having differentiated gonad (**Figure 3.9**). This likelihood creeps towards 100% as shell height increases, and at a shell height of 85mm, any one randomly sampled scallop would have a 96% likelihood of having differentiated gonad.

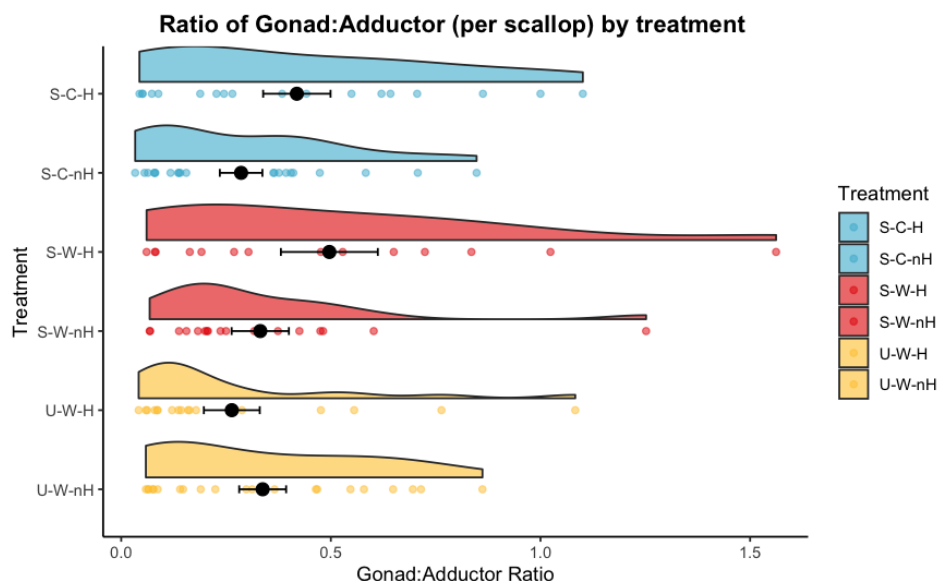


Figure 3.8. *Gonad:Adductor* ratio by treatment, where each datapoint represents the *Gonad:Adductor* ratio estimated for an individual scallop, color-coded and grouped by treatment. On the x axis is the unitless ratio of *Gonad:Adductor* tissue, and on the y axis is treatment (where S-C-nH: *Satiated-Cold-nonHeatwave*, S-C-H: *Satiated-Cold-Heatwave*, S-W-nH: *Satiated-Warm-nonHeatwave*, S-W-H: *Satiated-Warm-Heatwave*, U-W-nH: *Unsatiated-Warm-nonHeatwave*, and U-W-H: *Unsatiated-Warm-Heatwave*). Across each set of points is a black dot with whiskers, marking the mean and range in Standard Error of the mean (SEM) calculated for each treatment. Two outlier points are identified and labeled in treatments S-W-H and U-W-H; these two outliers were excluded from our calculation of mean and SEM. Finally, above each set of points is the density distribution for those data, modeled using the `geom_flat_violin()` function in R (package “PupillometryR”, Forbes et al., 2020).

Table 3.9. Summary of our full mixed-effects linear model estimating the ratio of *Gonad:Adductor* tissue, predicted by the fixed effects of Food Availability, Background Temperature, the presence / absence of a Heatwave, and their interactions, with tank modeled as a random effect (**Equation 6**). Here, two asterisks (**) denote an effect that is statistically significant to at least the 0.05-level, and effects with no asterisk are not statistically significant.

Factor:	Viscera blot weight (g)	Food	Background temperature	Heatwave	Food × Heatwave	Background × Heatwave
Factor effect size (95% Confidence Interval)	1.03** (1.02, 1.04)	0.91 (0.55, 1.50)	1.18 (0.72, 1.96)	0.67 (0.27, 1.62)	2.21** (1.05, 4.63)	0.99 (0.47, 2.08)
p-value	< 0.001**	0.716	0.506	0.365	0.036**	0.984

Table 3.10. Summary output from our simplified ANOVA model, where the ratio of *Gonad:Adductor* tissue is predicted by the fixed effects “Background Temperature, the presence / absence of a Heatwave, and the interactive effects between these two factors, with tank modeled as a random effect. Here, (**) denotes an effect that is statistically significant to at least the 0.05-level, and effects with no asterisk are not statistically significant.

Factor:	Viscera blot weight (g)	“Background” temperature	Heatwave	Background × Heatwave
Factor effect size (95% Confidence Interval)	1.02** (1.01, 1.03)	1.20 (0.74, 1.95)	1.46 (0.92, 2.32)	1.00 (0.50, 2.02)
p-value	< 0.001**	0.450	0.1100	0.990

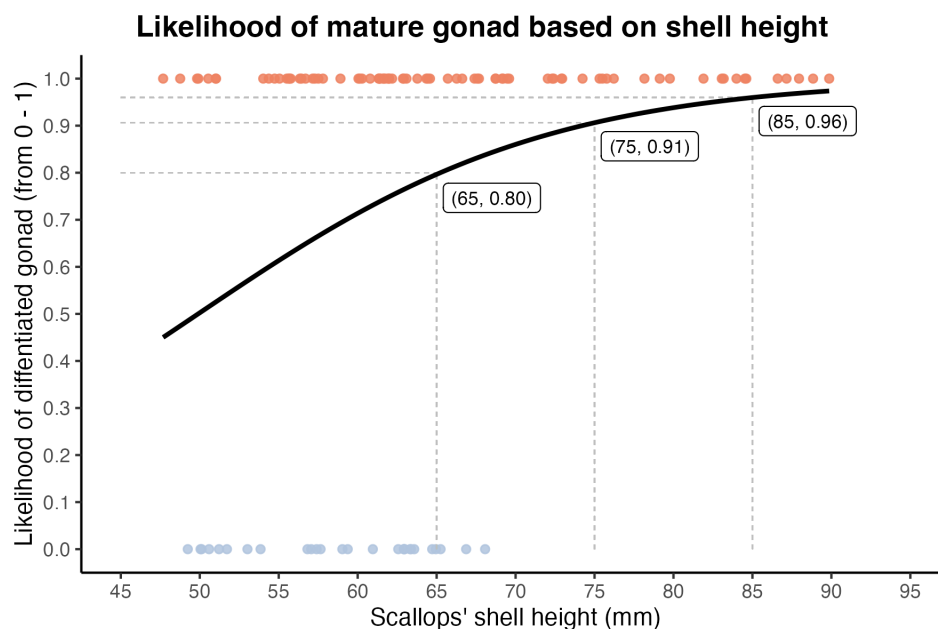


Figure 3.9. Binomial logistic regression (thick black line) showing the relationship between overall shell length (millimeters, x axis) versus the likelihood that any one scallop, at that size, will have sexually mature gonads (likelihood values range from 0 to 1, y axis). Here, each point represents an individual scallop that was dissected as part of the experiment. The color of each data point indicates whether or not that individual had differentiated (i.e., sexually mature) gonad tissue, where points shown in light blue were undifferentiated, and points shown in dark orange were differentiated.

Table 3.11. Summary table of results presented throughout *Sections 3.1–3.6*.

	Food (HIGH) High primary productivity (pp)	Background (HIGH) Warm-water conditions or previous thermal history	Heatwave (ON) Heatwave	Food x Background Interaction between high pp & warm- water conditions	Food x Heatwave Interaction between heatwave & high pp conditions	Background x Heatwave Interaction between heatwave & warm-water history
Survival Estimated likelihood of long-term survival	Negative effect (-) effect is significant but very small	Negative effect	Negative effect	N/A model did not report an interaction term, most likely due to collinearity	No effect	Positive effect (+) interaction between previously high background temperatures and heatwave exposure
RMR * routine metabolic rate	Positive effect *	Positive effect * temperature matters, but previous thermal history does not	Positive effect *	N/A *	N/A *	N/A *
Growth daily growth rates	Positive effect	Positive effect	No effect	Negative effect (-) interaction between high food availability and high background temperatures	No effect	No effect
Gonad gonad:adductor ratio	No effect	No effect	Positive effect suspected (+) effect is not statistically significant but close	N/A model did not report an interaction term, most likely due to collinearity	Positive effect (+) interaction between high food availability and heatwave exposure	No effect
Lethal Temperature Maxima average lethal temp. tolerance	No effect	No effect	Positive effect	N/A model did not report an interaction term, most likely due to collinearity	No effect	No effect
* Cell values demarcated with an asterisk (*) reflect expected effects. These cell values do not reflect direct results, but rather our interpretation of RMR results described in <i>Section 3.2</i> .						

4. DISCUSSION

Results from this study provide us with a few key takeaways about the effects of press-pulse climate stress on *N. subnodosus* (**Table 3.11**), along with potentially useful information for those interested in the effects of press-pulse stressors on bivalves and bivalve rearing. Ideally, these results will contribute to the restoration and management of Mano de León in Northwest Mexico, and we therefore highlight specific findings that may be useful for fisheries and aquaculture below.

4.1. HOW DO THESE ANIMALS (*N. SUBNODOSUS*) RESPOND TO PRESS VERSUS PULSE CLIMATE STRESS?

Evidence from the present study suggests that, for this particular species (*N. subnodosus*), mortality increases under both press and pulse stress. Meanwhile, the sub-lethal effects of low Food Availability, high Background Temperature, and the presence / absence of a MHW are numerous but not unilaterally negative, nor negative in the same ways. Here, we synthesize the effects of these factors / stressors, and their interactions, across all measured physiological indicators, in tandem (**Table 3.11**). We use this section to describe our results in the context of lethal and sublethal effects posed by press-pulse conditions to individual scallops and populations of *N. subnodosus* more generally. With respect to lethal effects, we measured scallops' mortality throughout the experiment (and estimated likelihood of survival), as well as their resistance to Lethal Temperatures at the end of the six weeks. With respect to sublethal effects, we measured estimates for scallops' routine metabolism, growth, and reproductive capacity (gonad size and differentiation).

Mortalities were highest in the *Satiated-Warm* tanks, dominated by one mortality event in particular that occurred before heatwave onset (from August 21st–22nd), in *Tanks 7B* and *6C* (**Figure 3.4**). During this time, the seven scallops in *Tank 7B* (*Satiated-Warm*) perished, along with three other scallops from *Tank 6C* (*Satiated-Warm*). While we cannot ascribe their cause of death with certainty, we can speculate based on physical clues noted at the time of the animals' mortality. Throughout the day on August 21st, scallops in *Tanks 7B* and *6C* did not clear their normal food ration and water in their tanks began to look green and sudsy (a tell-tale sign of gamete release). We found it unusual that the scallops were not eating and began to suspect that something was wrong in the afternoon of August 21st, at which point we also noticed that the animals looked 'unwell'. At that time, we took additional YSI measurements, all of which were normal except for dissolved oxygen (% DO), which was a little lower than usual, at about 80%. Mortalities occurred that evening and we conducted a full water change in both tanks that night; unfortunately, mortalities continued into the next day and the animals from *Tank 7B* could not be saved.

We speculate that this event was most likely the result of rapid and acute hypoxia, following unexpected spawning events in both tanks that (we assume) led to changes in the scallops' metabolism and appetite. Scallops released gametes and eventually stopped eating, at which point we noticed the tank's poor condition and began to monitor individuals for signs of mortality. Release of gametes likely led to a decline in the amount of dissolved oxygen available in the tank, that can, theoretically, be explained by a higher respiration rates among the scallops, their gametes, and bacteria inside the tank. Low-oxygen conditions, along with food left uneaten, may have contributed to eutrophication and asphyxiation. If this suspicion is correct, it would suggest that scallops living under higher temperature regimes — with lower oxygen and / or under higher nutrient loads (Carrier-Belleau et al., 2021) — might be more susceptible to mortality

during periods of reproduction and spawning. This is consistent with previous research by Salgado-García et al. (2020), who suggest that Mano de León's overall performance and survival may be challenged during peak reproductive stages and under extreme heat. Given the limits of our experimental design and the physical measures we took (or did not take), we cannot rule out the possibility that these mortalities were an artifact of the experiment itself (a “fluke”). If we choose to ignore these mortalities in *Tank 7B* (n= 7) and *Tank 6C* (n= 3), the highest mortality rates were observed among those individuals in the *Satiated-Cold-Heatwave* tanks and the *Unsatiated-Warm-nonHeatwave* tanks (**Table 3.3**). Remarkably, no mortalities (0%) were observed under “control” conditions (*Satiated-Cold-nonHeatwave*).

While the scallops reared under control conditions suffered the *least* in terms of mortality, they were also the most vulnerable to lethal heat stress imposed at the end of the experiment. According to results from our LTM assay, scallops from the *Satiated-Cold-nonHeatwave* tanks averaged a Lethal Temperature maximum of 34.4°C ($\pm$ SEM= 0.2) — a full 1.2°C lower than the population-wide mean (35.6°C $\pm$ SEM= 0.1°C). The average *Lethal Temperature maximum* of scallops from control conditions (*Satiated-Cold-nonHeatwave*) was statistically different from four of the five other treatments. Meanwhile, the average Lethal Temperature Maxima of scallops from the *Satiated-Cold-Heatwave* treatment was statistically indistinguishable from that of scallops in the *Satiated-Warm-Heatwave* treatment. This suggests that scallops' *immediate* thermal history and exposure to elevated temperatures may prime them to handle acute hyperthermia, while, in contrast, scallops' thermal history from *weeks prior* does not appear to be important in the same way. Cumulatively, these results suggest that exposure to elevated temperatures immediately preceding a MHW may pre-condition them to handle ensuing high heat, but that the full extent of their thermal history may not matter.

It appears as though all individuals of *N. subnodosus*, regardless of treatment conditions, hit a thermal “ceiling” somewhere between 34°C and 36.3°C, according to our LTM test; in fact, 92% of all observations from the LTM assay fall within this small temperature range. This finding is approximately consistent with results from a previous study conducted by González Estrada (2003), who reports an observed thermal maximum for Mano de León of 28°C–31.4°C, over 96 hours of exposure (note that our assay was much shorter, no more than 7 hours). While the differences in average thermal maxima observed between treatments are noteworthy, Mano de León scallops living in the lagoon ecosystem of Guerrero Negro do not (or very rarely) experience temperatures above 30°C. Thus, results from this assay may only tell us so much in terms of Mano de León’s “real-world” vulnerability to extreme heat, but can be useful when placed in a wider physiological context.

The evidence for a clear thermal maximum among *N. subnodosus* at very high temperatures goes hand in hand with results from our analysis of routine metabolism. We measured RMR among scallops from all six treatments at the end of the experiment, at the appropriate test temperature (21°C, 25°C, or 28°C). Results from our RMR analysis suggest a positive effect of temperature on metabolism between 21°C and 25°C, and 21°C and 28°C — with no statistical differences between the average RMR of scallops at 25°C and 28°C. This suggests that within the temperature range of 21°C and 25°C, *N. subnodosus* can upregulate their metabolism in response to rising temperatures, but, somewhere in the range of 25°C to 28°C, they hit a “metabolic ceiling” (some thermal maximum) and cannot up-regulate their metabolism any further (**Figure 3.5**). Estimates for RMR tell us roughly how much energy is required to maintain an animal’s normal bodily functions, including the energy required for the oxygenation of tissues, regulation of internal biochemical function, and minimum motor activity.

In ectotherms, RMR is directly proportional to growth, where higher metabolism is strongly correlated with higher growth rates (Zuo et al., 2012). This paradigm is consistent with the results from our mixed effects model for daily growth, where Food Availability and Background Temperature both had positive (but interacting) effects on daily growth rates (**Table 3.6**). We can look at our estimates of daily growth alongside our estimates for RMR for a better understanding about how much energy *N. subnodosus* needs to survive (i.e., RMR) versus thrive (i.e., grow) under various oceanographic conditions. Interestingly, it seems as though *N. subnodosus* may down-regulate their metabolism in response to lower food availability (**Figure 3.5**), as scallops reared in *Unsatiated* tanks had lower RMR values relative to their *Satiated* counterparts.

Considering these various lines of physiological evidence (i.e., mortality, resistance to Lethal Temperatures, metabolic rate, and growth rates), it seems as though high food availability may offset the thermal stress (and metabolic demands) imparted by higher temperatures. It also seems possible that these scallops may be able to “eat their way out of a bad situation,” up to a certain point, with “diminishing returns” on food availability at higher temperatures. There exists a likely tradeoff between growth and resistance to hyperthermic shock, since scallops from treatments with higher food availability appear to grow faster, but also appear to be more susceptible to Lethal Temperatures.

While the presence or absence of a MHW may not alter the overall growth of these organisms, MHWs may change how they partition energy and growth among certain organs. Evidence from our analysis of the scallops’ gonad tissue indicates that MHWs have a likely positive effect on the ratio of Gonad to Adductor mass that is near significant ($p > 0.11$), suggesting that MHWs may cause *N. subnodosus* to “ripen” faster under stressful heat conditions. This finding

is consistent with the Temperature Size Rule for ectotherms, which posits that, with increasing temperature, ectotherms mature faster and at smaller body sizes (Zuo et al., 2012). Because *N. subnodosus* relies on its adductor muscle for movement (e.g., when swimming or escaping predators), understanding how they partition their physiological resources in response to high heat, is likely of interest to those concerned with the population dynamics of this species in a warmer world.

4.2. LOOKING AHEAD: CLIMATE-RESILIENCE IN SCALLOP AQUACULTURE

Because of the low feed, space, technology, and energy required to successfully cultivate most bivalves, many view bivalve aquaculture as a highly promising source of “food for the future” (Costello et al., 2020). Evidence suggests that not only has aquaculture been underutilized as a source of global food security, it has the potential to grow sustainably as a practice / industry for decades to come (Costello et al., 2020). Integral to the success and sustainability of bivalve aquaculture, however, is a robust understanding of how target species may respond to increasing environmental change (Kluger et al., 2019; Costello et al., 2020).

Several scallop species exhibit poorly-understood cycles of population “boom-and-bust” that are thought to be linked to changes in climate (e.g., Kluger et al., 2019; Tomasetti et al., 2023). This dynamic is evidenced by the fisheries trajectory of Mano de León in Baja California (as discussed), and by other examples from scallop fisheries around the world (e.g., Arntz et al., 2006; Kluger et al., 2019; Tomasetti et al., 2023; Pales Espinosa et al., 2023). One notable example derives from the bay scallop fishery off the coast of Peru, where, beginning in the late 1990s, small-scale aquaculture production of bay scallops *Argopecten purpuratus* surged, only to crash catastrophically in 2017 (Kluger et al., 2019). Temperature spikes > 10°C and salinity drops (-9–30 PSU), associated with a localized El Niño, led to a near-complete die off of all benthic

organisms in the area, and financial hardship rocked the local aquaculture sector (Kluger et al., 2019). This is just one example where scallop busts can be clearly linked to changing oceanographic conditions. It is in this context then that we argue how the research presented herein serves as an important reference material for those who are interested in further establishing the link between environmental variability and changes in scallop populations. Likewise, we can use this information to help “ready” the Mano de León fishery and aquaculture sectors for a future under climate change.

5. CONCLUSION

We report the physiological outcomes associated with high and low food availability, background temperature, and the presence / absence of a MHW across observations of *N. subnodosus*' resting metabolic rate, growth, gonad mass, gonadal differentiation, mortality, and resistance to Lethal Temperatures. By recognizing, testing, and characterizing the effects of press and pulse stressors specifically, we can begin to understand the effects of a changing climate on organisms, like Mano de León, in a more nuanced way. We can use this information to develop our understanding of scallops' resistance and resilience to various types of environmental change, from low primary productivity, to extreme heat, and other multiple stressors. Based on our results and understanding of the local climate system in Northwest Mexico, we recommend future studies explore the effects of food and temperature along with changes in pH, salinity, and, in particular, dissolved oxygen on the health of *N. subnodosus*. Subsequently, we can apply this knowledge of multiple stressors to create more robust conservation and management strategies. To this end, it is our hope that the suite of results generated by this research will contribute to the effective restoration and management of *N. subnodosus* in Baja California, and serve as a helpful reference material for those interested in cultivating similar species of scallops in a changing ocean.

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SUPPLEMENTARY MATERIALS

A. HOBOS AND YSI DATA

HOBO sensors and a YSI multimeter were used during the experiment to collect time series data for temperature, light, oxygen concentration, salinity and barometric pressure inside each of the experimental tanks (n= 18) and LTM tanks (n= 3, described in **Section 2.1**). The HOBO Onset loggers collected data at 15-minute intervals from the start of the experiment (on August 2nd, 2021) to the end of experiment (end date varies by tank). Each logger was placed on the bottom of the tank, zip-tied to a small weight, and placed away from air pipes that might disturb temperature recordings throughout the experiment. Once the experiment was completed, the logger data were offloaded using HOBOWare¹⁵, and the data were then transferred into excel and R to generate useful graphs (**Figure 3.S1**).

Both the YSI and HOBOS were used to keep track of seawater quality and to ground-truth experimental accuracy over time. As stated, the HOBOS collected temperature and light measurements continuously, every 15 minutes, and were used for data analysis *after* the experiment ended, while the YSI was used to manually collect observations of temperature, dissolved oxygen, salinity and barometric pressure, *every morning* before feeding. In this sense, the YSI measurements were more immediately useful to us in terms of improving animal husbandry and responding to equipment malfunctions in real time.

