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Exploring connections between mesopelagic ecosystems, epipelagic predators, and a changing ocean climate in the California Current

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EXPLORING CONNECTIONS BETWEEN MESOPEALGIC ECOSYSTEMS, EPIPELAGIC PREDATORS, AND A CHANGING OCEAN CLIMATE IN THE CALIFORNIA CURRENT

A dissertation submitted in partial satisfaction
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Ilysa S. Iglesias

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Abstract

Exploring connections between mesopelagic ecosystems, epipelagic predators, and a changing ocean climate in the California Current

by Ilysa S. Iglesias

The deep-pelagic ocean represents one of the largest biomes, and is home to a diverse assemblage of organisms, whose collective vertical movements represent the greatest migration on earth. Deep-pelagic environments and denizens are often defined by their distance and distinctness from surface ecosystems. However, in this dissertation, I explore how mesopelagic communities are interconnected to pelagic food webs and impacted by changing oceanographic conditions at the surface. Focusing on the California Current, we use a combination of diet data, fisheries acoustics, and downscaled climate projections to investigate the role of mesopelagic fishes as prey to higher trophic level predators, the effects of a large marine heatwave on the deep scattering community, and the compression of mesopelagic habitat projected by the end of the 21st century. Our results suggest that mesopelagic communities provide prey for numerous federally managed and protected species, adjust their vertical position in response to marine heatwave events, and will experience vertical habitat compression as low oxygen conditions shoal due to global climate change. As anthropogenic threats to exploit and alter deep-pelagic ecosystems rise, our work demonstrates the need to consider more carefully the role of mesopelagic communities in supporting healthy and functioning ocean ecosystems.

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The text of this dissertation includes reprints of the following previously published material (Chapter 1) or work that is currently under review (Chapter 2):

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Introduction

The deep-pelagic ocean represents the largest habitable by volume on earth and is home to the greatest estimated biomass of vertebrates. Mesopelagic communities inhabiting depths from ~200-1000 m provide important prey for higher trophic level predators and transport carbon from the surface to the interior ocean (Davison et al., 2013), therein contributing to global climate regulation. Despite inhabiting daytime depths of ~200-1000 m, many mesopelagic animals undergo nightly vertical migration into the upper water column to feed, which connects mesopelagic animals directly to epipelagic processes and food webs. This movement also exposes mesopelagic fishes to anthropogenic impacts on the ocean, many of which are most pronounced at the surface. Despite the importance of mesopelagic communities to a functioning ecosystem, and increasing threats posed by a changing oceanographic landscape, limited research exists which explicitly evaluates the role of mesopelagic fishes as prey in epipelagic food webs, or the effects of changing oceanographic conditions on the distribution and abundance of mesopelagic fishes. Using a combination of data from predator diets, long-term fisheries acoustics, and downscaled climate projections, this work examines the role of mesopelagic fishes as prey to predators residing outside mesopelagic depths, quantifies the response of mesopelagic communities to a large marine heatwave, and examines how the vertical extent of mesopelagic habitat is likely to change by the end of the 21st century.

Previous research has emphasized the importance of mesopelagic animals as prey to higher trophic level predators (i.e., Northern Elephant Seals (Goetsch et al., 2018), seabirds (Watanuki and Thiebot, 2018), Tunas (Duffy et al., 2017) and King penguins (Raclot et al., 1998) amongst others, but these studies were narrowly focused on specific predator taxa. In the first chapter, *Mesopelagic fishes are important prey to a diversity of predators* (Iglesias et al., 2023), I use a large trophic database with >100,000 diet records from over 143 predator taxa collected from the California Current Ecosystem (CCE), to quantify the prevalence of mesopelagic fishes in the diet of a diverse assemblage of higher trophic level predators. Mesopelagic fishes occurred in the diets of 25% of all predator taxa in the database, including protected marine mammal species, 19 bony fishes, 15 of which support managed fisheries (e.g. Swordfish, Tuna, Rockfishes, Salmon, Hake); and 7 elasmobranchs. For 11 predator taxa, including species of dolphins, Swordfish and pelagic squid, mesopelagic fishes occurred in greater than 25% of all diet samples examined, highlighting their relative importance as prey. Compared to coastal pelagic forage fish, considered “essential” prey in the California Current, mesopelagic fishes occurred more frequently in 21 predator taxa. This work illuminated the value of mesopelagic fishes as prey to economically valuable and federally managed and protected species, as well as the interconnection of mesopelagic organisms and habitats to predators occupying different depths of the water column.

Whereas the first chapter highlighted trophic connections between mesopelagic communities the epipelagic predators, in the second chapter, Large marine heatwave deepens vertical distribution of mesopelagic fishes, we explore the connections between the mesopelagic community and changes in the oceanographic conditions near the surface. Marine heatwaves, defined as periods of intense ocean warming, have increased in intensity and duration as a result of climate change (Frölicher et al., 2018). During 2013-2016, a large marine heatwave event, referred to as “the blob,” led to unprecedented ecological impacts to epipelagic and coastal marine communities (Cavole et al., 2016), including mass mortality of seabirds (Jones et al., 2018), changes in the composition of zooplankton communities (Brodeur et al., 2019) and fisheries closures. The marine heatwave also led to changes in prevailing oceanographic processes, such as the compression of upwelling habitat closer to shore (Santora et al., 2020; Schroeder et al., 2022). However, it is less clear how these anomalous oceanographic conditions impacted mesopelagic communities inhabiting daytime depths typically considered stable.

Using fisheries acoustics data collected as part of the NOAA Rockfish Recruitment and Ecosystem Assessment Survey from 2013-2018 for the Central California Current, we examined how this heatwave event influenced the depth of the deep scattering layer (DSL). Our results revealed a significant increase (by >100 m) in the depth of acoustic backscatter during the warmest years of the heatwave (2015 and 2016) compared to pre-heatwave conditions. Using a generalized additive modeling approach, we then linked center of mass depth (mean depth weighted by acoustic backscatter) to light, backscattering intensity, upwelling strength and temperature. Based on these results, we hypothesize that a compression of upwelling habitat nearshore during the heatwave reduced the amount of primary production in the upper water column, contributing to increasing light at mesopelagic depths, which mesopelagic fishes responded to by descending deeper into the water column. This chapter highlights the response of mesopelagic fishes to changing oceanographic conditions in the near-surface, as well as the need to better incorporate monitor changes in the distribution and abundance of mesopelagic communities.

The long-term indirect effects of climate change on mesopelagic communities is poorly understood, but global declines in oxygen and the expansion of oxygen minimum zones by millions of kms (Breitburg et al., 2018) have led some researchers to speculate that the extent of vertical mesopelagic habitat is likely to shoal by the end of the 21st century (Proud et al., 2017) and possibly shift mesopelagic fishes poleward (Liu et al., 2023). The upper boundary of mesopelagic communities is limited by the intensity of light that penetrates down from the surface (Benoit-Bird et al., 2009; Aksnes et al., 2017), as mesopelagic organisms seek refuge from visual predators (Longhurst, 1976). From below, the limit of mesopelagic communities is often determined by the depth of low oxygen conditions (Netburn and Koslow, 2015; Urmy and Horne, 2016). Global warming contributes to deoxygenation by reducing the solubility of dissolved oxygen in seawater, increasing respiration (which consumes oxygen) and reducing exchange between the surface and deep ocean (Breitburg et al., 2018). In the third chapter, *Projected 21st century vertical compression of mesopelagic habitat in the California Current,* I examined how oceanographic conditions are likely to change as a result of climate change by the end of the century.

Using downscaled climate projections from three Earth System Models to force a coupled physical biogeochemical regional ocean model, we compared changes in ocean conditions from the beginning (2000-2030) to the end of the century (2070-2100).

We defined the vertical extent of mesopelagic habitat as the distance between isolume depth and the hypoxic boundary (60 mmol/m3). Our analysis suggest a ~58% (~45 m) compression of mesopelagic habitat by the end of the century, an increase in temperature by 1.1 °C at 200 m, increased depth of the 26.5 kg/m3 isopycnal (> 50 m) and declining oxygen concentrations (by ~10 mmol/m3 at the historical hypoxic boundary depth). Although the ensemble mean predicted declining mesopelagic habitat, the response varied spatially, with more declines in the north of the study domain because of disparate evolutions of ensemble members. One main difference between our three ensemble members, which were select to represent varying warming rates under the RCP8.5 scenario (GFDL- low, IPSL-moderate and Hadley-high rates of warming), was in the projection of future southern boundary conditions, with GFDL and IPSL predicting declines in oxygen and Hadley predicting increases, highlighting how equatorial processes may shape the availability of mesopelagic habitat in the future. Our results suggest that mesopelagic communities are likely to experience warmer, less deoxygenated conditions by the end of the century, which could lead to a homogenization of mesopelagic habitat globally and a loss of biodiversity (Stramma et al., 2010; Proud et al., 2017) in this biodiverse but understudied region of the ocean (Webb et al., 2010).