¹⁵ HOBOWare is available for free download at: <https://www.onsetcomp.com/products/software/hoboware#overview>

B. ANALYSIS OF HOBO AND YSI TEMPERATURE TIME SERIES

We organized all of the tank data collected by the HOBO sensors and YSI, and analyzed *in situ* conditions across tanks and treatment (see **Figure 3.2** or **Table 3.1**). As a reminder, the six treatments were as follows:

- S-C-H: *Satiated* x *Cold* x *Heatwave*
- S-C-nH: *Satiated* x *Cold* x *nonHeatwave*
- S-W-H: *Satiated* x *Warm* x *Heatwave*
- S-W-nH: *Satiated* x *Warm* x *nonHeatwave*
- U-W-nH: *Unsatiated* x *Warm* x *nonHeatwave*
- U-W-nH: *Unsatiated* x *Warm* x *nonHeatwave*

All animals were held at ~21°C prior to the starting the experiment (see **Section 2.1** for details), thus all of the tanks' temperature time series start out at ~21°C. They either remain at that temperature for the next several weeks if they are a “cold” tank, or experience a gradual (+1°C) increase every day for the next four days if they are a “warm” tank (plateauing at 25°C). The heatwave, which begins towards the end of the experiment (on August 29th), bumps the temperature up to 28°C at a rate of +2°C / day for all tanks of interest. Here, “Satiated” refers to tanks with adequate food availability, while “Unsatiated” indicates reduced food availability.

Within treatments, most of the tank replicates show similarities in terms of their physical seawater conditions. Of note, however, is the mortality event that occurred in *Tank 7B* (see **Section 2.2**), which resulted in the loss of this entire tank and the truncation of the timeseries (timeseries for that tank ended on August 22nd). Additionally, in *Tank 7C*, we discovered that there was a major drop in temperature, most likely due to temporary heater malfunction; we were, however, able to get the temperature for that tank back to “normal” within 24 hours.

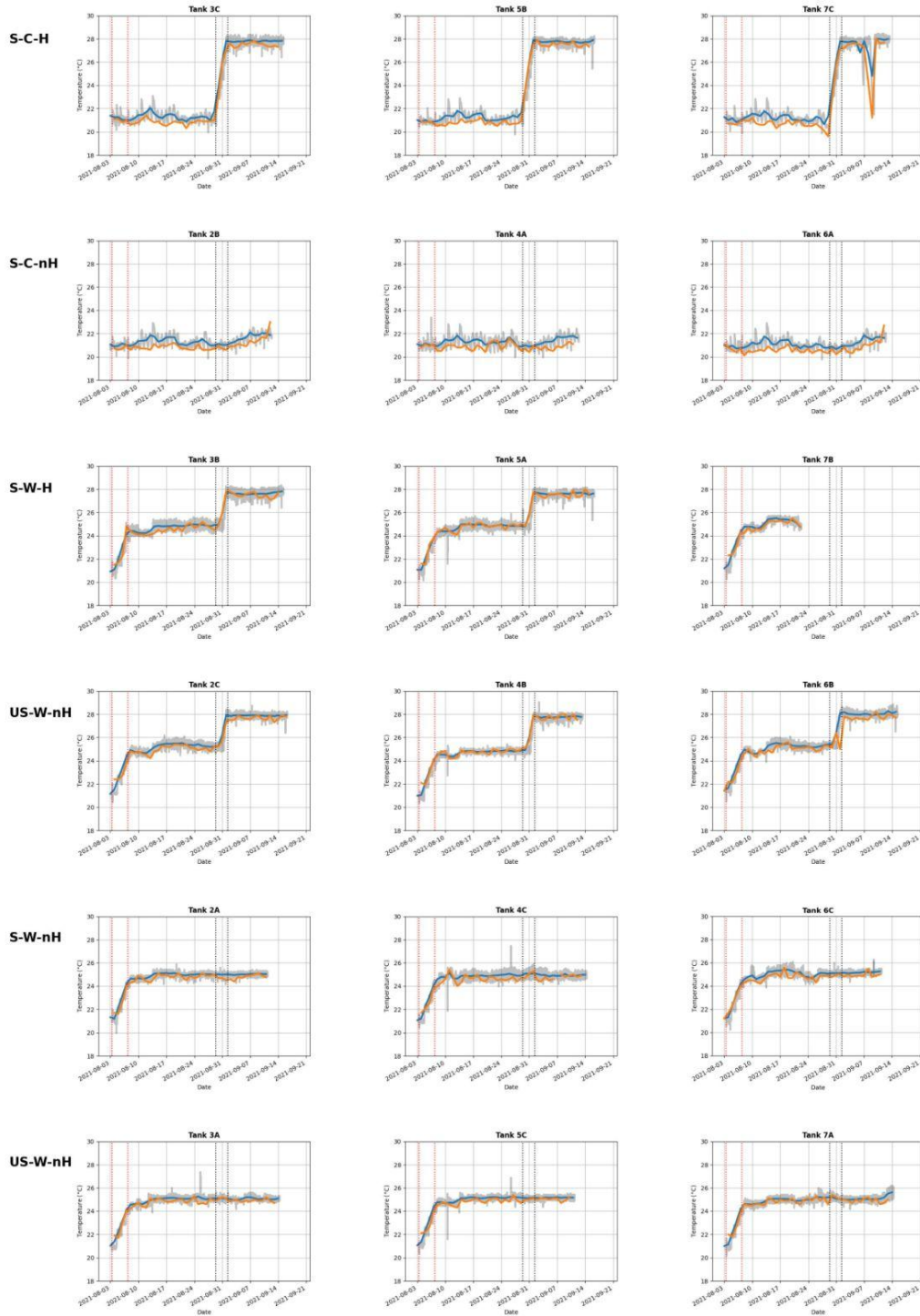
C. UNDERSTANDING THE DIE-OFF THAT OCCURRED PRIOR TO THE START OF THE EXPERIMENT

While the circumstances that led to the rather large die-off of scallops on July X were not immediately clear at the time, the situation improved fairly quickly and mortalities subsided after we conducted a full water change / flush of the holding tank's biological filter. Temperature, pH, and dissolved oxygen in the tank at the time of this event were all normal — that is, unremarkable according to our repeated YSI and HOBO measurements. Likewise, a variety of chemical assays revealed normal levels of ammonia and no detectable levels of chlorine in the seawater. Now, we are reasonably confident that this die-off was due to a prolonged period of exposure to excess nutrients, resulting from measurement error and equipment failure since the chemical kit we used to monitor nitrate concentrations in the bags of live phytoplankton was revealed to be faulty just a few days later (nitrate, NO_3^- is a proxy for iron loading). In short, we believe that it was the first introduction of live phytoplankton as food, dosed with high iron, that led to this event.

Figure 3.S1. Temperature measurements from each of our 18 experimental tanks, with three tanks per treatment (hence the 18 separate panels organized in six rows of three). Each tank was home to 6–7 scallops that experienced the temperature conditions shown here, from *Day 1* of the experiment (August 2nd) until *Day 45* of the experiment (September 16th). On the x axis is time (date), and on the y axis is temperature (°C). Each line depicts one of three alternate and complimentary timeseries collected for temperature: (1) temperature measurements over time, collected every 15 minutes, according to the HOBO sensors (grey line); (2) average daily temperature over time, according to the HOBO sensors (blue line); and (3) daily temperature over time, according to our YSI measurements (orange line). Red vertical lines indicate the initial acclimation period for each tank, and black vertical lines denote the period of marine-heatwave onset. Here, S-C-nH: *Satiated-Cold-nonHeatwave*, S-C-H: *Satiated-Cold-Heatwave*, S-W-nH: *Satiated-Warm-nonHeatwave*, S-W-H: *Satiated-Warm-Heatwave*, U-W-nH: *Unsatiated-Warm-nonHeatwave*, and U-W-H: *Unsatiated-Warm-Heatwave*.

Temperature Overtime by Treatment & Tank

— HOB0- 15min intervals
 — HOB0- daily average
 — YSI- daily measurement



CHAPTER 4

MEXICAN SMALL-SCALE FISHERIES REVEAL NEW INSIGHTS INTO LOW-CARBON SEAFOOD AND “CLIMATE-FRIENDLY” FISHERIES MANAGEMENT

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FEATURE

Mexican Small-Scale Fisheries Reveal New Insights into Low-Carbon Seafood and “Climate-Friendly” Fisheries Management

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Fishing at sunset. Photo credit: Octavio Aburto/Mares Mexicanos

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As a society, we are confronted with the question of how best to feed an expanding human population, and some have pointed to seafood as a “climate-friendly” option. To date, the contributions of small-scale fisheries (SSFs) have been largely excluded from studies on food footprint. Here, we calculated the Emission Intensity profiles for seven seafood types generated by Mexican SSFs. Based on these results—which indicate that there exist several low-carbon SSFs in Northwestern Mexico—we provide a coarse approximation for the total carbon footprint of Mexico’s motorized small-scale fleet. Finally, we scrutinize the utility of non-fuel data (such as GPS data) in predicting fuel consumption/carbon emissions across SSFs. To our knowledge, this is the first life-cycle assessment to compare multiple seafood products generated by Mexican SSFs, and the first published link between tracking data and carbon accounting for SSFs specifically. We discuss how these results, in combination with insights gained from monitoring efforts in Northwestern Mexico, might be used to inform and incentivize “climate-friendly” fisheries management. While carbon footprint represents just one component of sustainability, this article serves as a helpful case study for those preoccupied with carbon accounting and fishers sustainability in traditionally data-limited scenarios.

INTRODUCTION

Social-ecological functioning on our planet faces radical disruption due to anthropogenic climate change (IPCC 2018; IPBES 2019), with nature, Indigenous peoples, and low-income communities projected to bear severe climate injustices (IPCC 2018; IPBES 2019; Whyte 2019). Simultaneously, we are confronted with the question of how best to feed an expanding human population on a planet where increasing climate instability already threatens food security (IPCC 2018; FAO 2019). Some studies point to seafood as a source of “climate-friendly” protein (Hilborn et al. 2018)—that is, protein which has a negative, neutral, or low carbon footprint—while others are less conclusive (Nijdam et al. 2012).

Of the research that provides estimates for carbon dioxide (CO₂) or CO₂-equivalent (CO₂e) emissions associated with food, only a handful report information about seafood landed in small-scale fisheries (SSFs; Kelleher and Mills 2012; Alder et al. 2018). This underrepresentation of SSFs in the footprint literature is remarkable, given their contributions to the global food system. Worldwide, SSFs provide about one-half of all seafood landed for direct consumption, directly employ over 40 million people, and support many more millions in the post-production sector (Kelleher and Mills 2012; Alder et al. 2018). Their exclusion from the footprint literature is primarily attributed to lack of data (e.g., Hilborn et al. 2018; Parker et al. 2018), and because it can be difficult to make “generalizable” conclusions about them (Smith and Basurto 2019). Further, we speculate that emissions from SSFs are understudied due to the incorrect assumption that SSFs are too small to substantively contribute to food security (see Too Big to Ignore; Chuenpagdee 2019).

Here, we explore the carbon footprints associated with seafood from Mexico’s SSFs, based on over 4,900 catch records reported by fishers (Mascareñas-Osorio et al. 2020). We provide Emission Intensity estimates per kilogram of wet weight and kilogram of protein, followed by a coarse approximation for the carbon footprint produced by the country’s motorized (marine) small-scale fleet (defined as boats <12 m; FAO 2003, 2019). Finally, we demonstrate that GPS data can be used to predict the fuel footprint of SSF activities as a proxy for carbon emissions. To the best of our knowledge, this is the first carbon assessment of SSF products in Mexico, and the first published link between geospatial tracking data and carbon accounting in SSFs specifically. We conclude with a discussion about how this information might be leveraged to inform climate-friendly fisheries management in Mexico and beyond.

METHODS

Collecting GPS, Fuel Use, and Landings Data

Scientists with the Gulf of California Marine Program (GCMP) have worked collaboratively with small-scale fishers for over a decade to collect fisheries data from eight communities along the Baja California peninsula and around the Gulf of California, Mexico (Figure 1). This fisheries monitoring program employs portable GPS tracking devices to populate an SSF database with thousands of fishing tracks (> 25,000). Many of these tracks are appended with catch data reported by fishers. Approximately 4,900 of these records were single-species trips with information about geospatial movement, catch, and fuel consumption, collected from the years 2013–2018; these records represent the universe of data we used as our primary sample (Figure 2). The GCMP dataset (Mascareñas-Osorio et al. 2020) is assumed



Figure 1. A map showing the eight different communities in which we work and have collected samples from. (Map of Baja California Peninsula courtesy of Wikimedia commons, available: <http://bit.ly/3uZ6keZ>)

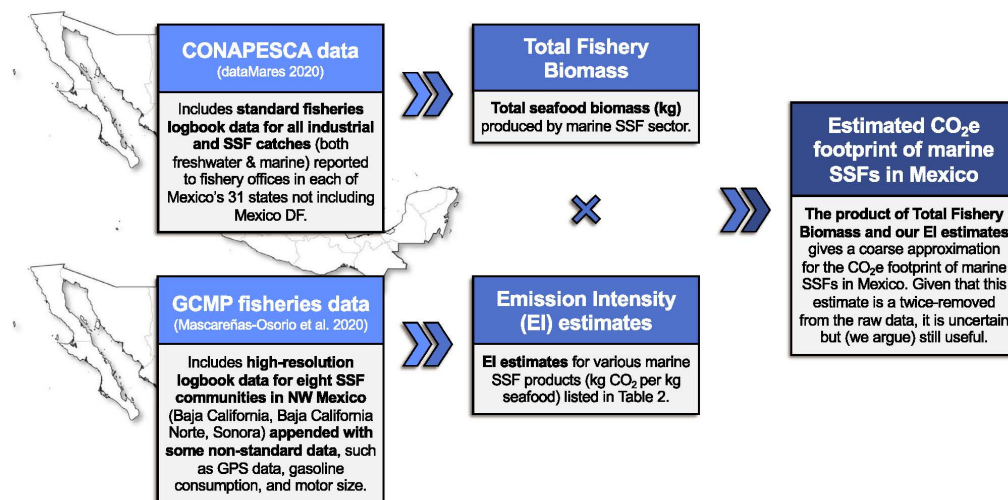


Figure 2. Shows the flow of data used throughout our analyses. Here, SSF = small-scale fisheries, GCMP = Gulf of California Marine Program, and CONAPESCA = Comisión Nacional de Acuacultura y Pesca.

to be representative of SSFs in Mexico (see Supplemental Material) and is available by request at dataMares.ucsd.edu.

Classing Organisms

In both the data set we collected (Mascareñas-Osorio et al. 2020), and in a supporting data set provided by Mexico's Comisión Nacional de Acuacultura y Pesca (CONAPESCA; dataMares 2020; Figure 2), taxa are reported to lowest taxonomic level possible. We grouped each taxa into 1 of 11 organismal classes: (1) small pelagic fishes (<30 cm), (2) large pelagic fishes (> 30 cm), (3) residential demersal fishes, (4) non-residential demersal fishes, (5) demersal molluscs, (6) non-shrimp crustaceans, (7) shrimp/prawns (hereafter shrimp), (8) cephalopods, (9) echinoderms, (10) primary producers, or (11) other.

In most cases, the class to which an organism was assigned was obvious and indisputable. However, some of the demersal fishes were difficult to class, given the diversity of life-history strategies these fish do, or could theoretically, employ. For some demersal fishes, their behavior and natural history are not well known. Here, “resident” refers to demersal fishes with high site fidelity and/or those consistently associated with complex substrate or biogenic structure (e.g., reefs, kelp forests, seagrass meadows, or mangroves). These fishes do not frequently traverse pelagic waters. We assigned resident versus non-resident status to demersal fishes based on: (1) known life history; (2) a preponderance of evidence one way or another, plus consensus among authors using FishBase (<https://www.fishbase.se/>; Froese and Pauly 2020) as well as other publicly available sources; or, as a last resort, (3) the known life history of the species' congener or family member. To give two examples of how this worked, a study by TinHan et al. (2014) found that, of individuals sampled, 50% of Leopard Grouper *Mycteroperca rosacea* showed high site fidelity, versus only 25% of Yellow Snapper *Lutjanus argentiventris*; we classified these fish as resident and non-resident species, respectively.

The CONAPESCA data included records pertaining to 527 distinct taxa spanning all 11 classes, 462 of which we included in this analysis. The remaining 65 taxa (which comprised 7.0% of landed biomass) were identified as (11) other and omitted from our analysis; this catch-all category consisted of freshwater species, unidentified bycatch, unspecified organisms, and a small number of cnidarians. Within the data we collected (Mascareñas-Osorio et al. 2020), 39 taxa were observed (Table 1), representing classes (1)–(7) and 32 genera. Of all landed biomass reported to CONAPESCA (dataMares 2020), 28.6% of biomass was derived from these genera specifically.

Calculating Emission Intensity Estimates for Different Types of Seafood

An Emission Intensity (EI) estimate tells us the emission rate of CO₂e, or the global warming potential per kilogram of product. These estimates are useful for comparing carbon footprint between foods and allow us to approximate the total emissions generated by a fishing fleet, using landings data alone (see Figure 2). Very often, EI estimates refer to the live/wet weight of product, but can also refer to butchered/filletted weight (Nijdam et al. 2012). We calculated EI estimates for each class of organism based on samples of seafood *wet weight* and fuel consumption (Mascareñas-Osorio et al. 2020). To encourage comparison between our EI estimates and those previously published, we applied estimation methods approximately consistent with Parker et al. (2018), with some minor caveats outlined below.

Out of 5,295 trips complete with gasoline data, less than 8% were flagged as multi-species trips. Thus, to avoid the numerous uncertainties associated with portioning fuel consumption among multiple species (Vázquez-Rowe et al. 2012), we only considered single-species trips ($n_{\text{single-species trips}} = 4,939$ samples). Unlike Parker et al. (2018), whose EI estimates are global but largely informed by industrial fleets powered by marine diesel,

Table 1. Lists the 39 taxa represented by the samples we collected in Northwestern Mexico (Mascareñas-Orsorio et al. 2020), grouped by class.

Small pelagic fish (< 30 cm)	Non-resident demersal fish
<i>Clupeidae</i> spp.	<i>Cynoscion othonopterus</i>
<i>Sardinops sagax</i>	<i>Cynoscion</i> spp.
	<i>Gnathanodon speciosus</i>
Large pelagic fish (> 30 cm)	<i>Lutjanus peru</i>
<i>Atractoscion nobilis</i>	<i>Lutjanus</i> spp.
<i>Isurus oxyrinchus</i>	<i>Micropogonias megalops</i>
<i>Mobula thurstoni</i>	<i>Mulloidichthys dentatus</i>
<i>Mustelus californicus</i>	<i>Paralichthys californicus</i>
<i>Prionace glauca</i>	<i>Stereolepis gigas</i>
<i>Rhinoptera steindachneri</i>	
<i>Scomberomorus concolor</i>	Demersal molluscs
<i>Seriola lalandi</i>	<i>Chione californiensis</i>
unspecified sharks	<i>Hexaplex</i> spp.
	<i>Panopea generosa</i>
	<i>P. globosa</i>
Resident demersal fish	
<i>Balistes polylepis</i>	Non-shrimp crustaceans
<i>Caulolatilus princeps</i>	<i>Callinectes bellicosus</i>
<i>Epinephelus labriformis</i>	<i>Panulirus interruptus</i>
<i>Hyporhamphus niphobles</i>	
<i>Mugil</i> spp.	Shrimp
<i>Mycteroperca jordani</i>	<i>Farfantepenaeus californiensis</i>
<i>M. rosacea</i>	<i>Litopenaeus stylirostris</i>
<i>Paralabrax maculatofasciatus</i>	
<i>P. nebulifer</i>	
<i>Paranthias colonus</i>	
<i>Sphoeroides annulatus</i>	

we calculated emissions borne from the combustion of gasoline (used by Mexican SSFs). We assumed a fuel-to-emissions conversion of 2.8 kg CO₂/L of gasoline, accounting for the direct (2.3 kg CO₂/L; Natural Resources Canada 2014) and indirect (0.5 kg CO₂/L; DEFRA 2011) emissions associated with combustion and upstream production. We assumed that non-fuel emissions directly associated with fishing contributed an additional 10% to total fishing emissions (supported by Gulbrandsen 2012), accounting for CO₂e sources like the production/consumption of ice. All data analysis was performed using R version 4.0.3, and graphs were generated using ggplot2.

To obtain EI estimates for each class of organism, we first generated EI estimates for individual trips by multiplying reported fuel consumption (L) by a factor of 3.11 CO₂e/L and dividing by the wet weight of catch (kg) reported for each entry. To limit the influence of outliers, we applied a 95% winsorization to all EI estimates (R DescTools package), except for small-pelagic fishes where $n = 7$. Using this data set, we produced mean EI estimates for classes (1)–(7) and bootstrapped a 95% confidence interval for each (R boot package). Due to lack of data, we were unable to generate EI estimates for classes (8) cephalopods, (9) echinoderms, and (10) primary producers, which are fished throughout Mexico and account for 22.7% total landed biomass reported to CONAPESCA (dataMares 2020).

Comparing to Other Types of Animal Protein

To contextualize our results for seafood landed by SSFs, versus other sources of protein, we provide an approximation for CO₂e emissions per kilogram of protein, derived from each class of organism (Table 2), employing methods approximately consistent with Nijdam et al. (2012) and Parker et al. (2018). We assumed protein content was equal to 20% of total edible catch (Nijdam et al. 2012; Parker et al. 2018), which we approximated as 40% of landed biomass (Nijdam et al. 2012; Parker et al. 2018), unless the catch was marked as prepared in some way. For example, about half of all entries were reported as having been “gutted,” “deshelled,” “beheaded,” or otherwise butchered. We treated these landings as *de facto* edible catch, while all other records were assumed to report unprocessed wet weight. Following this transformation, we multiplied the CO₂e estimate for edible catch by a factor of 0.2 to obtain kg CO₂e/kg protein. As was the case for our EI estimates, we winsorized estimates for CO₂e per kilogram of protein at the 95% level (grouped by class, sans small pelagics).

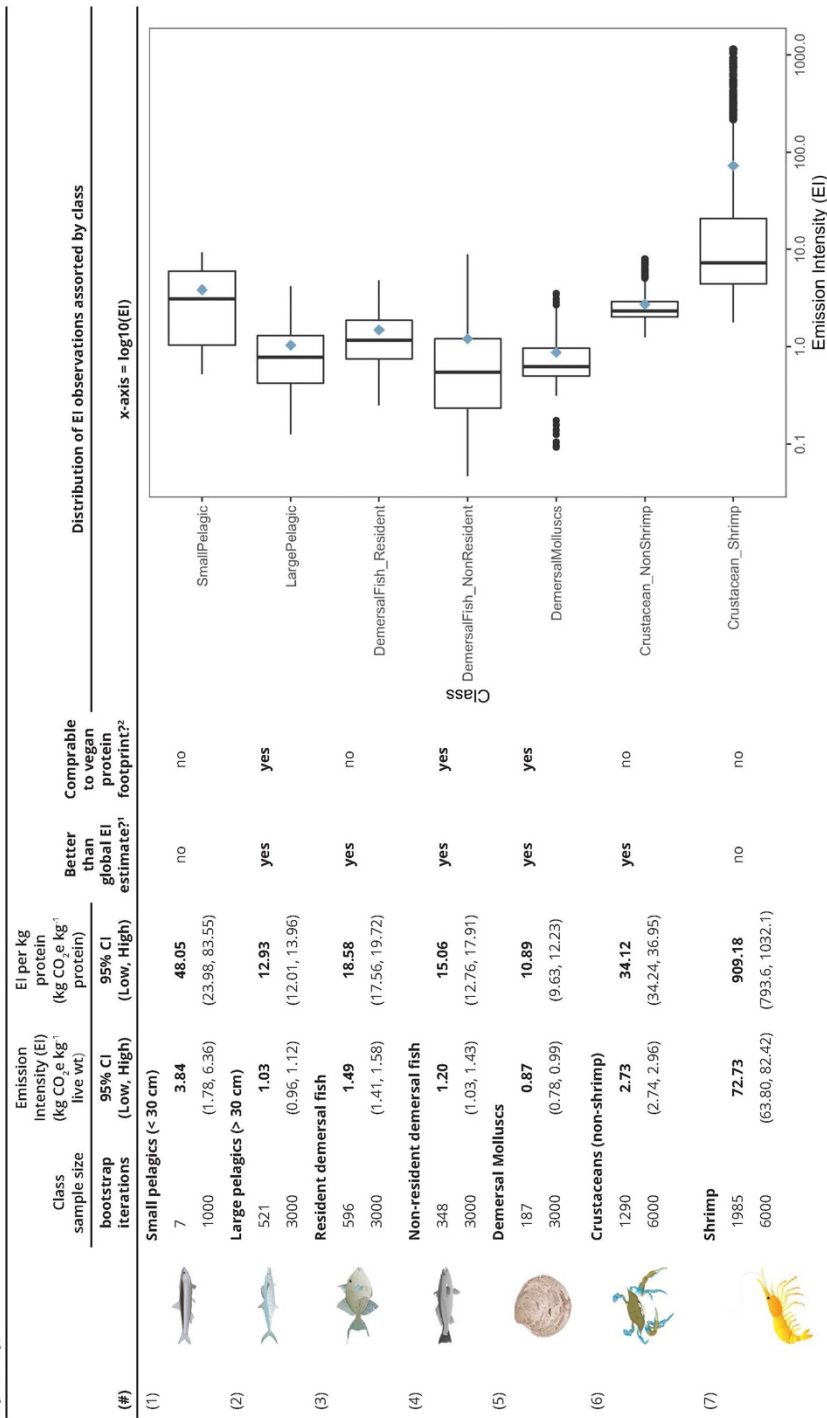
Unlike Parker et al. (2018)—though consistent with other “cradle-to-gate” life-cycle assessments (Vázquez-Rowe et al. 2012)—we assumed that the downstream emissions associated with processing and distribution of these products were equal to zero, primarily because the value chains of Mexican SSF products are non-uniform and poorly resolved. Thus, the estimates for EI per kilogram of protein reported here are conservative and may not reflect a 100% assessment of life-cycle emissions, but close to it. (Note that, when approximating the CO₂e emissions per kg of edible protein, Parker et al. [2018] added an additional 0.5 kg per landed kg of seafood. If we were to apply this extra source of emissions to our calculations, our estimates for emissions per kg of protein would increase by ~16%.)

Estimating Carbon Footprint of Mexico's Marine SSFs

To calculate the carbon footprint for marine SSFs in Mexico, we utilized our EI estimates in combination with SSF data reported in the country's 17 coastal states (Figure 2; dataMares 2020). We grouped records for SSF catch by class (total biomass, kg), and then multiplied these observations by the best available estimate for EI. For classes (1)–(7), we used the EI estimates produced directly by our analysis, and for classes (8)–(10) we supplied a “best guess” estimate.

For (8) cephalopods, we assumed that the EI was equal to that of the global estimate reported by Parker et al. (2018) of 2.8 kg CO₂e/kg. For (9) echinoderms and (10) primary producers, providing a best guess estimate was not so straightforward, since very little published data on their footprint exists. What data does exist is not readily applicable to SSF production in Mexico. For example, Purcell et al. (2018) estimate an EI of 3.5 kg CO₂/kg of fresh sea cucumber in Fiji, however, differences in habitat, fisher behavior, use of boats, and fleet size between sea cucumber fishing in Fiji and Mexico are notable. Similarly, we identified a handful of studies estimating the carbon footprint associated with industrially farmed plant products (e.g., Nijdam et al. 2012) and algae farmed for biofuel (Quinn and Davis 2015), which we did not feel were applicable to SSFs in Mexico. Thus, for classes (9) and (10), we supplied the most conservative EI estimate produced by our own data (which, as we report below, is that of demersal molluscs).

Table 2. Lists Emission Intensity (EI) estimates and protein footprint estimates for each class of organism, with 95% confidence intervals listed beneath each estimate; whether or not the EI estimate for that particular type of seafood is better than the global EI estimate generated by Parker et al. (2018), and comparable to vegan protein (Nijdam et al. 2012). Finally, the boxplot shows the distribution of EI estimates, among and within classes, where: the x-axis is $\log_{10}(\text{EI})$, the mean is marked by a blue diamond, and individual EI estimates that fell outside of the first and fourth interquartile range appear as individual black points. (Seafood icons courtesy of IAN/UMCES Symbol and Image Libraries, available: ian.umces.edu/imagelibrary/; image authors: Tracey, Saxby, Saxby, Saxby, Chen-ery, Tracey)



NOTE: EI estimates are not reported for (8) Cephalopods, (9) Echinoderms, or (10) Primary Producers due to lack of data. However, these classes of organisms are fished throughout Mexico and accounted for in our subsequent analysis.

¹EI estimates for the global fleet (including small-scale and industrial vessels) are reported by Parker et al. (2018).

²Comparable to the carbon footprint associated with a 100% plant based protein (i.e., legumes, 100% vegetal meat substitutes) reported by Nijdam et al. (2012), that is: 4–17 kg CO₂e/kg protein.

We ran our calculation for the total carbon footprint of Mexican SSFs three separate times: (1) using the mean EI estimates supplied by our data and best guesses, as well as the (2) high and (3) low EI estimates predicted by each 95% confidence interval. This allowed us to report the estimate for total carbon footprint in addition to a low–high “range” for that estimate, which we list in parenthetical notation as such: [*main estimate*] (low–high estimate). This low–high estimate was propagated throughout subsequent calculations and reported throughout the text as appropriate.

Estimating Footprint Using GPS Data

As a proxy for carbon emissions, we decided to test the utility of non-fuel data in predicting SSF fuel consumption over individual trips and a 100-member sample of trips (i.e., a small fishing fleet). Using the lme4 package in R, we generated three multiple linear regression models, each one more saturated than the last. In our first model (Y_1), we performed a multiple linear regression where fuel consumption was predicted by (i) the total distance travelled (continuous) and (ii) hours spent on the water (continuous), such that $Y_1 = \beta_1 x_1 + \beta_2 x_2 + e_1$. Our second model (Y_2) was similar to Y_1 with the additional predictor variable of (iii) class of organism fished (categorical), such that $Y_2 = Y_1 + \beta_3 x_3 + e_2$. Then, using only fuel records appended with information about the vessel’s motor size (which reduced our sample to $n_{\text{motor sample}} = 915$, excluding $n_{\text{small-pelagic}} = 1$), we performed a third multiple linear regression (Y_3), including (iv) motor size/horsepower (categorical), such that $Y_3 = Y_2 + \beta_4 x_4 + e_3$.

We scrutinized the predictive ability of all three models (Y_1 , Y_2 , and Y_3) when applied to a small fishing fleet using a Monte-Carlo Cross-Validation technique (Xu and Goodacre 2018), which calculated the percent error borne from the difference between predicted and observed fuel consumption over 100 fishing trips, bootstrapped/iterated 1,000 times, such that $n_{\text{trips}} = 100$ and $n_{\text{bootstrap iterations}} = 1,000$. Twenty-five percent of all available data was used to train the model(s) and generate predicted values, while the remaining 75% of the data points were retained. By iterating this process 1,000 times, we were able to generate the mean of, and range for, percent error borne from each model, providing a coarse picture as to how well each model might perform in the “real world.”

RESULTS

EI Estimates for Popular Seafoods in Mexico

EI estimates including 95% confidence intervals for each class of organism are reported in Table 2 and vary between classes and within trips. For example, shrimp—which have long been the target of environmentally hazardous fishing (Cisneros-Mata 2010; Aburto-Oropeza et al. 2017b)—contribute over 83 times as many carbon emissions per kilogram of catch than do demersal molluscs (EI = 72.73 versus 0.87 kg CO₂e/kg). Large-pelagic and non-resident demersal fishes contribute low- to moderate-carbon catches (EI = 1.03 and 1.20 kg CO₂e/kg, respectively), while resident demersal fishes have a slightly higher carbon footprint (EI = 1.49 kg CO₂e/kg).

Closer scrutiny of the data reveals that non-shrimp crustaceans, such as crabs and lobsters, contribute far fewer emissions per kilogram than do shrimp (EI = 2.73 versus 72.73 kg CO₂e/kg), likely explained by gear type used to fish them (see Table 3). For example, crabs and lobsters are landed using stationary traps, which are lightweight and easy to collect relative

to other types of gear. In contrast, shrimp are landed using trawls or large gillnets, which carry tremendous mass as they drag across the sea floor. Lending credence to this hypothesis are the results from previous studies (e.g., Kelleher and Mills 2012; Parker et al. 2018), and the observation that, on average, small-scale vessels fitted with “eco-friendly” trawls (*changos*) use 3–26 times less gas per kilogram of unprocessed shrimp than do vessels fitted with traditional trawl nets and large gillnets. Specifically, the EI estimates associated with shrimp landed using eco-friendly trawls is 6.19 kg CO₂e/kg ($n_{\text{records}} = 586$) versus 165.28 kg CO₂e/kg for traditional trawls ($n_{\text{records}} = 859$) and 21.29 kg CO₂e/kg for large gillnets ($n_{\text{records}} = 256$). Point estimates presented here are based on non-winsorized EI values. The decision to winsorize or not changes the point estimates but not the interpretation of our results. Given these discrepancies, we speculate that SSF vessels are particularly fuel-inefficient when it comes to towing heavy equipment (Gulbrandsen 2012).

When we partitioned the data by gear type, we still observed considerable variance across EI estimates for shrimp. A wide range in shrimp EI estimates is driven by high volatility in catch, where some trips were very successful (max = 272.58 kg beheaded), and others were not at all (min < 1 kg beheaded). We observed a similar pattern for the other classes of organisms, where trips with a low catch drove up the average EI, and trips with high catch drove down the average EI. This suggests that one way to lessen emissions associated with seafood is to improve the health of fishery stocks and increase the catch-per-unit effort (Kelleher and Mills 2012).

Certain Seafoods from SSFs Offer Low-Carbon Protein

Some of the seafood landed by SSFs in Mexico offer low-carbon harvests of animal protein (Table 2), consistent with the footprint of a vegetarian or vegan diet, and are potentially climate-friendly (Table 3). Although an exhaustive comparison between proteins is beyond the scope of this paper, previous studies support the following conclusions from our data:

- (1) Protein from demersal molluscs, large pelagic fish, and non-resident demersal fish has a low carbon footprint, comparable to protein from vegan meat substitutes (Nijdam et al. 2012; Hilborn et al. 2018; Parker et al. 2018).
- (2) Protein from resident demersal fish and non-shrimp crustaceans is about as carbon-intensive as protein from eggs, milk, and poultry (Nijdam et al. 2012; Hilborn et al. 2018; Parker et al. 2018).
- (3) Protein from small pelagic fish landed by SSFs may be carbon-intensive, similar to pork. However, this estimate is highly uncertain due to our small sample size, and is inconsistent with literature surrounding other small pelagic fisheries (Avadí et al. 2014; Hilborn et al. 2018; Parker et al. 2018).
- (4) Protein from shrimp is carbon-intensive, on par with protein from ruminant herbivores like cows and sheep (Nijdam et al. 2012; Hilborn et al. 2018; Parker et al. 2018).

The Carbon Footprint of Mexico’s Small-Scale Fleet

Using the latest available catch records reported to CONAPESCA (dataMares 2020), in combination with our EI results (Table 2), we estimate that the carbon footprint for Mexico’s SSFs was 3.35 million metric tons of CO₂e in 2014 (with a low–high estimate of: 2.96–3.86 million metric tons). Since there exist ~74,000 small-scale motorized vessels in Mexico (Alder et al. 2018), we estimate that the mean

Table 3. Characteristics of each small-scale fishery (SSF) beyond Emission Intensity (EI) estimates, including relevant measures of economic and ecosystem impacts. (Seafood icons courtesy of IAN/UMCES Symbol and Image Libraries [available: ian.umces.edu/imagelibrary/]; image authors: Tracey, Saxby, Saxby, Saxby, Saxby, Saxby, Saxby, Saxby, Saxby, Tracey)

#	Class	Emission Intensity (EI)		EI per ex-vessel peso ¹		Ratio of ex-vessel revenue : biomass ²		Typical trophic level		Commonly-used gear	
		(kg CO ₂ e kg ⁻¹ live wt)	(kg CO ₂ e kg ⁻¹ live wt)	(kg CO ₂ e peso ⁻¹)	(kg CO ₂ e peso ⁻¹)	higher- vs. lower-revenue landings	8.7 : 1	common role in the food web	Low	% of trips using gear X	NA*
(1)	 Small pelagics (< 30 cm)	3.84		1.082		lower-revenue landings	8.7 : 1	often primary consumers	Low		*sample too small to generalize: hook & line (n = 4), cast net (n = 3)
(2)	 Large pelagics (> 30 cm)	1.03		0.086		lower-revenue landings	11.4 : 1	generally apex predators	High		Gillnets 82% gillnets; 13% trawls
(3)	 Resident demersal fish	1.49		0.078		lower-revenue landings	21.8 : 1	many meso predators	Medium - High		Mixed 35% traps; 26% trawls; 20% gillnet; 18% hook & line
(4)	 Non-resident demersal fish	1.20		0.108		lower-revenue landings	17.7 : 1	many meso predators	Medium - High		Gillnets 86% gillnets; 10% hook & line
(5)	 Demersal Molluscs	0.87		0.007		lower-revenue landings	11.0 : 1	often primary consumers	Low		Hookah 100% hookah
(6)	 Crustaceans (non-shrimp)	2.73		0.072		lower-revenue landings	27.5 : 1	some secondary consumers	Low - Medium		Traps 100% traps
(7)	 Shrimp	72.73		0.671		higher-revenue landings	49.5 : 1	some secondary consumers	Low - Medium		Trawls 79% trawls; 21% gillnets

¹Values based on individual records of fuel consumption and ex-vessel sales from communities in Northwest Mexico (Mascareñas-Osorio et al. 2020).

²Ratio of total ex-vessel revenue (pesos) to total landed biomass (kg), based on records from marine SSFs throughout all of Mexico in the year 2014 (dataMares 2020).

annual emissions per vessel is 45.3 metric tons of CO₂e (low–high estimate: 40.0–52.2 metric tons) or ~14,597 L gas/year (low–high estimate: 12,909–16,825 L gas/year). Uncertainties associated with this result are discussed in Supplemental Material, however, our estimate appears consistent with findings by Martínez-Cordero and Sanchez-Zazueta (2017), who report median CO₂ reductions in Mexico's SSF fleet resulting from a motor replacement program (not including non-fuel emissions).

Our estimate for fuel use among Mexican SSFs suggests that, relative to other *motorized* SSF fleets, the average SSF vessel in Mexico is “middle of the road” to high in terms of its carbon footprint. For example, compare the average footprint of a small-scale vessel in Mexico (~14,597 L gas/year) to: 1,349 L/male fisher/year for the sea cucumber fishery of Vanua Balavu-Fiji (a sparsely motorized fishery; Purcell et al. 2018); 2,963–15,416 L/vessel/year for the Peruvian Anchoveta *Engraulis ringens* fishery (degrees of motorization; Avadi et al. 2014); and an average 15,000 L/vessel/year among eight SSFs in the European Union (fully motorized; Guyader et al. 2013).

Evidence that Tracking Technologies May Enable Footprint Estimation

We performed three multiple linear regressions (Y_1 , Y_2 , and Y_3), where fuel was predicted by an increasing number of variables: (i) the total distance travelled (continuous), (ii) hours spent on the water (continuous), (iii) class of organism fished (categorical), and (iv) motor size (categorical).

Our simplest model (Y_1) was significant ($F(2, 4931) = 552.8$, $p < < < 0.05$), but only explained 18% of the variance in our data ($R^2_{adj} = 0.18$); both predictor variables (i) and (ii) were significant ($p < < < 0.05$). Our second regression equation (Y_2) included the third predictor variable (iii) class of organism fished, and was significant ($F(8, 4925) = 859.8$, $p < < < 0.05$), explaining 58% of the variance in our data ($R^2_{adj} = 0.58$); all Y_2 predictor variables were significant ($p < < < 0.05$), except for small-pelagic fishes. Finally, our third multiple linear regression (Y_3), which was applied to a smaller subset of the data containing information about vessel motor size ($n_{\text{motor sample}} = 915$), was significant ($F(10, 904) = 407.1$, $p < < < 0.05$), and explained 82% of the variance in our data ($R^2_{adj} = 0.82$); and all Y_3 predictor variables (i)–(v) were significant ($p < 0.01$). This makes sense given that Y_3 is more saturated than Y_2 , and Y_2 more saturated than Y_1 , at the expense of model parsimony.

Using a Monte-Carlo Cross-Validation method (Xu and Goodacre 2018) to test the utility of our regression models in predicting real-world outcomes (where $n_{\text{trips}} = 100$ and $n_{\text{bootstrap iterations}} = 1,000$), Y_1 predicted the observed fuel footprint of a 100-member fleet with a mean percent error of -0.2% (95% CI: $-0.5, 0.1$), and a range of -16.4% to 15.3% error. Y_2 had a mean percent error of -0.02% (95% CI: $-0.2, 0.2$), with a range of -10.6% to 11.0% error. And, Y_3 had a percent error of -0.2% (95% CI: $-0.4, 0.0$), with a range of -11.5% to 11.5% error. In all cases, percent error is close to normally distributed around zero, and dissipates as n_{trips} increases.

A visual assessment of model output suggests that models Y_1 and Y_2 do not accurately predict individual trips with unusually high fuel consumption (Figure 3A), but perform reasonably well over a small fleet (Figure 3B). Since model Y_3 was applied to a smaller and more “normal” subset of the data, it is unknown how Y_3 would predict fuel consumption for trips or fleets with unusually high values.

Cumulatively, these results suggest that in a real world application of models Y_1 through Y_3 , Y_2 would most accurately predict the fuel footprint of a small fleet (Figure 3B), closely rivaled by Y_3 , then Y_1 . This is interesting in that one might expect Y_1 to have more predictive power than Y_2 , given that Y_3 explains a larger amount of variance observed among individual fishing trips. While this may be an artifact of disparate sample size, it still hints at a useful takeaway: while information about motor size is useful, even without it, a large sample size makes it such that Y_2 performs reasonably well at predicting fuel consumption over several trips. Even Y_1 , which only contains information about (i) total distance travelled and (ii) hours spent on the water, performs moderately well at predicting fuel consumption over a small fleet, suggesting that footprint estimation may be possible based on GPS data alone.