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Chapter 1

Mesopelagic fishes are important prey for a diversity of predators

1.1 Abstract

Through daily vertical movements, mesopelagic fishes contribute to global carbon export and, when eaten, link primary consumers to higher trophic level predators. Although the importance of mesopelagic fishes as prey to individual predator species has been explored, a comprehensive assessment of mesopelagic fishes as prey at the scale of a large marine ecosystem would advance our observing, modeling, and predicting of biodiversity and ecosystem function. We use diet samples from over 105,000 individual predators from 143 taxa in the California Current Ecosystem (CCE) to quantify and evaluate the role of mesopelagic fishes as prey. For 11 predator taxa, including protected mammal species, pelagic squids, a shelf-edge-associated rockfish and highly migratory species, mesopelagic fishes occurred in greater than 25% of all diet samples, likely comprising an important source of prey. Of the 143 taxa represented, individuals from 36 taxa, or 25% percent of all predator taxa in the database, consumed at least one mesopelagic fish species, including economically important fishery species such as Bluefin tuna (16% of all non-empty diet samples), Albacore (19%), Swordfish (50%), Humboldt squid (52%), and Pacific hake (4%). Compared with coastal pelagic fish species (essential prey in the CCE), mesopelagic fish were more frequently encountered in the diets of 21 predator taxa. Lanternfish (family Myctophidae) were the most common prey and consumed by the greatest diversity of predators (32 taxa), but an additional 16 families of mesopelagic fishes were also consumed by predators, highlighting the diversity of organisms

inhabiting mesopelagic depths. Mesopelagic fishes were found in the diets of predators collected from shelf depths to well offshore, accentuating the role of mesopelagic fishes as prey across habitats, especially for predators foraging over the slope and further offshore. Our work illuminates the importance of mesopelagic fishes as prey to a diversity of economically valuable and protected species, underscoring the need to incorporate mesopelagic fishes more comprehensively into food web models, global carbon budgets and ultimately our understanding of ecosystem function.

1.2 Introduction

Mesopelagic fishes are among the most abundant vertebrates on earth, with a biomass likely exceeding that of total global fisheries landings (Beamish et al., 1999; Irigoien et al., 2014). Historically, mesopelagic fishes have been of little direct economic value due to their small size, waxy composition, and difficulty of capture in loose aggregations at deep depths. In recent years, however, there has been growing interest in developing industrial fisheries, particularly as potential fishmeal and fish oil for aquaculture operations that produce more desirable fish species (Standal and Grimaldo, 2020). Beyond economic value, mesopelagic organisms contribute to global carbon export through their vertical migration into surface waters to feed and their subsequent return to depth. In the California Current, mesopelagic fishes are estimated to account for 15–17% of all carbon exported from surface productivity (Davison et al., 2013). In addition to their role as consumers, mesopelagic fishes are vital as prey to higher trophic-level predators, including economically valuable fish species and protected marine mammals (Pauly, 1998; Brodeur and Yamamura, 2005; Duffy et al., 2017). While the importance of mesopelagic fishes as prey to individual predator species is regularly stated, the complex trophic interactions between diverse mesopelagic species and potential predators can be best examined at an ecosystem level. As a case study, we use a unique database of diet data from diverse predators within the California Current Ecosystem (CCE) to investigate the role of mesopelagic fishes as prey. This work benefits future biodiversity and ecosystem function modeling and provides context to inform ongoing and potential future fisheries management actions.

The mesopelagic zone, occurring at depths of ~200–1000 m, is one of the largest habitats on earth, and one of the least understood (St. John et al., 2016). Organisms inhabiting mesopelagic depths often form complex aggregations of diverse taxa referred to as "deep scattering layers"; their initial discovery was via strong acoustic backscatter (Eyring et al., 1948). The mesopelagic environment is connected to epipelagic processes such as upper thermal mixing and pycnocline layers that structure and concentrate primary production and secondary consumers in pelagic systems. Mesopelagic organisms typically depend on raining organic matter from the surface for food or interact with upper waters directly during a daily vertical migration to feed. During these nighttime sojourns to the surface, mesopelagic organisms are prone to predation by epipelagic nocturnal predators. While it is assumed that most mesopelagic fishes return to depth during the day to avoid predation by visually oriented predators (see review by Longhurst, 1976), which can vary by species and life-history (Benoit-Bird et al., 2017), some predators are capable of hunting mesopelagic prey during the daytime by foraging at mesopelagic depths. Thus, mesopelagic fishes are vulnerable to predation by both daytime diving predators as well as nocturnal predators foraging near the surface.