DISCUSSION

Our results provide a baseline understanding for scientists and fishery managers who seek to incorporate carbon footprint into their calculus surrounding SSFs and carbon management. Additionally, they indicate that SSFs in Mexico contribute substantially to food security (FAO 2003, 2019; Kelleher and Mills 2012) with relatively low carbon impacts. Yet, carbon footprint represents only one dimension of fisheries sustainability to be aware of, and characteristics for each SSF class (summarized in Table 3) lend valuable context to our understanding of what it means for a fishery to be truly climate-friendly. For example, meso and apex predators are known to play an important role in structuring healthy and resilient marine ecosystems (Estes et al. 2011), which, in turn, support carbon sequestration and regulation of Earth's climate (e.g., Atwood et al. 2015). Thus, intense fishing of large pelagic and non-resident demersal fishes may negatively impact carbon reductions overall, despite their apparently low EIs.

To help incentivize climate-friendly fishing, managers might employ various strategies, such as communications campaigns (Merayo et al. 2019), support for cooperative fisheries management (Hilborn 2004; Cota-Nieto et al. 2018), and direct financial transfers to fishers and their communities as they transition away from high-carbon fishing (Cisneros-Montemayor et al. 2016; Merayo et al. 2019). Managers might also consider removing “harmful” subsidies, which artificially decrease the price of fuel, as these tend to encourage unsustainable fishing practices (Sumaila and Pauly 2007; Sumaila et al. 2010; Merayo et al. 2019; Cisneros-Montemayor et al. 2020).

On the supply side of fisheries production, fuel subsidies disincentivize fuel consciousness among existing fishers and lower the barrier to entry for new fishers, contributing to fleet overcapacity (Sumaila et al. 2010; Merayo et al. 2019). While on the demand side, cheap fuel leads to distortions in seafood prices (Sumaila et al. 2010; Merayo et al. 2019), obscuring the costs of harvest and undermining consumers' propensity to select for low-carbon seafood products. Such subsidies give rise to a socially inefficient outcome, where fisheries are more vulnerable to overexploitation (Sumaila et al. 2010; Merayo et al. 2019; Cisneros-Montemayor et al. 2020), and likely increase fishery emissions on net.

At the same time, it is important to understand that these harmful subsidies disproportionately fall to industrial fisheries (Cisneros-Montemayor et al. 2020), and holistic SSF management must account for the various

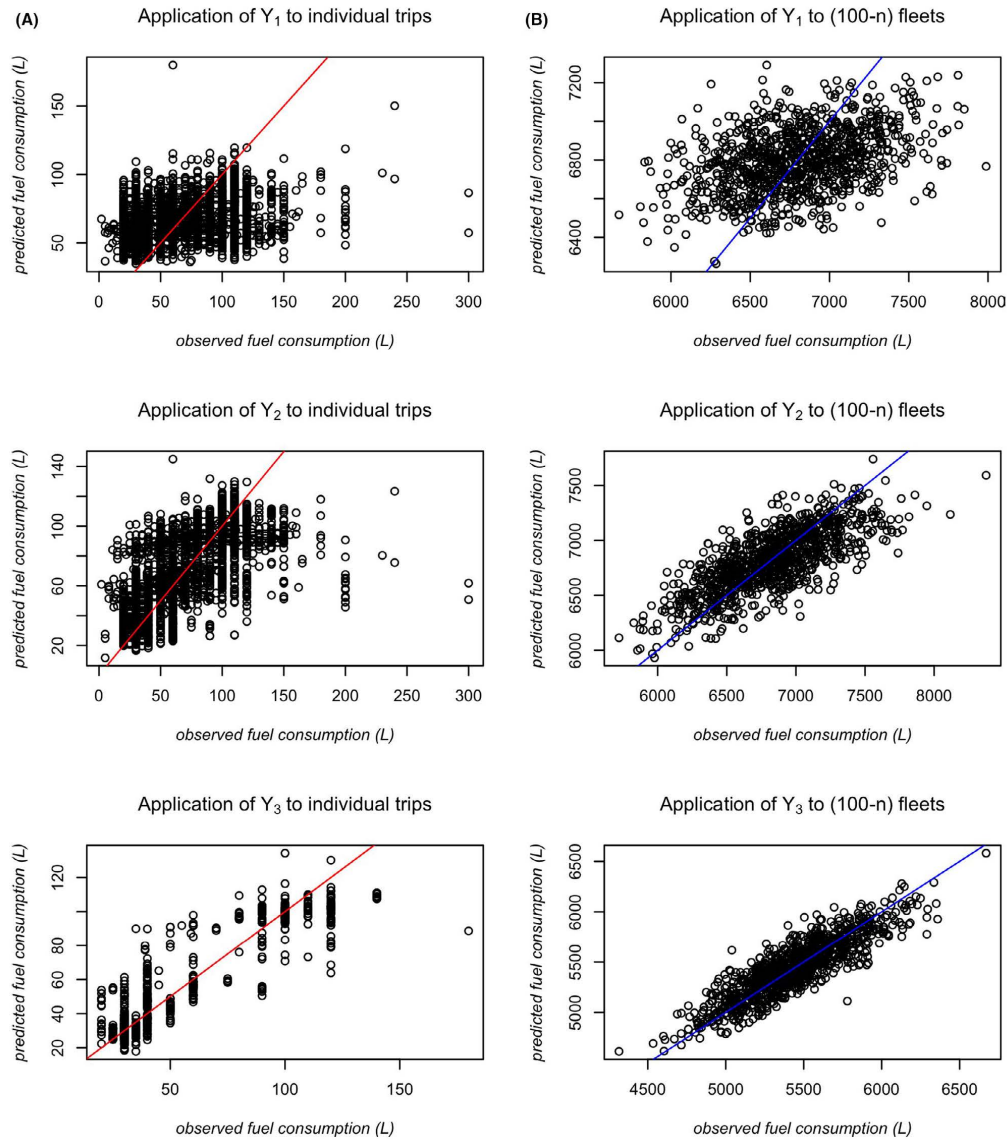


Figure 3. Graphs depicting goodness-of-fit results for multiple linear regression models Y_1 , Y_2 , and Y_3 , when applied to individual trips (A) and small (100-member) fleets (B). Accordingly, in graphs on the left, each point indicates the fuel consumption for an individual fishing trip. In graphs on the right, each point indicates the total fuel consumption for 100-member “fleet,” randomly sampled from the wider universe of data (described in “Estimating Footprint Using GPS Data”). Respectively, red and blue lines indicate a perfect 1:1 relationship between the observed and predicted values generated by each multiple regression when applied to individual trips and 100-member fleets, such that points clustered close to the red/blue line indicate a good model fit, and points far from the red/blue line indicate a poor model fit.

socio-economic benefits conferred by a particular subsidy or style of fishing. Our results suggest that shrimp landed by SSFs in Northwestern Mexico, for example, carry a high carbon footprint per kilogram of protein, but a much lower

carbon footprint per peso (Table 3). Thus, policies designed to promote climate-friendly fishing need be considered on a case-by-case basis and in the wider context of fisheries “sustainability.”

To monitor and address uncertainties between our estimates for fishing emissions and our carbon reality, emergent technologies may provide new and improved information. As evidenced by our results, tracking devices may enable SSF carbon accounting with relatively little adaptation to tracking/monitoring efforts already underway. For example, in an effort to curb illegal, unreported, and underreported fishing, geopositioning technologies such as Automatic Identification Systems and Vessel Monitoring Systems have become commonplace within the world's industrial fishing fleet. These technologies produce massive amounts of automated and semi-automated data, which can be readily utilized by scientists and managers alike through platforms such as the Global Fishing Watch (<https://globalfishingwatch.org>). We reason that the Global Fishing Watch (and platforms like it) may be able to provide estimates for fishery emissions in nearly real time and at a relatively low cost, based on ground-truthing studies such as ours, plus subsequent modifications to its machine learning algorithms.

Fisheries tracking data has proven valuable for reasons beyond surveillance, in both industrial (Kroodsma et al. 2018) and small-scale settings (e.g., Metcalfe et al. 2016; Cardiec et al. 2020), though fishers' feelings towards tracking technologies are generally mixed. Some are suspicious that tracking data will lead to management decisions that penalize participants who fish honestly, while others benefit from access to geospatial information. Among SSFs, GPS data has been demonstrated to enhance cooperative fisheries management (Metcalfe et al. 2016; Cardiec et al. 2020), observance of Marine Protected Areas (Cardiec et al. 2020), and compensation for area closures (Aburto-Oropeza et al. 2017b).

Fishers' willingness to help with monitoring and management increases when they are included in leadership and decision making (Hilborn 2004; Cota-Nieto et al. 2018; Alder et al. 2018). In our experience, fishers' local ecological knowledge not only provides better context for program design, implementation, and data analysis, fishers are well equipped to identify and communicate issues particular to their community and the resources they fish (e.g., Aburto-Oropeza et al. 2017a, 2017b). Furthermore, establishing trust and equity among stakeholders has been identified as integral to sustainable transformation and restoration of ecosystems, fisheries, and human communities (Bennett et al. 2019; Whyte 2019; Merayo et al. 2019). Therefore, administrators of novel tracking platforms should strive to include fishers as both participants and leaders in program development and implementation.

Our findings demonstrate that there exist several low-carbon SSFs in Northwestern Mexico, and that it may well be possible to monitor and improve upon climate-friendly fishing in the region. The methods described here may prove useful for studies in other countries, in data-limited scenarios, and for monitoring programs already underway. Ideally, this work will serve as stepping stone for novel research in SSF science and contribute to our understanding of sustainable seafood production in a rapidly changing world.

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DATA AVAILABILITY STATEMENT

The primary data sources used herein (Mascareñas-Osorio et al. 2020; dataMares 2020) are available by request at dataMares.org. Individuals who are interested in specific details of the analysis should carefully review the Methods section or contact the corresponding author.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.
Supplementary Material [S3](#)

CHAPTER 5

OVERFISHING INCREASES THE CARBON FOOTPRINT OF SEAFOOD PRODUCTION FROM SMALL-SCALE FISHERIES

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Overfishing Increases the Carbon Footprint of Seafood Production From Small-Scale Fisheries

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Small-scale fisheries (SSFs) and the foods they produce are extremely important, contributing 25–50% of global seafood landed for direct consumption. In some cases, SSFs provide seafoods with an exceptionally low carbon footprint, but like all food, it is important to understand the factors that regulate that footprint in the face of increasing demand and a worsening climate-ecological crisis. We utilize long-term fisheries monitoring data from Northwest Mexico to generate novel stock assessments and, subsequently, test the relationship between underlying fishery biomass and fuel intensity observed among several motorized SSFs. Using fuel data from over 4,000 individual fishing trips, in combination with estimated biomass data for 19 regional stocks, we show that the fuel footprint per kilogram of seafood increases sharply as the stock's underlying annual biomass (B) falls below its estimated biomass at Maximum Sustainable Yield (B_{MSY}). We find an inverse relationship between B/B_{MSY} and fuel intensity using a test for simple correlation between the two ($r = -0.44$), a linear regression analysis ($R^2_{adj.} = 0.17$), and a mixed-effects model with gear type, year, and genus modelled as random effects. These results indicate that efforts to end overfishing, rebuild fishery stocks, and/or minimize intensive fishing practices will help to decrease the carbon emissions generated by motorized wild-catch fishing. We anticipate that this study will contribute an important “missing link” to discussions on how best to secure climate-resilient fisheries and, ideally, help SSF stakeholders garner recognition and support for SSFs in this context.

Keywords: artisanal fisheries, carbon footprint, fuel intensity, management, maximum sustainable yield, Mexico, overfishing, small-scale fisheries

INTRODUCTION

Fisheries are an integral source of animal protein to nearly 1-in-5 of the world's roughly 7.2 billion people (FAO, 2017; FAO SOFIA, 2018), making them a key element in all considerations related to global food security. While the production of wild-caught seafood has reached something of a plateau in terms of annual landed biomass (Pauly and Zeller, 2016), demand for seafood (and other animal products) has been steadily increasing over the last several decades and is projected to grow for the foreseeable future (Kearny, 2010; FAO SOFIA, 2018; Costello et al., 2020). Because seafood,

like all food, bears some environmental footprint, it is important to understand the factors that maintain, diminish, or grow that footprint in the face of increasing demand and a worsening climate-ecological crisis (IPBES, 2019; IPCC, 2022).

Fishing is inextricably linked to nearly all marine landscapes, flora, and fauna — and the act of *overfishing* has been shown to have deleterious effects on abiotic and biogenic habitat, dramatically altering species abundance and the preservation of biodiversity, with often negative impacts on coastal communities of people (e.g., Turner et al., 1999; Worm et al., 2006; Sumaila and Tai, 2020; Sumaila et al., 2021). In the 1990's, scientists began to document the serial depletion of fisheries stocks worldwide (e.g., Pauly et al., 1998), namely at the hands of industrial/large-scale fisheries, and several high-profile papers drew public attention to the fact that a large proportion of the world's fish populations were experiencing overfishing or were already overfished (Pauly et al., 1998; Worm et al., 2006). Since then, numerous governmental and non-governmental policy agendas have been dedicated to ending overfishing and rebuilding stocks (FAO SOFIA, 2018). While these efforts have been met with some success (Duarte et al., 2020; Hilborn et al., 2020), overfishing remains a serious problem (FAO SOFIA, 2018), particularly for stocks which lack formal assessments (Costello et al., 2012; Hilborn et al., 2020).

SSFs produce anywhere from 25–50% of all seafood landed for direct consumption (Pauly and Zeller, 2016; FAO, 2017; FAO SOFIA, 2018; Greer et al., 2019) and, in some cases, serve as a source of food with an exceptionally low carbon footprint (Nijdam et al., 2012; Hilborn et al., 2018; Ferrer et al., 2021). SSFs can be motorized or non-motorized, targeting thousands of taxa and supporting millions of jobs in both the fishing and post-production sectors (FAO, 2017; FAO SOFIA, 2018). At the same time, SSFs tend to be "data-poor," and often lack formal fishery stock assessments (Costello et al., 2012; FAO SOFIA, 2018; Hilborn et al., 2020). This makes them often difficult to manage (Costello et al., 2012; FAO SOFIA, 2018; Hilborn et al., 2020) and notoriously underrepresented in socio-political discussions surrounding (sustainable) global food production (e.g., Cohen et al., 2019). Given their diversity, there does not exist a universal definition for SSFs (Hidden Harvest Report, 2012; Smith and Basurto, 2019), but for the purposes of this article, we define SSFs to be those fisheries targeted by vessels < 12m in length (FAO, 2022).

Key considerations vis-à-vis "sustainable" seafood are the existence or non-existence of overfishing within that fishery/particular region, as well as gear type, and extent of fishing effort. Ending overfishing is a valuable endeavor in its own right, with several co-benefits, such as increased ecosystem biomass and avoided damages to aquatic habitat (Sumaila and Tai, 2020). A decrease in the total carbon footprint and/or fuel intensity of fisheries are two *additional* co-benefits that have been theorized by fisheries scientists; the logic behind this idea being that an end to overfishing would require a decrease in overcapacity of the world's fishing fleets, shrinking the total fuel footprint of fisheries while growing available biomass across a number of stocks, and effectively increasing the Catch per Unit Effort (CPUE) (The

World Bank, 2017; Sumaila and Tai, 2020). This idea is compelling and largely intuitive, yet the relationship between overfishing and emissions is supported by a limited number of empirical studies and relevant inquiries focused on SSFs are noticeably scant (see Parker and Tyedmers, 2015; Rousseau et al., 2019; Bloor et al., 2021).

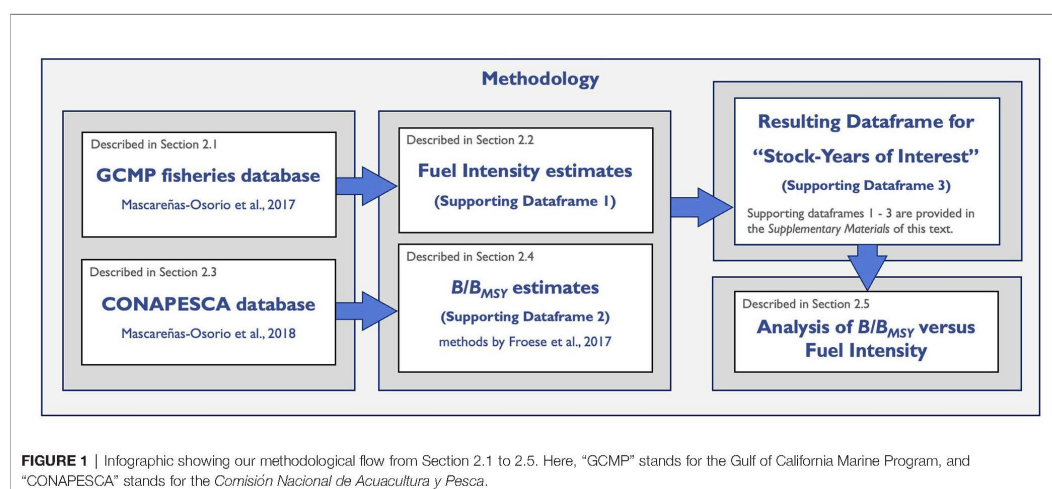
Here, we utilized long-term fisheries monitoring data from Northwest Mexico to generate novel stock assessments and to, subsequently, test the relationship between underlying stock status and fuel intensity among several SSFs in the region [note that we use fishery biomass as a proxy for stock status]. Like others have alluded to (e.g., The World Bank, 2017; Sumaila and Tai, 2020), we hypothesize that there exists an inverse relationship between fishery biomass (B/B_{MSY}) and fuel intensity — that is to say, as fishery biomass decreases, the fuel required to land one unit of seafood increases. To substantiate this hypothesis, we utilized two independent fishery databases, in combination with methods for "data-poor" stock assessment (developed by Froese et al., 2017), to explore the relationship between estimated B/B_{MSY} and fuel intensity across 19 Stocks, and 39 "Stock-Years of Interest" (defined in Section 2.3). We end with a discussion on the theoretical climate-fishing feedbacks that have been proposed in the literature to date, and discuss the importance of our results in the context of overlapping social, climate, and biodiversity objectives.

METHODS

To test the relationship between fishery biomass (B/B_{MSY}) and fuel intensity, we draw from the following independent data sources: (i) fuel and catch data from the Gulf of California Marine Program (GCMP) Fisheries Monitoring Network, hereafter referred to as "the GCMP database" (Mascareñas-Osorio et al., 2017); and (ii) fisheries landings data supplied by the Mexican governmental agency known as *Comisión Nacional de Acuacultura y Pesca* (CONAPESCA), hereafter referred to as "the CONAPESCA database" (Mascareñas-Osorio et al., 2018). Both of these databases are updated periodically, and the data used herein reflect observations from the GCMP database recorded through March, 2018, and from the CONAPESCA database recorded through December, 2019. See **Figure 1** for a stylized representation of our methodology, and consult the **Supplementary Material** section to access relevant dataframes. All analyses were performed using Microsoft Excel in combination with R version 4.0.3 (R Core Team, 2020).

Collecting High-Resolution Catch and Fuel Data From SSFs in Northwest Mexico (Utilizing "the GCMP Database")

Northwest Mexico is home to two of the country's most productive fishery zones: the southern extension of the California Current Ecosystem, and the Gulf of California (GoC) (Cisneros-Mata, 2010; FAO, 2022). Indeed, from our own interrogation of the CONAPESCA database, we found that from 2006 to 2014, SSFs in Northwest Mexico contributed



52% of the total biomass generated by the nation’s marine SSFs (Ferrer et al., 2021).

Understanding the critical importance of SSFs in and around the GoC, colleagues with the GCMP and local small-scale fishers have worked collaboratively for over a decade to collect high-resolution fisheries monitoring data from in and around the Baja California Peninsula (see <http://gulflprogram.ucsd.edu/slider-home/projects/>). This monitoring program employs portable GPS tracking devices to populate a database with thousands of fishing tracks (> 25,000), about 5,000 of which are further appended with information related to catch and fuel consumption. These records within the GCMP database comprise the universe of data we used to generate the fuel intensity estimates described below.

Fuel Intensity Estimates From the GCMP Database

A fuel intensity estimate (FIE) is a measure of fuel efficiency, telling us the fuel consumption per unit of X, where in this case X is one kilogram of wet weight^{1,2} seafood. To generate FIEs, we divided the gasoline consumption (in liters) by the wet weight of catch reported for each single-species fishing trip identified/located in the GCMP

¹Key assumption: About half of the fishing records we analyzed reported total landings in terms of wet weight (kilograms), while the other half were marked as having been butchered or prepared in some way. We assumed that, in most cases, prepared weight accounted for 40% of total wet weight (Nijdam et al., 2012), such that $wet\ weight = prepared\ weight \cdot (0.40)^{-1}$, with two notable exceptions to this rule: beheaded shrimps, where we assumed that the rest of the shrimp’s body accounted for 65% of total wet weight (<https://louisianadirectseafood.com/seafood-handbook/>), and shark / ray fins (“aletas”), which we assumed accounted for just 5% of total wet weight (Cortes & Neer, 2006). For fishing trips where the style of preparation was not explicitly noted, we assumed that the catch was reported in terms of wet weight. Note that the statistical significance and interpretation of our results appears robust to alternative conversion factors of prepared-to-wet weight, where some conversion factors actually increased the statistical-significance and effect size of our results.

²See: <https://www.epa.gov/nutrientpollution/sources-and-solutions-fossil-fuels>

database. To avoid the numerous uncertainties associated with partitioning fuel consumption among trips targeting multiple species (Vázquez-Rowe et al., 2012), we constrained our analysis to records for single-species trips. We also excluded any records that were obviously duplicated, incomplete, split, or erroneous (e.g., average boat speed > 80 km/hr). The resulting dataframe ($n_{records}=4,795$) is included in the **Supplementary Material** section of this text, entitled “**Supporting Dataframe 1**”. The raw data for this analysis (Mascareñas-Osorio et al., 2017) are available upon consultation at dataMares.ucsd.edu.

Extracting Time Series Data From the CONAPESCA Database Based on Two “Criteria for Inclusion”

To generate stock assessment profiles (described in Section 2.4), we first needed to extract catch time series from the CONAPESCA database (Mascareñas-Osorio et al., 2018). The particular version of the CONAPESCA database that we used is a repository consisting of tens of thousands of records for small-scale and industrial fishing activities, targeting over 500 taxa, reported in all of Mexico’s Pacific states. Thus, to extract the relevant time series from this rather large database, we needed to identify the “Stocks of Interest” for which we would eventually require estimates of B/B_{MSY} (Section 2.4); we did so based on the definition of a “Stock,” and the two “Criteria for Inclusion,” we describe below.

We define a “Stock” (S) as any genus (G) living in fishing zone (Z), such that $S = G_Z$. Subsequently, we define a “Stock-Year” (S_Y) as a stock (S) in a specific year (Y), such that one $S_Y = G_{ZY}$. So, for example, we consider *Callinectes-Lower Pacific-2015* and *Callinectes-Lower Pacific-2016* as two separate “Stock-Years” borne from the same “Stock” of swimming crab (*Callinectes* sp.). We defined fishing zones (Z) *a priori*, based on expert knowledge of the area and a large geographic separation of recorded ports (Figure 2). The fishing zones relevant to our analyses are as follows: (1) the “Central Pacific” (CP), which includes ports circa

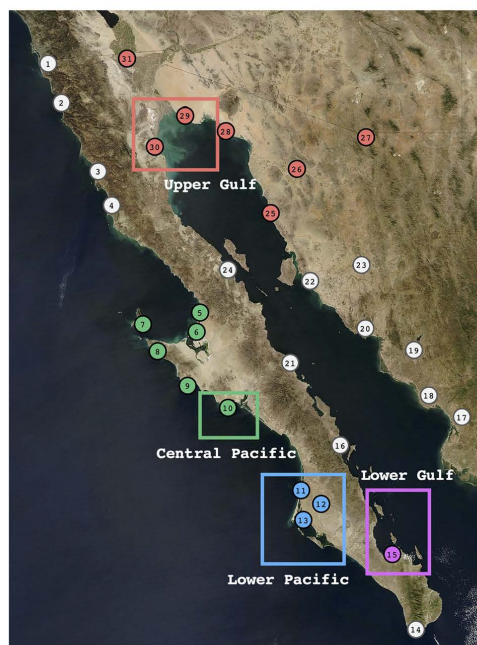


FIGURE 2 | Map of Baja California, where each circle represents a fishery office recorded in the CONAPESCA database, and each square demarcates the approximate spatial footprint of fishing trips for which there exist records of fuel consumption in the GCMP (Gulf of California Marine Program) database. For a complete roster of CONAPESCA office names, see **Table S1**. Respectively, the offices shown in green (#5 - #10), blue (#11 - #13), purple (#15), and red (#25 - #31), represent those with fishery reports that we used to generate stock assessment profiles for “Stocks of Interest” in the “Central Pacific”, “Lower Pacific”, “Lower Gulf”, and “Upper Gulf” (as described in Section 2.4). Conversely, we did not utilize CONAPESCA landings data reported by those offices shown in grey. (Underlying map of Baja California is courtesy of the MODIS Rapid Response Team and NASA, and is available for download at: [https://commons.wikimedia.org/wiki/File:Baja_peninsula_\(mexico\)_250m.jpg](https://commons.wikimedia.org/wiki/File:Baja_peninsula_(mexico)_250m.jpg)).

Punta Eugenia; (2) the “Lower Pacific” (LP), which includes major ports on the Pacific side of Baja California Sur, near Bahía Magdalena; (3) the “Lower Gulf” (LG), which we’ve defined as the ports in and around La Paz, south of Loreto; and finally, (4) the “Upper Gulf” (UG), which spans the region from the Colorado River Delta to the Midriff Islands in the GoC. Note that, on average, small-scale fishers in the region only travel about 63 kilometers in a given fishing trip (see “**Supporting Dataframe 1**”), and it is unlikely — though not impossible — that fishers in, for example, the LP would land and register their catch in the LG.

With these definitions in mind, we decided upon two “Criteria for Inclusion,” that is, two criteria used to determine whether or not a stock would be included in our final statistical analyses and therefore in need of assessment. First, we stipulated that a stock (S) can be found in the CONAPESCA database with ≥ 10 -years’ worth of landings data; and second, that that stock has at least one Stock-Year (S_Y) represented in the GCMP database with ≥ 10 paired observations of fuel consumption and catch. Ultimately, these “Criteria for Inclusion” produced a list of 19 “Stocks of Interest” for which we were able to extract landings time series from the

CONAPESCA database, and which are associated with the 39 “Stock-Years of Interest” listed in **Table S2**.

The reason for our first “Criteria of Inclusion,” in which we have stipulated that n years of CONAPESCA catch data must be ≥ 10 , has to do with the number of years required to generate a reliable stock assessment. According to Froese et al. (2017), it is sometimes possible to generate a stock assessment profile with as little as five-year’s worth of catch data, however, the fewer the number of years, the larger the uncertainty. Moreover, for species with low or very-low intrinsic population growth (e.g., ocean whitefish *Caulolatilus princeps*), about 10 years’ worth of landings data are required to generate an informed prior about the fishery’s catchability and, in turn, its Maximum Sustainable Yield (Froese et al., 2017). The second criteria we have defined, that n paired observations of fuel use & catch in the GCMP database must be ≥ 10 , has to do with the methods we used to test the relationship between B/B_{MSY} and fuel intensity among “Stock-Years of Interest” (described in Section 2.5); summarily, we wanted to include only those Stock-Years for which it would be possible to generate a reliable estimate of mean fuel intensity.

Methods for Stock Assessment: Synthesizing B/B_{MSY} Values for "Stock-Years of Interest"

B/B_{MSY} is often used as a measure for stock status and a proxy for "overfishing," where B is the current (available) stock biomass, and B_{MSY} is the estimated stock biomass at "Maximum Sustainable Yield" (MSY). MSY is the theoretical level of extraction equal to the rate of added population growth over an indefinite period of time — the highest level at which it is possible to extract fish from a population while still maintaining that stock's standing biomass. By fishing a stock at MSY, the biological stability, economic value, and contribution to fishers' livelihoods (derived from that stock) are more likely to be preserved in the long-term (Giron-Nava et al., 2021). Meanwhile, fishing a stock at levels *above* MSY is considered "overfishing," which, if allowed to persist, will eventually diminish or crash that population (e.g., New England Cod; Pershing et al., 2015).

Herein lies a key distinction between "overfishing" and "overfished". Overfishing, estimated as the current fishing mortality versus fishing mortality at MSY (F/F_{MSY}), is the actual *act* of fishing beyond MSY at any given point in time. In contrast, B/B_{MSY} tells us if a stock is currently overfished, which, if it is, is usually the direct result of habitual or chronic overfishing. We contend that, in this respect, B/B_{MSY} carries some amount of "memory" vis-à-vis fisher behavior in response to stock status over time. We have therefore elected to use B/B_{MSY} as our proxy for overfishing, where biomass (B) exists on a gradient from "pristine" ($B/B_{MSY} = 2$) to "overfished" ($B/B_{MSY} \leq 0.5$), such that when B is precisely equal to biomass at MSY, the ratio of B/B_{MSY} is equal to 1.

To generate B/B_{MSY} estimates for the 39 "Stock-Years of Interest" described above (in Section 2.3), we applied a data-poor method for fishery stock assessment developed by Froese et al. (2017) to the catch time series we extracted from the CONAPESCA database. Summarily, this method, which Froese et al. (2017) dub the "Simple CMSY," applies a Bayesian model to fisheries-dependent time series to generate most-likely values for B/B_{MSY} over time. It does so based on the landings data combined with informed priors about the stock's intrinsic population growth (r) and starting biomass (B_0). To better understand the theoretical and mathematical underpinnings of the Simple CMSY method, we recommend reviewing the original research by Froese et al. (2017) as well as a subsequent application of their methods to SSFs in Mexico executed by Giron-Nava et al. (2019). The resulting stock assessment profiles we generated using this method are included in *Supplementary Materials* - "Supporting Dataframe 2".

Examining the Relationship(s) Between B/B_{MSY} and Fuel Intensity

To test for a relationship between B/B_{MSY} and fuel intensity across the 39 "Stock-Years of Interest," we employed three complementary statistical analyses. We reasoned that if there exists a strong (linear) relationship between B/B_{MSY} and fuel intensity across SSFs, it would be apparent *via* a simple

correlation test and, likely, a simple linear model. Thus, we began with (i) a Pearson's correlation test between estimated values for B/B_{MSY} and *mean* values for fuel intensity ($Fuel Intensity_{mean}$). We then constructed (ii) a simple linear regression, where $Fuel Intensity_{mean}$ values are predicted by B/B_{MSY} . Each $Fuel Intensity_{mean}$ value is calculated as the arithmetic mean of all FIEs associated with that particular Stock-Year. Here, we compared B/B_{MSY} values to $Fuel Intensity_{mean}$ values in an effort to control against the influence of uneven sample sizes across Stock-Years (sample sizes for each are listed in Table S2).

The third and final analysis we conducted was (iii) a mixed effects model where any individual estimate for fuel intensity is predicted by its corresponding value for B/B_{MSY} as a fixed effect, along with three random effects: gear type, genus, and year. One might reasonably expect that the fuel-use per kilogram of landed seafood on any given trip is borne from a number of factors beyond the fishery's underlying stock biomass which could cause or covary with B/B_{MSY} . We know, for instance, that fishing patterns, fleet (over)capacity, management schemes, underlying ecosystem dynamics, weather patterns, and changes in climate are all important factors that can determine fishery outcomes (e.g., Worm et al., 2006; Pershing et al., 2015; Schuhbauer et al., 2017; Hilborn et al., 2020; Giron-Nava et al., 2021). For the most part, these dynamics lie beyond the scope of this paper, or the data are not available at this time. We can, however, begin control for *some* of this complexity — both observed and unobserved — by incorporating the additional information we have access to *via* the GCMP database about gear type, genus, and year (at the trip-level).

We controlled for gear type as a random effect based on findings from previous studies, which indicate that gear type plays an important role in the overall emissions borne from fishing activities (Parker and Tyedmers, 2015; Parker et al. 2018; Ferrer et al., 2021). Likewise, we included genus and year as random effects since target taxa and unobserved changes over time likely play important roles in predicting fuel expenditures. We chose to model these three factors as random effects because, while we anticipate that they do matter, we are not explicitly interested in the *fixed* effects of gear type, genus, nor temporal factors on the observed discrepancies among individual estimates for fuel intensity. Rather, our primary interest lies in understanding the generalized relationship between B/B_{MSY} (a fixed effect) and fuel intensity (a continuous output) *across* gear types, target genera, and years.

We generated the mixed effects model using the "lme4" package in R (Bates et al., 2015), and utilized the R "lmerTest" package to generate associated p values (Kuznetsova et al., 2017). Notably, the "lmerTest" package applies "Satterthwaite's method" (Fai and Cornelius, 1996) to estimate degrees of freedom, covariance, and significance values for unbalanced samples in mixed effects models. Thus, in contrast to our first and second analyses, it was not necessary to test B/B_{MSY} against $Fuel Intensity_{mean}$ values here, due to the very nature of the mixed effects model itself. Instead, we compared estimates for B/B_{MSY} against *individual* estimates for fuel intensity, generated over 4,491 single-species fishing trips. (Data associated with each

of these trips can be accessed in *Supplementary Materials - "Supporting Dataframe 3."*

RESULTS

Stock Assessment Profiles

We have included the results from our stock assessments in *"Supporting Dataframe 2"*. Specifically, we report estimated values and confidence intervals for B/B_{MSY} and F/F_{MSY} for all 19 "Stocks of Interest" over time (2001–2019), as generated by the Simple CMSY method.

Stocks that are both overfished and experiencing overfishing are those with a $B/B_{MSY} < 1$ and a $F/F_{MSY} > 1$ (e.g., Giron-Nava et al., 2019; see also UW - Sustainable Fishing 101: <https://sustainablefisheries-uw.org/seafood-101/overfished-overfishing-rebuilding-stocks/>). Conversely, stocks that are fished "sustainably" are those that are neither overfished ($B/B_{MSY} > 1$) nor experiencing overfishing ($F/F_{MSY} < 1$). There are many cases in between, where stocks can be overfished but recovering ($B/B_{MSY} < 1$, $F/F_{MSY} < 1$), or not yet overfished but experiencing overfishing ($B/B_{MSY} > 1$, $F/F_{MSY} > 1$). With these definitions in mind, we found evidence of at least some overfishing in every year for which we were able to generate assessment data. We also found evidence that many of these stocks are currently overfished.

In 2019, the most recent year for which we were able to generate assessment data, we found that out of the 19 stocks, nine (47%) were overfished and experiencing overfishing ($B/B_{MSY} < 1$, $F/F_{MSY} > 1$); zero (0%) were overfished and recovering ($B/B_{MSY} < 1$, $F/F_{MSY} < 1$); two (11%) were not overfished but were experiencing overfishing ($B/B_{MSY} > 1$, $F/F_{MSY} > 1$); and eight stocks (42%) were being fished sustainably ($B/B_{MSY} > 1$, $F/F_{MSY} < 1$). Of the eight stocks that were fished sustainably that year, six of them were located in the LP, one in the LG, and one in the UG.

Our results for B/B_{MSY} , on which we've based our assessment of overfishing, are largely consistent with anecdotal evidence, ecological research (e.g., Lluch-Cota et al., 2007), and local ecological knowledge about the region's fish populations (e.g., Sáenz-Arroyo et al., 2005). For example, as of 2016, Giron-Nava et al. (2019) found that in the GoC, 69% of the stocks analyzed ($n = 121$) were overfished and still being fished at unsustainable levels; 13% were overfished but recovering; 11% were not overfished but were being fished at unsustainable levels; and just 7% were fished "sustainably," neither overfished nor experiencing overfishing.

Relationship Between B/B_{MSY} and Fuel Intensity

A visual assessment of the data (Figures 3A, B) suggests that, the relationship between B/B_{MSY} and fuel intensity is inverse and exponential of some type, and we therefore report our results for B/B_{MSY} against $\log_{10}(\text{Fuel Intensity})$ or $\log_{10}(\text{Fuel Intensity}_{\text{mean}})$ values where appropriate. We've elected to report the results of our first two analyses in terms of B/B_{MSY} versus $\text{Fuel Intensity}_{\text{mean}}$ for reasons explained above (in Section 2.5), however, the interpretation of our results does not change if we compare values of B/B_{MSY} to demeaned values for fuel intensity (Figure S1).

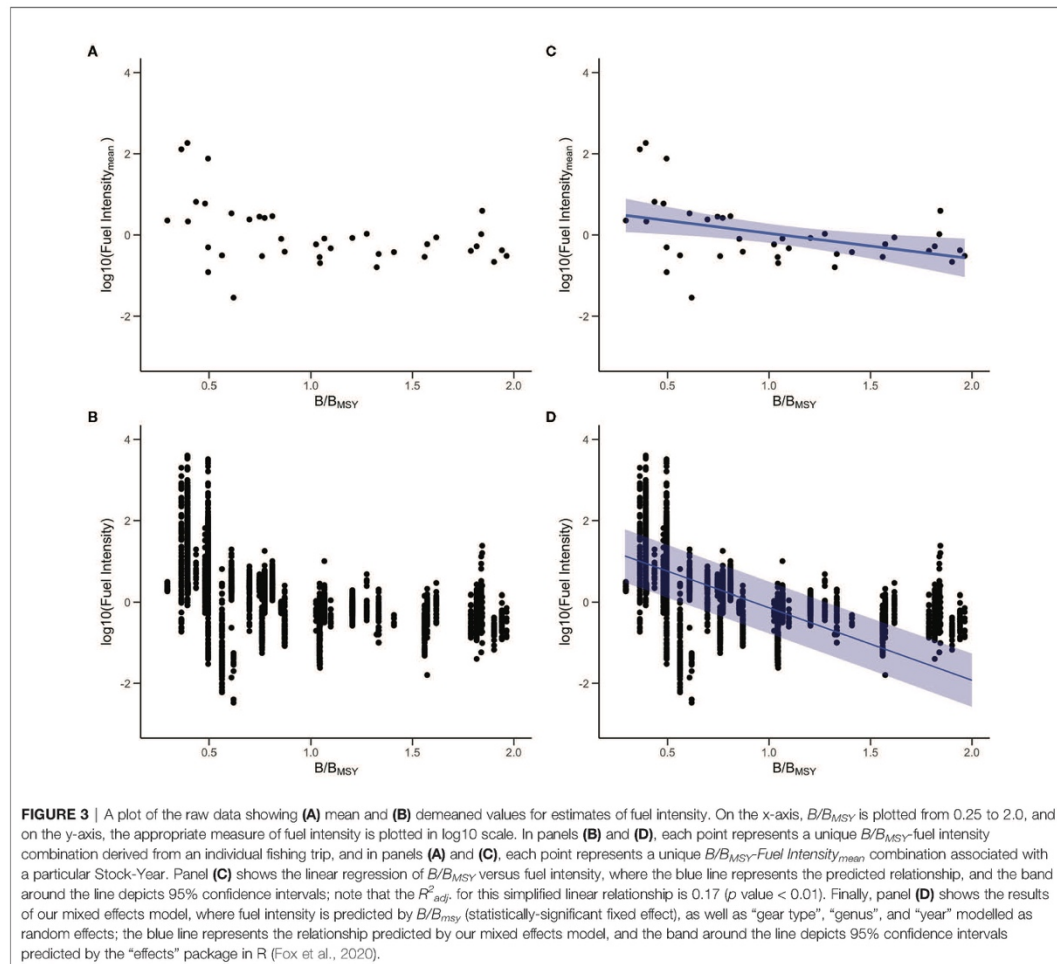
We found a statistically-significant negative correlation between B/B_{MSY} and $\log_{10}(\text{Fuel Intensity}_{\text{mean}})$ using a Pearson's test for correlation, where $r(df = 37) = -0.44$ (p value < 0.01). Subsequently, we conducted a simple linear regression, where $\log_{10}(\text{Fuel Intensity}_{\text{mean}})$ was predicted by B/B_{MSY} with an $R^2_{\text{adj}} = 0.17$ ($df = 37$, p value < 0.01) (Figure 3C). Finally, the existence of an inverse relationship between B/B_{MSY} and fuel intensity was further corroborated by the results of our mixed effects model (Figure 3D), where B/B_{MSY} is a statistically-significant predictor of $\log_{10}(\text{Fuel Intensity})$ (p value < 0.01), when accounting for gear type, genus, and year as random effects. According to this model parameterization, the association between B/B_{MSY} and $\log_{10}(\text{Fuel Intensity})$ has a negative correlation of $r = -0.36$. Notably, B/B_{MSY} remained a significant predictor of both fuel intensity and $\text{Fuel Intensity}_{\text{mean}}$ under a variety of controls and robustness checks (Figure S1).

DISCUSSION

Projections indicate that as the effects of climate change continue to manifest, many fisheries (though not all) will be negatively impacted (Allison et al., 2009; Free et al., 2019). As fisheries change or degrade, fishing effort may increase while, on net, CPUE declines. As net CPUE declines, fishers working in both small-scale and large-scale fishery settings may burn more fuel in an effort to land the same amount of fish, contributing more CO_2 to the atmosphere along with other fossil fuel-derived pollutants. Burning more fuel is likely to increase the costs of production, while depleting regional air and water quality², and potentially contributing to other social and environmental consequences (Aburto-Oropeza et al., 2018). To sustain their livelihoods, fishers may expend more effort fishing — be it in the form of more time spent on the water, gear deployed, etc. — increasing the expense/labor associated with fishing as well as the likelihood that stocks will become overfished. Thus, one can hypothesize a "positive" feedback loop (albeit small and asymmetrical) where, as overfishing increases, the fuel intensity of seafood grows and climate change continues, resulting in increasingly negative fishery outcomes (Sumaila and Tai, 2020).

Our results indicate that at least one aspect of this theoretical feedback loop very likely exists, in that the fuel intensity per kilogram of seafood appears inversely related to underlying stock biomass among several SSFs in Northwest Mexico. One cannot necessarily infer causation from our results, however, the relationship between B/B_{MSY} and fuel intensity proves suggestive and predictive under a variety of controls. Given the inverse and log-linear nature of this relationship, fuel intensity increases sharply for those seafood products generated by fisheries with a $B/B_{MSY} < 1$. This lends credence to the theories we described earlier (The World Bank, 2017; Sumaila and Tai, 2020), which posit that the act of habitual overfishing contributes to the carbon footprint associated with fishing.