Mesopelagic fishes have been recorded in the diets of cephalopods, elasmobranchs, fishes (including tuna, salmon, and groundfish species), seabirds, pinnipeds, and cetaceans (Gjosaeter and Kawaguchi, 1980; Pauly, 1998; Brodeur and Yamamura, 2005; Spear et al., 2007), among others. Myctophids, one of the most abundant and diverse families of fish in the mesopelagic, are noted for their high energy density (Van de Putte et al., 2006), which makes them a particularly important prey for predators with high energy demands. While Myctophids are an important link between primary consumers and higher trophic level predators in epipelagic surface waters, they additionally connect surface production to deep-ocean food webs (Choy et al., 2017). While some predator species specifically target mesopelagic fishes (e.g., Northern elephant seal (Goetsch et al., 2018)), other predators may rely on mesopelagic prey during times of decreased coastal prey (e.g. Kittiwakes, Paredes et al., 2014). Myctophids are also important consumers of krill, and in their central role between primary consumers and higher trophic level predators, they may stabilize krill-dominated food webs, such as in the Southern Ocean, during periods of warming temperatures and declining krill (Saunders et al., 2019). In the CCE, mesopelagic fishes may likewise be important as prey for higher trophic level predators during periods of variable oceanographic conditions. Survey data from both the southern and central California Current indicates mesopelagic fishes may fluctuate out of phase with other forage species, with mesopelagic taxa tending to be more abundant, (Hsieh et al., 2009; Koslow et al., 2011; Ralston et al., 2015; Santora et al. 2021), and more diverse (Santora et al., 2017), in years defined by warmer ocean temperatures. Thus, during warm periods, when other forage species are likely to decline, mesopelagic fishes may provide similar resiliency for predators in the CCE.

The California Current is an eastern boundary current upwelling ecosystem that is characterized by seasonally strong upwelling-favorable conditions and associated high levels of primary productivity (Checkley and Barth, 2009). This productivity supports robust coastal pelagic species and economically important fisheries, considered indispensable to the CCE food web (Miller et al., 2010). The biomass of mesopelagic fish has been estimated to be approximately equivalent to that of the epipelagic forage community (Davison et al., 2015), but with far greater uncertainty regarding total abundance and species composition. Although previous work in the region has attempted to summarize trophic relationships between mesopelagic prey (and other forage species) and higher trophic level predators (Dufault et al., 2009; Szoboszlai et al., 2015), these studies were based on literature reviews rather than analysis of raw diet data and were consequently limited in their ability to evaluate the importance of mesopelagic prey to predators with fine-scale taxonomic resolution. Our study is the first to use a meta-synthesis of raw diet data to conduct a comprehensive examination of the role of the full suite of mesopelagic fishes as prey to the broader predator community of the CCE. The results should inform future ecosystem modeling efforts, by providing guidance on complex trophic interactions and aid ongoing management efforts, such as the current moratorium on new fisheries for mesopelagic fishes and other forage species in the California Current.

1.3 Methods

Examining the diet of higher trophic level predators is an imperfect method for describing predator consumption patterns and trophodynamics. While there are limitations with sampling a snapshot in time, the inferences that can be made regarding the diet composition and relative importance of distinct prey items make gut content analysis nonetheless an indispensable method for understanding trophic interactions (Baker et al., 2014). In this study, we use the "California Current Trophic Database," referred to as the CCTD (Bizzarro et al., 2023), available publicly via the NOAA Environmental Research Division's Data Access Program (ERDDAP). The CCTD combines 24 separate datasets from 1967 to 2019 on food habit studies from predominately stomach, and some scat samples, from over 100,000 individual predators, including taxa of squids (*n* = 5), elasmobranchs (*n* = 13), bony fishes (*n* = 118), and marine mammals (*n* = 7).