Our results give us some idea of the carbon emissions that could be avoided with even slight improvements to stock biomass. Given that the majority of carbon emissions



associated with wild-caught seafood are generated by burning fossil fuels while fishing (Vázquez-Rowe et al., 2012; Parker and Tyedmers, 2015), we can devise a short back-of-the-envelope calculation as follows: the average $Fuel Intensity_{mean}$ of seafood landed among Stock-Years with a $B/B_{MSY} \geq 1$ is 0.66 L fuel/kg catch, and for those with a $B/B_{MSY} < 1$ is 22.31 L fuel/kg catch. Thus, if we assume a fuel-to-emissions conversion factor of 2.3 kg CO₂-equivalent per liter of gasoline (Natural Resources Canada, 2014)³, the carbon footprint generated by Stock-Years examined herein with a $B/B_{MSY} < 1$ contributes (on average) an

additional 50 kilograms of CO₂-equivalent per kilogram of wet-weight seafood, compared to those with a $B/B_{MSY} \geq 1$.

Evidence of this nature might motivate climate-oriented policies designed to restore fisheries and alleviate fishing pressure, or perhaps generate novel possibilities for those countries that seek to better incorporate the ocean and blue carbon into their Nationally Determined Contributions under the Paris Agreement ("NDCs") (see Gallo et al., 2017). Indeed, our results expand our understanding of, and appreciation for, the ways in which the protection of biodiversity and a stable climate are inextricably linked: abating climate change will help to conserve healthy fish populations, and, vice versa, the conservation of healthy fish populations may help to mitigate climate change (IPBES, 2019; IPCC, 2022). The conservation of marine ecosystem services (IPBES, 2019) and fish populations as

³This conversion factor only accounts for the quantity of greenhouse gases emitted directly by the burning of gasoline. It does not, for example, account for the upstream emissions associated with the production of fossil fuels, nor the downstream emissions associated with seafood production and transport.

"blue carbon" sinks (e.g., Mariani et al., 2020) are two popular examples of how ending overfishing might be considered a form of climate action. Now, we have evidence to suggest that, in addition to conserving ecosystem services and blue carbon sinks, ending overfishing is likely to make it more carbon-efficient to supply seafood security going forward.

To be clear, SSFs, in all their importance, diversity, and abundance, likely account for a relatively small portion of greenhouse gas emissions borne from total seafood production. While the carbon footprints of SSFs are heterogeneous and can be high (see Purcell et al., 2018; Ferrer et al., 2021), Greer et al. (2019) estimate that SSFs land about a quarter of the world's wild catch for a little less than a quarter of all fishery emissions. At the same time, we know that the carbon emissions borne from the fishing sector in general are non-negligible (accounting for ~1% of all global CO₂ emissions; Sumaila and Tai, 2020), and it's possible that the relationship we've identified here is generalizable to the fishing sector more broadly. While this remains a largely open question, we posit that, independent of the answer, investing time and resources towards ending overfishing presents a prime opportunity for stakeholders with varied interests (e.g., fisheries management, fisheries livelihood, blue carbon) to collaborate in protecting and rebuilding healthy fish populations.

To this end, we argue that it is important to continue designing and investing in culturally-relevant and participatory management schemes that support fishers in fishing sustainably (e.g., Bloor et al., 2021; Gómez and Maynou, 2021; see also FAO SOFIA, 2018). For fisheries in Northwest Mexico, successful community-based efforts to ensure sustainable fishing among SSFs are already underway, and have been for some time. The Community Catch Monitoring Program in the Upper GoC (see Juárez, 2021), and the SCPPPA cooperative that governs fishing in the town of Punta Abreojos (Cota-Nieto et al., 2018), are just a two notable examples. For the former, Juárez (2021) describes how local rights-based management efforts have helped to stabilize the Gulf Corvina fishery over the last decade — and for the latter, Cota-Nieto et al. (2018) describe how a number of strategic, participatory management actions taken by fishers and other community members have ensured the town's fishing success over multiple generations.

Strategies for ending overfishing more broadly include: eliminating harmful fishing subsidies while supporting those that are beneficial, particularly among SSFs (Schuhbauer et al., 2017; Sumaila et al., 2021); protecting SSFs from exclusionary or exploitative fishing and management practices, including those conducted by industrial fisheries and other large-scale industry interests (see Schuhbauer et al., 2017; Cohen et al., 2019); improving our fishery assessments among historically "data-poor" stocks (Costello et al., 2012; Hilborn et al., 2020) and prioritizing SSF data needs (e.g., Smith and Basurto, 2019); working to alleviate illegal, unreported, and unregulated fishing (IUU) (World Bank, 2017); closing tax loopholes and shuttering tax havens that undermine biodiversity objectives and have, in some cases, been shown to contribute to IUU (Dempsey et al., 2021); and finally, investing in the restoration of ecosystems upon with healthy fisheries depend (Sumaila et al., 2012; Duarte et al., 2020).

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**. Further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

EF conceived of the initial idea for this article and implemented its execution. AG-N helped establish the methods underlying this article, contributed to analysis, and edited the manuscript. OA-O helped contribute to the vision, methods, and execution of this research, including production of the results and manuscript. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2022.768784/full#supplementary-material>

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CHAPTER 6

CONCLUSIONS

Understanding the effects of climate change on both ecosystems and organisms is essential for identifying sustainable seafood options and fishery management strategies. Acting in reverse, identifying sustainable seafood options will help us to maintain healthy marine ecosystems and organismal populations under mounting anthropogenic stress. Here, I conclude with the major insights I've generated from each chapter, as well as the insights I've gained by understanding these projects in tandem.

In Chapter two of my dissertation, I synthesize the impacts of deoxygenation across the aquatic realm, and within the context of the Planetary Boundary Framework. I identify five control variables associated with important thresholds of dissolved oxygen (DO), including: (1) hypoxia cutoffs, (2) percent DO saturation, (3) presence, absence, and behavior of sentinel species, (4) the Metabolic Index, and (5) the “velocity” of the Metabolic Index. I go on to describe known interactions between DO and six of the nine other planetary boundaries: climate change, loss of biodiversity, biogeochemical flows, ocean acidification, land-use change, and aerosol loading. In this chapter, which is primarily intended as a science-policy piece, I synthesize new and emerging areas of research that might help us understand, mitigate, and adapt to the effects of deoxygenation in a changing climate.

Understanding the importance of climate change in the realm of fisheries and fisheries management, I explore effects of press versus pulse climate stress on *Mano de León* scallops (*Nodipecten subnodosus*) in Chapter three. I report on changes in scallops' survivorship and physiology from across six phenomenologically-relevant treatments, designed to mimic an El Niño

and / or a marine heatwave (MHW) events. From this study, I found that scallop mortality increases slightly under both press and pulse stress, with statistically-significant effects of food availability, background temperature, and MHWs on the likelihood of their survival. I also find evidence to suggest that scallops may be down-regulating their metabolism and shunting energy towards reproduction (gamete growth) under MHW conditions. This research bears tremendous promise in terms of helping to identify the vulnerabilities of Mano de León scallops to fishing pressure and aquaculture production in a warmer and more climatologically volatile world. Results from this study may also be helpful for those interested in cultivating similar species scallop when and where El Niño and MHWs are likely to occur.

In Chapters four and five, I pivot away from the study of biogeochemical stressors on fisheries and fishery species, towards an investigation of fishing in relation to global warming. Specifically, I chose to investigate the importance of small-scale fisheries (SSFs) and the seafoods they provide, in the context of climate change and greenhouse gas emissions. I demonstrate how many of the SSFs in Mexico provide low-carbon seafood products, and examine what it means for a seafood or fishery to be truly “climate-friendly” in my fourth chapter. In my fifth chapter, I show that seafood generated by stocks that are fished sustainably (at or below MSY) has a significantly lower carbon footprint than seafood derived from stocks that are overfished. This relationship suggests that an end to overfishing would likely lower the carbon footprint of seafood, which reflects an exciting opportunity for us to overlap our climate and fisheries management goals. This research is further supported by an ancillary study that I conducted with colleagues, presented in Appendix A, which demonstrates an association between rebuilt stock biomass and increased fuel efficiency (for the hake fishery in Northwest Europe).

Results from my dissertation research have led me to conclude that fisheries and fishery species are probably more resilient to changes in climate than we think, but their resistance and resilience to future change will depend heavily on conscientious fisheries management, and in particular our efforts to ameliorate overfishing. Attempting to fish, protect, or rebuild fisheries and fishery stocks with an incomplete understanding of future climate change, though necessary, is a lot like trying to find something in the dark: we are basically guaranteed to overlook some important details. Thus, moving forward, I hope to use this body of work help “illuminate” the best pathways forward in terms of sustainable fisheries harvest and management in a warmer world. I also hope to expand the network of tools we use to understand climate-fishery interactions by publishing each chapter of this research through peer-review, and by connecting what I’ve learned throughout my PhD experience to my future research and scientific endeavors.

APPENDIX A

Appendix A, in full, is a reprint of the material printed in *Frontiers in Marine Science*, and appears as: Martin, A. H., Ferrer, E. M., Hunt, C. A., Bleeker, K., and Villasante, S. *Frontiers in Marine Science*. (2022). The dissertation author was the secondary investigator and co-author of this paper.



Exploring Changes in Fishery Emissions and Organic Carbon Impacts Associated With a Recovering Stock

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International objectives for sustainable development and biodiversity conservation require restoring fish populations to healthy levels and reducing fishing impacts on marine ecosystems. At the same time, governments, retailers, and consumers are increasingly motivated to reduce the carbon footprint of food. These concerns are reflected in measures of the EU Common Fisheries Policy (CFP) and the CFP Reform Regulation, which highlighted a need to move from traditional single-stock management toward an ecosystem approach to fisheries management (EAF). Using publicly available landings and effort data combined with estimates of adult population biomass, we develop methods to explore the potential for lowering emissions intensity and impacts on organic carbon stocks through ending overfishing and rebuilding stocks. We use the recent recovery of European hake (*Merluccius merluccius*) stocks in the Northeast Atlantic as a case study. With a focus on the hake fisheries of France, Spain, and the United Kingdom, we compare 2008 and 2016 fishing years. We make an initial estimate of the influence of changing stock status on greenhouse gas emissions during the fishery phase from fuel use and investigate the potential disturbance of organic carbon in the ecosystem, specifically via identification of bottom trawling overlap with organic-rich muddy sediments, and directly on storage in hake biomass. Our findings indicate that recovery of the hake stock was associated with reductions in overall emissions intensity from fuel and proportional impact on hake populations, however, total emissions from both fuel and landings increased, as did likely disturbance of sedimentary organic carbon in surface sediments due to benthic trawling. Ultimately, the aims of this analysis are to further explore the climate impacts of fisheries and overfishing, and to inform development of EAF in the EU.

Keywords: fisheries, carbon emissions, hake (*Merluccius merluccius*), stock recovery, sedimentary organic carbon, sustainable fisheries, ecosystem based management (EBM), ecosystem based approach for fisheries management

INTRODUCTION

Unsustainable resource extraction, biodiversity loss, and climate change threaten the health and longevity of marine ecosystems and fish populations worldwide (IPBES, 2019). Reducing greenhouse gas emissions (GHGs) is essential for reducing the ecological and social impacts of climate change and remains an international priority (United Nations General Assembly resolution [UNFCCC], 2015). Simultaneously, restoring fish populations and marine ecosystems to achieve healthy oceans are cited as international objectives for sustainable development (United Nations General Assembly resolution [UNFCCC], 2015) and conservation of biodiversity (Convention on Biological Diversity, 2021). In the European Union (EU), these objectives are reflected in measures outlined by the Common Fisheries Policy (CFP) (European Union [EU], 2013). The latter reform of the CFP proposed a new framework to manage European fisheries, and amongst several new initiatives, it highlighted a need to move from traditional single-stock management towards an ecosystem approach to fisheries management (EAF) (Prellezo and Curtin, 2015). The CFP Reform Regulation defines the EAF as "... an integrated approach to managing fisheries within ecologically meaningful boundaries which seeks to manage the use of natural resources, taking account of fishing and other human activities, while preserving both the biological wealth and the biological processes necessary to safeguard the composition, structure and functioning of the habitats of the ecosystem affected, by taking into account the knowledge and uncertainties regarding biotic, abiotic and human components of ecosystems" (European Union [EU], 2013).

Ecosystem approach to fisheries management prioritises the wellbeing of ecosystems over economic and social objectives since ecosystem wellbeing is considered a prerequisite for the latter two objectives (Murawski et al., 2008; Baudron et al., 2019). While the current CFP advocates for the implementation of some form of EAF, it remains largely unclear how to include conservation objectives within fisheries management measures in practice. The CFP aims to fish at levels consistent with achieving Maximum Sustainable Yield (MSY) for all exploited stocks (European Union [EU], 2013), an approach which does not necessarily account for impacts on the ecosystem (Ulrich et al., 2017). In Northern European waters, these fishing levels are proposed by the EU's International Council for the Exploration of the Sea (ICES) which delivers scientific advice for the management of northern European fish stocks. This advice provides biological reference points for commercial stocks, including the level of fishing mortality (F) needed to achieve MSY (F_{MSY}). According to the latest Scientific, Technical and Economic Committee for Fisheries (STECF) CFP monitoring report, stock status of the NE Atlantic (both EU and non-EU waters) has significantly improved since 2003, although many stocks remain overexploited (STECF, 2020a). Among the stocks which are fully assessed, the proportion of those that are overexploited decreased from around 75% to close to 40% over the last ten years. This trend is promising, however, in 2019, the proportion of overexploited stocks (i.e., $F > F_{MSY}$) for which there are data increased slightly (STECF, 2020a).

Regarding the climate impacts of EU fisheries, many national governments, retailers, and consumers are increasingly motivated to reduce greenhouse gas emissions (GHGs) associated with food production, including fisheries, as a form of climate change mitigation (Iribarren et al., 2010). When considering direct emissions, such as fuel use, trawl fisheries are known to produce, on average, more GHGs per kilogram of catch than virtually any other fishing gear (Tilman and Clark, 2014). The carbon footprint of seafood landed using trawl nets may be similar to, and in some cases exceeds, the footprint of terrestrial staples such as poultry or pork (Tilman and Clark, 2014; Hilborn et al., 2018). Trawl fisheries are also known to have negative effects on the marine environment via significant alterations to abiotic and biogenic structure (Chuenpagdee et al., 2003). Evidence from vessel Automatic Information Systems (AIS) data suggests that the continental shelf surrounding the EU is among the world's most trawled, although the Celtic and Greater North Seas are slightly less impacted than the waters west of Iberia and within the Mediterranean (Amoroso et al., 2018a).

In addition to direct emissions, fishing activity can affect organic carbon (OC) stocks in the marine environment, with implications for both climate and ecosystem function. One such stock is held in marine sediments, which store substantial amounts of carbon (Atwood et al., 2020; Legge et al., 2020), the active burial of which provides a climate regulation service over thousand-year timescales (Bernier, 2003). Where trawling gear interacts with marine sediments, it can introduce oxygen into sub-surface sediment layers, increasing the potential loss of buried carbon through aerobic remineralisation (Aller, 1994; Hulthe et al., 1998). Sediment type is an important factor in the storage of sedimentary OC (Diesing et al., 2017; Smeaton et al., 2021), where OC is largely controlled by the proportion of clay or mud (Hedges and Keil, 1995). Trawling has a larger physical impact on muddy-sediment environments in terms of resuspension, causing significantly higher volumes of OC to be resuspended compared to sandy-bottom environments (O'Neill and Summerbell, 2011), with implications for both carbon flux and the resilience of local biodiversity (Pusceddu et al., 2014; Paradis et al., 2017). There is currently a lack of comprehensive evidence to fully demonstrate the effects of trawling on sedimentary OC stocks, but one likely outcome of regular trawling is prevention of sediment settling processes and, in turn, localised carbon sequestration (Epstein et al., 2022 PREPRINT; Oberle et al., 2016). Furthermore, using the definition outlined in Scheffold and Hense (2020), fish populations are living pools containing stocks of OC. In addition to affecting OC stocks in sediments, by removing fish biomass, fishing activity may prevent OC from sinking in the form of fish carcasses and facilitate conversion of OC in biomass to atmospheric CO_2 (Mariani et al., 2020).

In this study, we make a first attempt at combining an established approach for estimating the fuel use of a specific fishery, with novel insights into the additional perturbation of OC stocks caused by fishing. We use landings and effort data associated with the Northern and Southern stocks of European hake (*Merluccius merluccius*) from 2008 and 2016, which enables a comparison of fishing emissions and OC impacts of the fishery

when the Northern stock was depleted (2008) and subsequently rebuilt (2016) (ICES, 2021a). The Northern stock of European hake (hereafter “hake”) encompasses those populations living within the Greater North Sea, Celtic Seas, and the northern Bay of Biscay, while the Southern stock consists of those populations living in the southern Bay of Biscay and Iberian Coast (Figure 1). The combined range for Northern and Southern hake stocks is provided by ICES in terms of the following subareas and divisions: Subarea 4, 6, 7, Divisions 3.a, 8.a-d, 9.a (ICES, 2021a,b).

Hake are predatory, demersal fish, usually found at depths of 75–400 m, above muddy or sandy sediments (Lloris et al., 2005; Froese and Pauly, 2021). The Northern and Southern hake stocks may not be two distinct populations biologically but nevertheless are assessed separately for the purpose of fisheries management (Milano et al., 2014). The Northern stock is managed using the MSY approach and as such, the spawning stock biomass (SSB) is estimated during assessment of stock status by ICES. Conversely, the Southern stock is managed under the precautionary principle and SSB is not estimated. The Northern stock was overfished from at least the 1990s to the late 2000s (Murua, 2010; Villasante et al., 2011); on multiple occasions during this time, fishing mortality (F) substantially exceeded the agreed landings target (ICES, 2021a,b). However, in 2004, a recovery plan for hake was introduced which required a 70% reduction in F. Subsequently, the SSB of the Northern stock increased substantially, likely due to the reduced fishing pressure (Baudron and Fernandes, 2014). Between 2008 and 2016, SSB of the Northern stock increased by approximately six-fold, catches more than doubled, and F declined substantially (ICES, 2021a). Overall, catches of hake reported by ICES for 2016 were landed predominantly by long lines (39%), trawls (33%), and gillnets (24%) (ICES, 2017). Each gear type comes with trade-offs from varying levels of ease of use, to efficacy, to selectivity. Trawls, which trap fish as they scrape across the seafloor, are known as “active” gear types as they are continuously dragged by a moving vessel, while long lines and gillnets are considered “passive” gear types as they drift or hang idly in the current. It is worth noting that, despite modifications made to each of these gear types to increase selectivity, all three of these gear types have some issues.

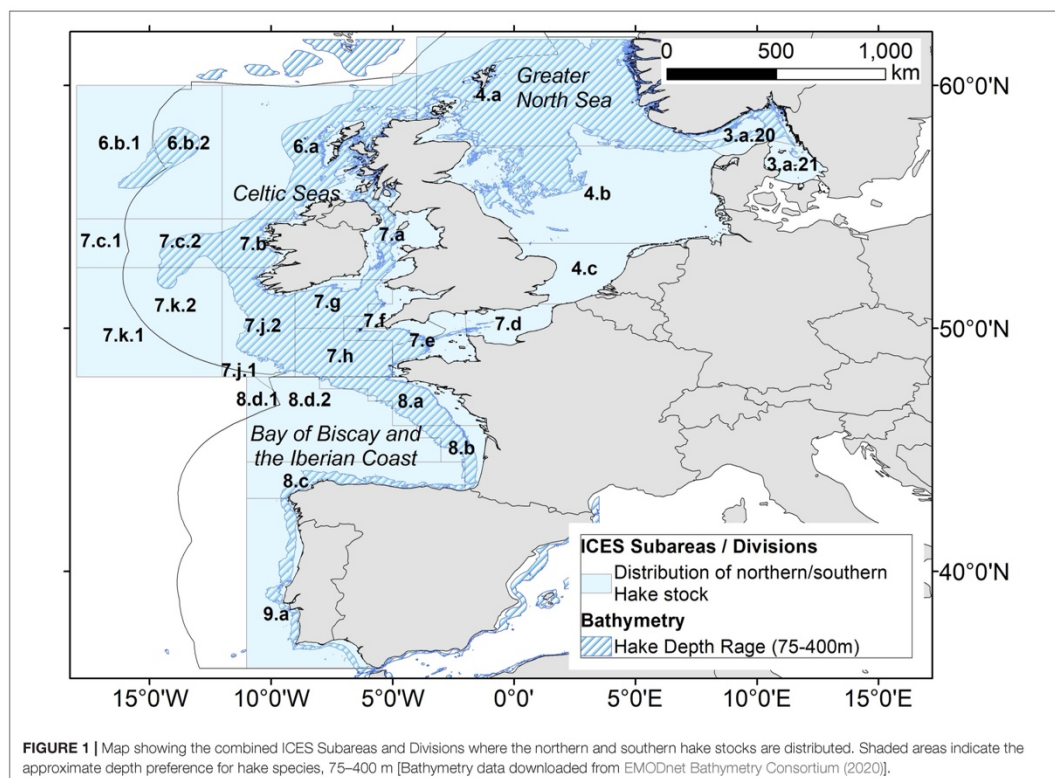
In this paper we focus on the relationship between the carbon impact of the fishery, namely GHGs generated from vessel fuel use, and consider the potential perturbations to the OC stocks in the sediment and hake population, against the rebuilding of the Northern hake stock, from 2008 to 2016. We do not consider emissions from non-fuel inputs associated with fishing, for which estimates vary (for example Parker et al. (2018) assume 25% of total emissions arise from non-fuel sources). The purpose of including a preliminary ecological perturbation analysis in this paper is to introduce the impacts of fishing on OC stocks, in addition to the direct carbon footprint of boats on the water, and to advance information available for the development of ecosystem-based approaches for EU fisheries. Given the nexus between climate change, sustainable resource use, and biodiversity conservation (Sumaila and Tai, 2020), we consider whether the GHG footprint of the hake fishery overall and per tonne of catch were reduced by ending overfishing.

MATERIALS AND METHODS

We used publicly available data collected by STECF through the Fisheries Dependent Information (FDI) data call (STECF, 2017) in combination with data we requested from STECF (STECF, 2020b), which included detail on hake landings, fuel use and intensity (litres per tonne of total landings) at the level of individual fishing fleet segments (i.e., vessel size, gear type). The requested data, hereafter referred to as dataset 1, were extracted from the STECF database (STECF, 2020b) for every second year from 2008 to 2018 inclusive, according to the following selection criteria: (i) fleets operating in the North Atlantic Ocean (FAO Area 27 - NAO) and (ii) EU fishing fleet segments in which, in 2018, hake accounted for at least 1% of total landings. France, Spain, and the United Kingdom landed 91% of total hake landings in 2008 (27,416 tonnes), and 78% in 2016 (23,764 tonnes) (STECF, 2020b). Thus, fishing mortality of the hake population within the NEA was dominated by the activities of these three countries, indicating that hake was an important target species for these nations. As such, we used the landings, effort, and fuel data for these three nations to investigate the impacts of the hake fishery in terms of fuel use, sedimentary disturbance, and extraction of OC in biomass. To compare the carbon impacts of the European hake fishery eight years apart, with two vastly different estimates of SSB, we emphasised the relative fuel use and impacts on OC per kg of hake landings, as opposed to focusing on the total emissions and impacts of the fishery. Landings data from STECF (STECF, 2020b) were used in kilograms, and, unless otherwise stated, this is the basic unit of measure we refer to hereafter.

To analyse the GHG footprint associated with fishing activity we focused on the carbon generated by vessels' fuel use, which includes travel to and from fishing grounds and gear operation. These data were entirely available in dataset 1 (STECF, 2020b). We estimated fuel intensity (FI) (the amount of fuel burned while fishing hake per kilogram of hake landed), and emissions intensity (EI) (the estimated GHGs released while fishing hake per kilogram of hake landed) which is directly related to FI. Estimates for mean FI values were calculated for year and gear type. There were eight types of gear listed in dataset 1 (STECF, 2020b): (1) polyvalent passive gears (PGP), i.e. polyvalent nets, (2) drift/fixed-net gears (DFN), (3) gears with hooks (HOK), (4) demersal trawlers and seiners (DTS), (5) pots and traps (FPO), (6) vessels using active and passive gears (PMP), (7) vessels using “other” active gears (MGO), and (8) pelagic trawlers (TM). For this analysis, we grouped polyvalent passive gears (PGP) and drift/fixed-net gears (DFN) together as “DNGN”. In addition to reporting the cumulative FI value for hake fished by all gear types in 2008 and 2016, we also report on FI values for the “DNGN”, “HOK”, and “DTS” gear types only, as these were relatively well sampled in both 2008 and 2016 ($n > 2$ for both years) and were responsible for the overwhelming majority of hake landed (>95% of total landings) in both years.

To estimate the disturbance of OC in muddy sediments caused by bottom-contacting otter-trawlers, we used swept area (SA), a measure of the seabed surface area that has been in contact with, or altered by, bottom-contacting fishing gear, such as trawls,



and report SA per kg of hake landed. SA is determined by the width of the gear and vessel speed (Church et al., 2016). We calculated and mapped the total SA by country using publicly available FDI data (STECF, 2017), hereafter referred to as dataset 2. Although this calculation does not quantify the amount of OC lost or consider the specific mechanisms by which OC may be lost, the areal overlap provides spatial information about where the biggest impacts of the trawl fishery on surficial sedimentary OC stocks are likely to be.

We calculated SA per kg of hake landed for France, Spain and the UK using the landings data in dataset 1 (STECF, 2020b), which included hake landings, hake landings as a percentage of total landings, and effort by fishing segment (STECF, 2020b), but did not contain spatial data. Instead, dataset 2 (STECF, 2017), which included fishing effort available per ICES rectangle, was downloaded for annexes IIA, IIB, BOB, and CEL1 and years 2008 and 2016 (see Table 1). The data were filtered for otter trawling gears only (OT) and for the following countries: France, Spain, and the United Kingdom (data were available for England, Northern Ireland, and Scotland). Dataset 2, which provided effort, landings, and spatial data (STECF, 2017), did not contain hake landings for otter trawlers in France or Spain in 2008, or hake landings as a percentage of total landings. As such, all hake

landings data for both 2008 and 2016 for France, Spain, and the United Kingdom were used from dataset 1 (STECF, 2020b). Dataset 1 were filtered by gear type “DTS”, which includes demersal trawlers and demersal seiners, on the assumption that these were mostly otter trawls, since, in European waters, effort by otter trawlers is an order of magnitude greater than that of demersal seiners (Eigaard et al., 2016; Supplementary Table 1). To see clearer differences in SA between depleted and recovered stocks it would be best to compare fleets that landed a high percentage of hake, as detailed in dataset 1, however, we were unable to disaggregate the effort of those fleets in dataset 2, which contained the spatial data. Therefore, for the purpose of making a comparison between two years with different stock statuses, the use of OT spatial data from dataset 2 with the total landings for France, Spain and the United Kingdom from the DTS segment in dataset 1 was the best possible approach given the limitations of the data.

Finally, to estimate the fishery’s impacts on the OC stock of the hake population, we first calculated the carbon removed by each country and by the different fleet segments using the landings reporting in dataset 1 for 2008 and 2016. We again grouped polyvalent passive gears (PGP) and drift/fixed-net gears (DFN) together as “DNGN,” and report OC removal values

TABLE 1 | International Council for the Exploration of the Sea (ICES) Annexes and the fishing areas they encompass.

Annex	ICES area
IIA	IV; VII d
IIB	VIII c and IX a
BOB	VIII a; VII b
CEL1	VII b, VI c, VI e, VII f, VII g, VII h, VII j and VII k

for the “DNGN,” “HOK,” and “DTS” fishing segments for 2008 and 2016. We also estimated the OC stock in the adult hake population for 2008 and 2016 and the proportion of OC in hake stock removed by total landings by France, Spain, and the United Kingdom cumulatively using dataset 1 and SSB estimates for the northern stock only (ICES, 2021a). This analysis was limited to using SSB estimates for the Northern stock as a proxy for the adult hake population of both stocks as SSB estimates were not available for the Southern stock, and the landings data in dataset 1 could not be disaggregated spatially to ascertain whether landings were from the Northern or Southern stocks. We reasoned that this approach was appropriate for our purpose of comparison between the two years given that total landings estimated by ICES for the Northern stock were much higher at 47,822 tonnes in 2008, and 107,530 tonnes in 2016 (ICES, 2021a), than for the Southern stock, at 16,773 tonnes for 2008 and 12,443 tonnes for 2016 (ICES, 2021b). We note that our results are therefore underestimates of the OC stock in the adult hake population of the NEA for 2008 and 2016, and overestimates of the OC removed by landings as a proportion of the adult hake population in those two years.

Hake are caught as part of a mixed-species fishery with several other target species, which makes it challenging to partition and confidently assign impacts to hake versus other species that end up in the same net. Nonetheless, we provide estimates for FI, emissions intensity (EI), and SA for hake landed by all trawlers, noting that the figures reported herein are useful for comparing the fishery impacts between a depleted and recovered stock, and do not represent precise point estimates for hake's total carbon footprint. Estimates and statistical analyses were calculated in R version 4.0.3 (R Core Team, 2020), ArcGIS version 10.1, and Microsoft Excel.

Fuel and Emission Intensity Estimates Over Time

Extrapolating Fuel Use and Calculating Fuel Intensity (FI)

To estimate the amount of fuel consumed in the pursuit of hake, we assumed that the fuel used to land hake was directly proportional to the ratio of hake landings to total landings for that fishing segment. That is, for each fishing segment reported in dataset 1 (STECF, 2020b), we assumed:

$$\frac{F_{hake}}{F_{total L}} \propto \frac{L_{hake}}{L_{total}} \quad (1)$$

Where F is fuel and L is landings. Thus, we assumed that the quotient of total fuel consumption over total catch (i.e., the FI for

total catch) was a reasonable proxy for the FI of hake. On this basis, we estimated FI using the following equation:

$$FI_{hake} = \frac{F_{hake}}{L_{hake}} \propto \frac{F_{total landings}}{L_{total}} \quad (2)$$

Where F_{hake} is estimated as:

$$F_{hake} = L_{hake} * \frac{F_{total L}}{L_{total}} \quad (3)$$

Mean FI values for the three gear types were calculated by first summing the estimated values for $F_{hake,G}$ (in litres) and then the reported values for $L_{hake,G}$ (in kg), and subsequently dividing these as follows:

$$Mean FI_{hakeGY} = \frac{\sum \text{estimated } F_{hakeGY}}{\sum \text{reported } L_{hakeGY}} \quad (4)$$

Where G is gear type and Y is year.

Converting FIs to Emission Intensity Estimates

To convert FI to emission intensity (EI), we assumed that most of the fishing vessels in the EU operate using marine diesel (Borrello et al., 2013), which has a published density of 890 kg/m³ (ExxonMobil, 2021), equivalent to 890 g/L. The fuel-to-emissions conversion factor for marine diesel (MD), as published by the International Maritime Organisation (IMO, 2015), is 3.206 g of CO₂/g of MD. After converting between units, we arrived at the conversion factor of 2.853 kg CO₂/L of fuel. Note that this number does not account for the carbon-dioxide equivalent of: (i) other GHGs released during combustion, e.g., methane and nitrous oxide; (ii) upstream emissions associated with fuel production, e.g., drilling and refining; nor (iii) downstream emissions borne from processing, e.g., freezing, packaging, and distribution. In this respect, our estimates for GHGs released by fuel consumption are likely quite conservative.

Emission intensity estimates (reported as kg CO₂ per kg hake) were derived by multiplying FI values by a factor of 2.853 kg of CO₂/L of fuel, using the following equation:

$$EI_{hake} = FI_{hake} * 2.853 \left(\frac{kg \text{ CO}_2}{L} \right) \quad (5)$$

Sediment Disturbance

Calculating Swept Area

Swept area was calculated using standardised values for door width (km) and trawl speed (knots) for the Otter trawl class BENTHIS métier code: “OT_MIX_DM_F_PEL,” which is used to target hake (Eigaard et al., 2016). Following recommendations in the OSPAR CEMP guidelines (OSPAR Commission, 2017) (Agreement 2017-09) and Gerritsen et al. (2013), we used the equation:

$$Swept Area = Effort (hours) \times 0.07621 \text{ km} \times 3.4 \text{ knots} \times 1.852 \quad (6)$$

Where Effort (fishing hours) from dataset 2 (STECF, 2017) was provided with spatial data (standardised ICES rectangles), 0.07621 km is the reported average door width and 3.4 knots

is average trawl speed (ICES, 2016; OSPAR Commission, 2017); and 1.852 is the conversion factor for knots to km/hr. The final SA estimates between the countries and two fishing years are compared on a relative basis. Only the average door width and vessel speed were reported by ICES (2016) and OSPAR Commission (2017), yet the width of the trawl doors is a function of the vessel size and length of the sweeps, which can vary between 25 and 250 m, and the towing speed can vary from 2 to 4 knots (Eigaard et al., 2016). Thus, there is a degree of uncertainty within the estimated SA results.

Resulting SA estimates were spatially mapped for individual countries and as combined totals for 2008 and 2016, using a Natural Breaks Classification scheme (Holt, 2008). Swept Area Ratios (SAR), i.e., the proportion of each grid cell area that is trawled, were not deemed a suitable metric for this study due to the large area of the ICES rectangles (at $0.5^\circ \times 1^\circ$, these are approximately 4,000 km²) in combination with the low spatial resolution of dataset 2 (STECF, 2017), as it was not possible to determine where within the ICES square the reported activity occurred (Amoroso et al., 2018b). As outlined above, SA per kg of hake was calculated using total annual estimated SA (km²) and hake landings (kg) data for each country as reported in dataset 1 (STECF, 2020b).

Combining With Sediment Type

Shapefiles for seabed substrate classified to the simplified Folk 5 classification were downloaded from EMODnet Geology (EMODnet Geology, 2016; **Supplementary Figure 1**). The total SA polygons for 2008 and 2016 were overlaid with the classified sediment layers and a spatial analysis was performed that extracted the areas of 'mud to muddy sands' (having the highest relative OC contents; e.g., Smeaton et al., 2021) directly swept by the otter trawls, and therefore considered to be impacted. We calculated the total area of the sediments considered to be impacted for both years.

Carbon Stock in Hake Populations

Using carbon measurements from six hake, 15–20 cm long and 25–35 g in wet mass, as recorded by Czamanski et al. (2011), where dry weight was $42.9 \pm 6\%$, we calculated that OC was approximately 11.33% of hake wet weight. Dataset 1 was used to estimate the OC removed from the hake population (combined Northern and Southern stocks) in landings by country for France, Spain and the UK (STECF, 2020b), using the equation:

$$OC_{Removed} = Landings_{CY} \times 0.113256 \quad (7)$$

Where Landings are in kg, C is country, and Y is year. Using a 94% conversion rate of landed OC to CO₂ emissions described by Mariani et al. (2020), CO₂ emissions from total hake landings for gear type (DNGN, HOK, and DTS), for all three countries cumulatively, for 2008 and 2016 were calculated using the following equation:

$$Emissions_{Landings} = Landings_{GY} \times 0.113256 \times 0.94 \quad (8)$$

Where G is gear type and Y is year. To calculate the OC stock in the adult hake population for 2008 and 2016, estimates of SSB

were used for Northern stock only (ICES, 2021a), since ICES does not estimate the SSB for the southern stock, using the equation:

$$OC_{SSB} = SSB_Y \times 0.113256 \quad (9)$$

Where Y is year. The range of OC in SSB was calculated using the high, mean, and low estimates of SSB reported by ICES (2021a). Finally, to make a meaningful comparison between 2008, when the stock was considered overfished, and 2016, when it was considered rebuilt, the proportion of OC removed in total hake landings for the three countries was calculated as a percentage of the total OC stock in the hake population, again using the SSB for Northern stock only and the years 2008 and 2016. For this, we used the equation:

$$\frac{OC_{Removed}}{OC_{SSB}} \quad (10)$$

Again, the range was calculated using the high, mean, and low estimates of SSB.

RESULTS

Fuel Use, FI, and EI

Between 2008 and 2016, the total fuel consumption for all fishing segments that landed hake for France, Spain, and the United Kingdom increased by 29% (from ~49M litres to ~63M litres), relative to hake landings more than doubling (from ~45M kg to ~95.5Mkg). Simultaneously, the FI (and by extension, EI) for hake landed by the gear types DNGN (polyvalent passive gears and drift/fixed-net gears), HOK (gears with hooks), and DTS (demersal trawlers and seiners) decreased by 11–54% (**Figure 2** and **Table 2**). Additional analyses on these differences are included in the **Supplementary Information**. The sample size was extremely small for those fishing segments that landed primarily hake (i.e., where hake accounted for $\geq 50\%$ of the total landings), and therefore not particularly viable for statistical analyses. However, there was a declining trend in FI over time (**Supplementary Figure 2**) and, as FI is directly related to EI, the same can very likely be said for emissions per kg of hake.

The CO₂ produced in pursuit of hake (and, realistically, other species associated with the fishery) was influenced by the type of gear used to target them. For example, in 2016, hake that was landed using demersal trawlers or seiners (DTS) was approximately 37% more carbon intensive than the mean FI for the entire fishery and approximately 65% more carbon intensive than hake landed by vessels using polyvalent-, drift-, or fixed-net gears (DNGN) (**Figure 2** and **Table 2**).

Disturbance of Sediment

An increase in effort by vessels using otter trawls, and subsequently total SA, occurred for all three nations from 2008 and 2016, although the hake landings by otter trawl decreased overall (**Figure 3**). Vessels that landed hake for France, Spain, or the United Kingdom using otter trawls swept a cumulative total area of 230,103 and 520,856 km² in 2008 and 2016 respectively. Conversely, the total reported landings of hake by otter trawls were reduced from approximately 27,416 tonnes in 2008, to

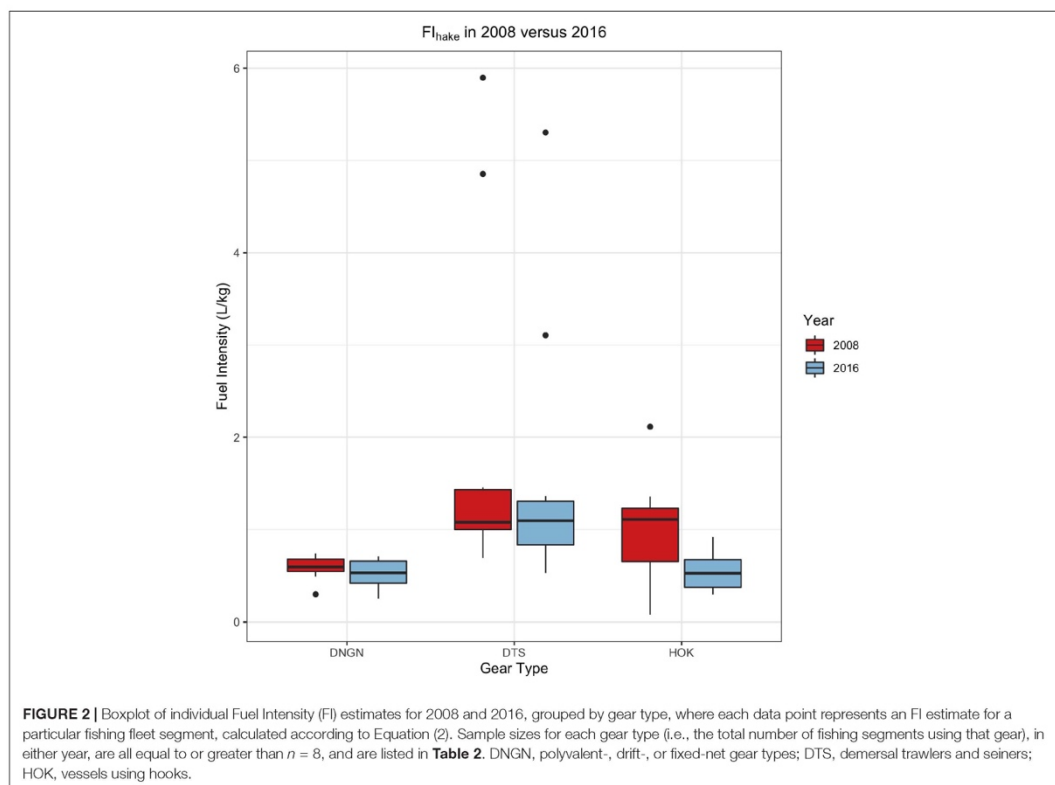


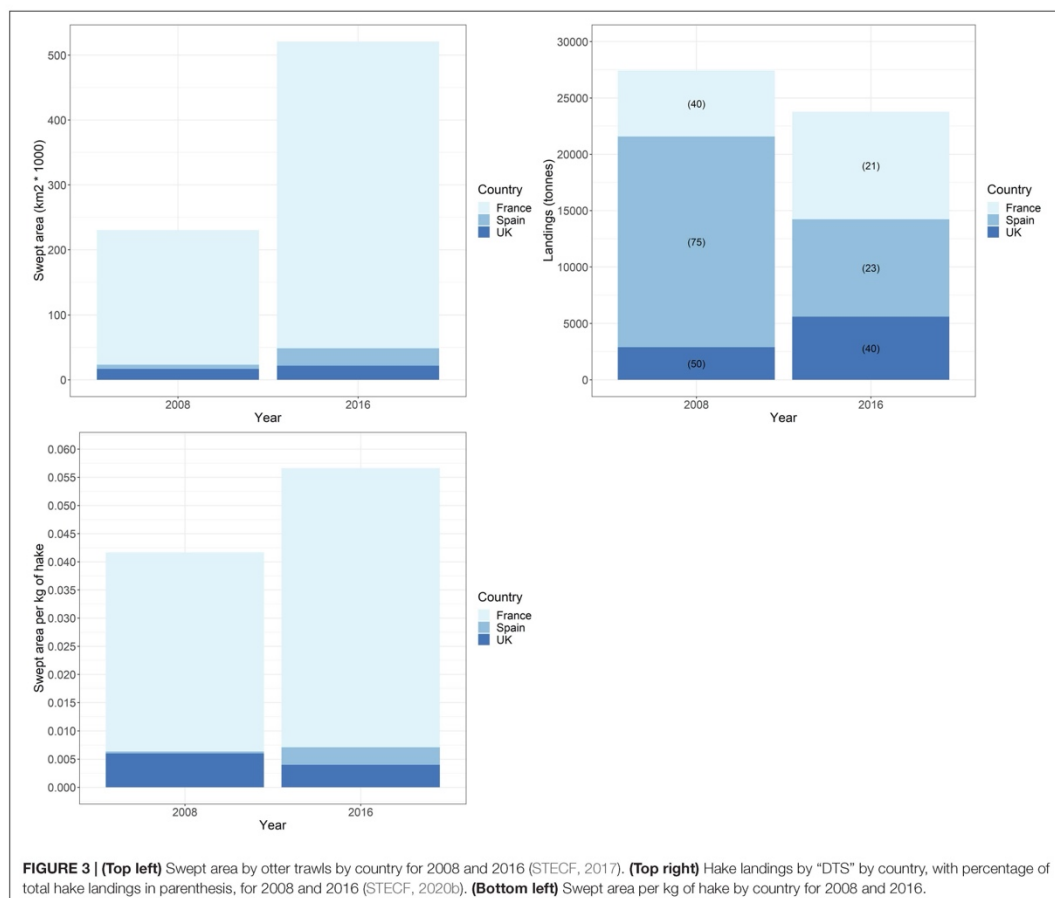
TABLE 2 | The reported total landings and estimated total fuel, mean Fuel Intensity (FI), and mean Emission Intensity (EI) for hake landed by vessels equipped with particular gear types (DNGN, HOK, DTS, or all gear types) in years 2008 and 2016.

Year	Measure	DNGN	DTS	HOK	All gear types
2008	Number of Individual fishing segments	12	10	8	37
	Total Fuel _{Gear} (L)	6,150,847	32,894,188	8,903,432	49,195,015
	Reported Total Landings _{Gear} (kg)	10,000,827	27,416,490	6,230,559	44,973,215
	Mean FI (L of fuel/kg hake)	0.615	1.200	1.429	1.094
	Mean EI (kg CO ₂ /kg hake)	1.755	3.423	4.078	3.121
2016	Number of Individual fishing segments	12	10	8	37
	Total Fuel _{Gear} (L)	26,726,954	21,546,642	12,364,812	63,110,975
	Reported Total Landings _{Gear} (kg)	48,654,256	23,763,605	18,743,699	95,547,292
	Mean FI (L of fuel/kg hake)	0.549	0.907	0.660	0.661
	Mean EI (kg CO ₂ /kg hake)	1.567	2.587	1.882	1.885
Change in FI and EI estimates from 2008 to 2016 (%)		-11	-32	-54	-40

Here we use "fishing segment" to refer to the combined gear type and size of vessel. DNGN = Polyvalent-, drift-, or fixed-net gear types; DTS, demersal trawlers and seiners; HOK, vessels using hooks. Respectively, units for FI and EI estimates are: litres of fuel per kg of hake landed, and kg of CO₂ per kg of hake landed. Percent changes in mean FI and EI estimates from 2008 to 2016 are listed at the bottom of each column. Mean FI estimates were calculated according to Equation (4). Note that, mechanistically, EI estimates are directly related to FI estimates by a factor of 2.853 kg CO₂/L fuel.

23,764 tonnes in 2016. The total SA values for the two annual snapshots are presented spatially in **Supplementary Figure 3**. In terms of SA per kg of landed hake, when comparing the

depleted stock of 2008 to the rebuilt stock of 2016, only the United Kingdom exhibited a lower result (33% decrease), while SA per kg of landed hake increased for France by 40% and Spain



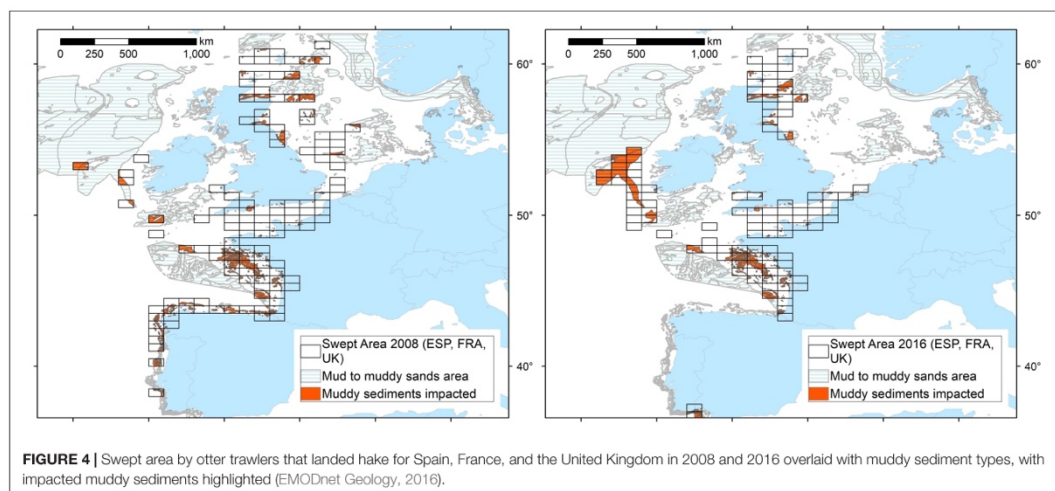
by 8-fold (Figure 3). For France, this is a result of a combined increase in effort and landings; however, for Spain, while there is a large increase in effort in 2016, reported hake landings were greatly reduced: less than 50% of 2008's catch.

As we have emphasised throughout the text, it is important to note that this is a mixed fishery and that hake forms a percentage of the overall landings, thus the SA is not attributable to the hake fishery alone. However, irrespective of which species were caught, the area of sediment swept represents the disturbance caused in relation to the hake landed. The spatial distribution of SA per individual nation for each year is shown in **Supplementary Figure 4**. Overall, the total spatial distribution of effort is quite similar for both years. The most intense activity occurred within the Bay of Biscay, following the western coastline of France, and within the Moray Firth region of the Greater North Sea. The English Channel sees increased effort in 2016, albeit consistent in distribution. In 2008, there was activity within the southern North Sea and along the northern and western coastline of Spain

which is not seen in 2016; instead, in 2016, a larger distribution of activity in the Celtic seas to the south-west of Ireland occurred. Using a somewhat crude area calculation provided by the spatial resolution of the ICES rectangles, we calculate an increase in the area of specifically muddy sediments disturbed by otter trawls from 5.72 km² in 2008 to 31.82 km² in 2016 (Figure 4). In 2008, disturbance of muddy sediments occurred off the west coast of France; northern coastline of Spain and west coast of Portugal; within the northern North Sea; and in the Celtic Sea to the west of Ireland. In 2016, there was less disturbance, and less activity generally, around the coasts of Spain and Portugal and the North Sea, and relatively consistent disturbance on the west coast of France. However, disturbance of a larger area of muddy sediments occurred in the Celtic Sea to the west of Ireland.

Impacts on Carbon Pool in Hake Stock

The total OC in hake landings increased between 2008 and 2016 for all three countries, with an additional 5,728 tonnes of



OC landed in 2016 cumulatively compared to 2008 (Table 3). Subsequently, total CO₂ emissions from OC in landed hake increased from 4.8M kg in 2008, to 10.2M kg in 2016, including increases in CO₂ emissions from hake landed using polyvalent passive gears, drift/fixed-net gears, and gears with hooks (Figure 5). However, a decrease of 0.4M kg CO₂ was observed for hake landed using demersal trawlers and seiners, as fewer hake overall were landed using that gear type in 2016. Despite total OC removal and emissions from OC in hake landings increasing between the two years, the proportion of the OC stock in the hake pool removed by landings in 2016 was much lower (31%) than that in 2008 (96%) (Table 3), and the OC stock in the adult hake population was approximately 6.5 times larger in 2016 than in 2008 (Figure 5).

DISCUSSION

Despite the limitations of the data, comparisons between the relative impacts of the fishery when the stock was overfished, as in 2008, and rebuilt, as in 2016, were possible. We have demonstrated improvements in efficiency and proportional OC storage in living stocks in 2016 compared to 2008. However, increased fishing in 2016 also resulted in increased total emissions from both fuel and landed hake, and increased ecosystem disturbance. First, we found that all gears were more fuel efficient in 2016 compared to 2008, suggesting an increase in catch per unit effort, where the unit of effort is fuel. Second, in 2016, when stocks had been rebuilt, more OC remained in the living pool of hake compared to when stocks were depleted in 2008, both in terms of total biomass and proportionally. Third, increased fishing effort in 2016 using bottom trawling resulted in higher disturbance of sedimentary OC, however, the hake catch from trawling was lower in 2016, suggesting this increase may have been due to trawls targeting other species than hake. Finally,

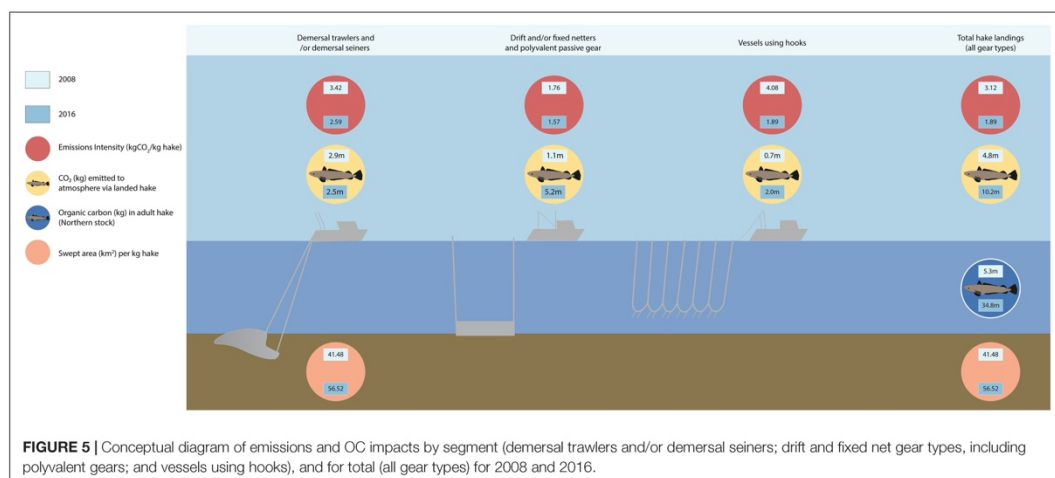
as may be expected with increased landings, higher total fuel emissions and CO₂ release from hake landings in the Northeast Atlantic occurred once stocks were rebuilt. However, this analysis does not consider the displacement of effort and catch that may occur when a stock in one geographic location is depleted, while demand for that seafood remains constant. For instance, in 2008 frozen hake imported to Spain from outside the EU was higher than imports reported for the five subsequent years (EUMOFA, 2015), which suggests that the full emissions and OC impacts borne from the depleted stock may be higher, perhaps substantially so, from a global perspective. Likewise, we did not consider post-processing differences in our analysis, which may undergo changes when fish are imported rather than landed and marketed fresh. While our aim was to provide insights on the impacts of fisheries that will ultimately be useful for the development of EAF, such additional assessments would also improve the information available to the consumer at the point of purchase.

Overall, the increase in available hake biomass once the stock was rebuilt correlates with increased efficiency across passive gear types and proportional reduction of fishing impacts on the living pool of OC. We found that the volume of CO₂ emissions produced by vessels landing hake was influenced by the type of gear used, with the passive gillnets, hook and line, and polyvalent gears generally outperforming trawls in terms of emissions and EI. With regard to sediment disturbance, the rebuilt fishery (2016) performed better than the depleted fishery (2008) in instances where hake landings produced by trawlers were more-or-less consistent between the two years (in France and the United Kingdom for example), compared to instances where the landings from trawlers between 2008 and 2016 were substantially reduced (as in the case of Spain). These observations are likely linked to the improved stock status of hake in 2016 compared to 2008, however, the hake fishery is a mixed fishery, thus the changes in EI and impacts of the benthic trawl gear

TABLE 3 | Organic carbon (OC) impacts of hake fisheries in France, Spain, and the United Kingdom.

OC estimates	Year	Country			Total
		France	Spain	UK	
OC in landings (tonnes)	2008	1,633	2,805	656	5093
	2016	5,005	4,221	1,596	10,821
OC in stock (tonnes)	2008	5,280 (± 375)			
	2016	34,780 (± 2671)			
Proportion of OC stock landed (range)	2008	96% (90–100%)			
	2016	31% (29–34%)			

OC in stock refers to Northern hake stock only as SSB not estimated for Southern stock.



on sediment cannot be attributed to hake stock status and hake landings alone. A greater proportion of the overall disturbance due to trawling effort in 2016 is likely to be attributable to other species, given the decline in hake landings by trawlers observed in 2016, particularly for the Spanish fleet. Unfortunately, we were unable to explore this observation further due to the limitations of the datasets. Nevertheless, the SA analysis provides useful insights into the potential disruptions to sedimentary OC posed by trawlers that land hake. Notably, hake habitat typically encompasses muddy sediments, which generally hold more OC (Diesing et al., 2017; Smeaton et al., 2021) and are resuspended for longer periods of time relative to other sediment types (O'Neill and Summerbell, 2011), implying a greater potential for OC loss via remineralisation or lateral transport offshore (Paradis et al., 2019; Epstein et al., 2022). This is not to suggest, however, that other types of seabed sediments are impervious to the impacts of trawling, both in terms of carbon and biodiversity—impacts relevant to EAF. For example, while both muddy and gravelly sediments experience relatively high benthic community depletion rates following a trawl, recovery rates for infaunal benthic communities are higher in mud than gravel due to the presence of faster-growing species (Pitcher et al., 2022).

As an early attempt to consider fishery impacts on OC in sediments and biomass using current publicly available data, there are limitations to what we could surmise. Firstly, we recognise the limitations of using two datasets which cannot be consistently filtered either by gear type or by landings with spatial data and, as such, note that the final estimates for SA per kg of hake are unreliable. Furthermore, our estimates of SA are likely to be over-estimated, not least because of the overlap of ICES rectangles with land area along coastlines (Figure 3). This is a function of the spatial scale of available data. We carried out a comparative analysis using a recent, much higher resolution dataset to illustrate this point (i.e., $0.05^\circ \times 0.05^\circ$ as opposed to $0.5^\circ \times 1^\circ$), however, we note that the SA data themselves are not comparable due to differences in the way that STECF (2017) and ICES (2021c) aggregate data. For instance, while landings data for hake are available at a country level by year from STECF (2020b), the data are aggregated into a broader gear type, for example “demersal trawls and seines” are categorised simply as “DTS.” Conversely, while the ICES data are disaggregated into specific designs of otter trawl (seven spatial layers exist for otter trawls within the high-resolution ICES dataset), the data comprise all landed species and for all countries per year.

To illustrate the advantages of high-resolution spatial data, we compared our 2016 SA calculated using dataset 2 (STECF, 2017) with the ICES (2021c) dataset of the 2016 spatial layer for the BENTHIS métier code “OT_DMFE” which refers to otter trawling of demersal fisheries. This BENTHIS métier code includes hake as a target species according to Eigaard et al. (2016) although hake is not specifically mentioned for this gear type by ICES (2021c). We compared the spatial distribution of SA for the area of high-intensity SA values off the west coast of France and north coast of Spain using these two datasets (**Supplementary Figure 5**). The higher resolution ICES dataset visibly reduced the estimated footprint and provided a much-improved spatial analysis of areas that are heavily impacted by trawling. An analysis of this nature might inform highly targeted management interventions, if required. The second analysis relates to estimates of the overall area of muddy sediment impacted using data of different scales/resolutions (**Supplementary Figure 6**). When we extracted the areas of muddy sediment that overlap with the SA data from dataset 2 and the ICES data (ICES, 2021c), we did not see a large difference in the disturbed area estimated by the two different resolutions. Overall, despite the data limitations described above, it is evident that the results of any spatial analysis strongly depend on the spatial scale of the dataset (Amoroso et al., 2018b) and highlights the importance of data resolution when estimating and considering fishing impacts. Therefore, with finer spatial resolution of effort data, combined with sediment maps and OC content estimates, quantification of disturbance to sediment OC are likely to improve.

Our analysis of fishing impacts on the living OC stock is focused on hake biomass only, due to the data available. Including dynamics between the target species, competitors, predators, and prey would improve the analysis and better inform management of living OC stocks under different fishing conditions. Consideration of the fishing impacts on bycatch and, when assessing a mixed fishery such as hake, other target species would be necessary, thus reporting catch composition and bycatch by segment would enable a more thorough analysis of fishing impacts on living OC stocks. Furthermore, better understanding and incorporation of a target species' natural history and trophic dynamics into the analysis could shed further light on the impact of fisheries on OC in living stocks. For instance, consideration of the age at which a species is fished may provide insights on the longevity of the OC stock in that population. The recorded maximum longevity for hake ranges from 20 to 25 years (Vitale et al., 2016); if individuals live for 20 years, they can effectively store OC for two decades. Hake occupies different trophic levels as their diet changes throughout their life stages, thus the prey controlled by juvenile and adult hake are different. Adult hake over 30cm in length, which are the target of hake fisheries, prey on demersal fishes such as blue whiting and, where adult and juvenile hake distributions overlap, they show a preference for cannibalism (Mahe et al., 2007). Removal of large hake may therefore release smaller hake from predation, increasing the chances that juveniles will reach adulthood and recruit to the fishery, while a reduction in fishing pressure on larger hake could

have the opposite effect (Mahe et al., 2007). At the same time, larger hake females may facilitate faster rebuilding where stocks are depleted, as they have a higher fecundity than smaller hake females and produce more eggs (Cervino et al., 2013). Overfishing of predators can cause widespread changes in the ecosystem as prey are released from predation, with implications extending beyond the biomass of the target population, to food webs, habitats, and ecosystem services (Östman et al., 2016; Norderhaug et al., 2021). While they are not considered a deep-sea species, hake can be found at depths down to 1000m (Morales-Muñiz et al., 2018), thus may provide a link between shallower and deep sea habitats, which play a key role in global ecological and biogeochemical processes (Danovaro et al., 2008).

The objectives of this study were to explore how ending overfishing of hake and stock recovery affected (i) the carbon emissions from fuel use during fishing activity; (ii) disturbance of OC in sediments by trawling; and (iii) impacts on the OC stocks in the population of the target species. Earlier analysis of emissions from the hake fishery in Spain considered the entire life cycle of the fishery, from extraction to processing and consumption (Vázquez-Rowe et al., 2011). However, our approach was to consider the fishery from the perspective of EAF, and thus, the only fuel emissions we considered were those caused by fishing activity directly. Our study was also limited to a snapshot view of fisheries impacts when the hake stock was depleted, in 2008, and rebuilt, in 2016. As such, we did not seek to establish the reasons for stock depletion and recovery, thus, the effects we report are not necessarily a product of ending overfishing. However, it is likely that reduced fishing pressure, required by the recovery plan introduced in 2004, contributed to the increase in hake biomass of the Northern stock (Baudron and Fernandes, 2014).

Exploration of the OC impacts of fisheries is timely given that the interaction between trawl fishing activity and sediments is increasingly recognised as an important impact for consideration in EAF (De Borger et al., 2021); recent research has highlighted the roles of fish in the carbon cycle and flux (Bianchi et al., 2021; Saba et al., 2021); and there is significant overlap between fishing grounds and areas of high productivity (Cavan and Hill, 2021). Furthermore, EU targets to end overfishing by 2020 have not been met, yet overfishing is known to affect the resilience of fish stocks to climate change and other stressors (Sumaila and Tai, 2020). During this study, we used only publicly available fisheries data and, as such, found various limitations which have resulted in unreliable estimates, particularly for SA and OC in hake stock. Improving the reliability and accuracy of estimates is necessary. Ensuring that data can be consistently disaggregated across public databases, such as by country, fishery segment, BENTHIS métier, effort, and landings, would go a long way toward improving the accuracy of estimates of the impacts of fishing on landed populations and the environment. In addition, spatial data at finer scale resolutions than ICES rectangles are especially important for generating estimates of impacts on benthic environments.

The need for EAF which can lead to better outcomes for climate, biodiversity, and people is widely recognised but not easily operationalised (Link et al., 2020). Climate-based fisheries management must go beyond a target of MSY to include climate-based objectives in EAF. This would, presumably, call for management decisions based on consideration of emissions from fuel, disturbance to OC in sediments and living pools, and the carbon functions of the ecosystem. Reference levels for what constitutes sustainable fishing and desirable stock size could then be decided across priorities, such as carbon sequestration, harvest, ecosystem health, and social and cultural facets. This analysis represents a first step towards ensuring that relevant information from emerging fields of research can be included in the development of EAF approaches and has illuminated some of the complexity involved when using publicly available data to assess fisheries impacts on ecosystems.

DATA AVAILABILITY STATEMENT

Publicly available datasets were analyzed in this study and are referenced. The data provided by STECF (2020b) upon our request can be found here: <https://github.com/angela-m/Hake-fishery-recovery-and-climate>.

AUTHOR CONTRIBUTIONS

AM, EF, and SV contributed to the initial discussion. AM and EF led the writing of the manuscript. AM, EF, CH, and KB designed the figures and compiled the tables. All authors contributed to the literature survey, drafted and reviewed the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2022.788339/full#supplementary-material>

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