We investigated and summarized the role of mesopelagic fishes in the diet of higher trophic level predators in the CCE. To identify which prey species could be categorized as "mesopelagic," we reviewed all prey fish species from the CCTD database (total of 323 fish taxa). For each of these taxa, we searched Fishbase (https:// www.fishbase.se/) for available depth range values. In those cases where data were missing for a given species, or for higher level taxonomic groupings (i.e., family or genus as opposed to species), we additionally looked up the taxon of question in "Pacific Coast Fishes,"(Eschmeyer et al., 1983) "Guide to the coastal marine fishes of California," (Miller and Lea, 1972) and/or "Deep-sea fishes" (Priede, 2017), and in some cases the broader literature (see Supplementary Table S1 for additional references). We define a taxon as "mesopelagic" if its daytime adult distribution is pelagic and occurs at depths of ~200–1000 m. Many "mesopelagic" taxa have distributions that extend beyond 1000 m into the bathypelagic zone. In this study, what we consider to be "mesopelagic" also includes those prey species with distributions extending into the bathypelagic zone. For specifics, see Supplementary Table S1. For broader taxonomic categories, we chose depth criteria based on representative species within a given taxa in the prey list, or other representative species from those taxa available in Fishbase, and only included the broader grouping as "mesopelagic" if all available representatives were mesopelagic. In total, there were 62 taxa that we consider to be mesopelagic, or ~19% of all identified fish prey species within the database (62/323 fishes).

Frequency of occurrence (FO) is a robust metric in diet analysis studies for quantifying prey prevalence, while avoiding the pitfalls inherent in other gut content metrics (Baker et al., 2014), especially as methods of diet sample collection and processing varied across taxa and collections. FO is calculated as the total number of stomachs [or scats for marine mammals inhabiting onshore colonies, see (Lowry et al., 2022)], containing a prey taxon of interest, divided by the total number of non-empty stomachs for that given predator taxa. We first determined which of the predators in the CCTD database had consumed any mesopelagic fish prey (Figure 1A). The FO was then calculated as the number of predator diet samples containing mesopelagic fish prey divided by the total number of non-empty diet samples for that predator (Figure 1B). To compare the relative contribution of mesopelagic fishes to that of coastal pelagic fishes, as defined by the Pacific Fishery Management Council, and considered to be essential prey in the CCE, we calculated a combined FO for Pacific sardine *Sardinops sagax*, Pacific (chub) mackerel *Scomber japonicus*, Northern anchovy *Engraulis mordax*, Jack mackerel *Trachurus symmetricus*, Pacific herring *Clupea pallasii pallasii*, and Jacksmelt *Atherinopsis californiensis*. We then compared the relative contribution of mesopelagic fishes to that of the combined coastal pelagic fish species for predator taxa that consumed mesopelagic prey (Figure 1B).

Of the mesopelagic fish consumed (Figures 2A, B), we were also interested in which mesopelagic fish taxa were most frequently encountered in predator diets, as this could indicate abundance and/or trophic importance of specific mesopelagic prey types. We chose to group by mesopelagic fish family as opposed to individual taxa due to challenges associated with reliably identifying gut/scat material to the species level between different collections. We calculated a FO per mesopelagic fish family as the number of unique predator stomachs containing prey from each family of mesopelagic fish, divided by the total # of non-empty stomachs per predator species. We then plotted this family level FO value for each predator taxa and examined trends in predator diet across mesopelagic fish families (Figure 3). Myctophids were the most frequently encountered mesopelagic fish prey, so we further examined the percentage occurrence of specific species of Myctophids contributing to this abundance (Figure 2C).

The CCTD database contains information on the method and location of predator diet sample collections. Predator collections were identified with a collection id that was unique in time and space, although the number of predator samples collected in any given collection was variable. Although collection information is not necessarily unique to an individual predator, the position of each collection provides valuable information on predator foraging habits and the proportion of predators at a given location that consumed mesopelagic prey. Location information was available for > 90% of mesopelagic predator collection records. For each predator collection location record in the database, we plotted the proportion of predators that had consumed mesopelagic fishes (Figure 4). For each collection record, we then assigned "habitat" type based on bottom depth: shelf (0–200 m), slope (200–1000 m), deep (> 1000 m), or scat samples from onshore marine mammal colonies (for California sea lion and Northern fur seal). We removed records for diet samples that were collected from strandings, as these samples did not accurately reflect foraging position. We used NOAA bathymetry data from the R package {marmap} (Pante and Simon-Bouhet, 2013) to extract information about the underlying bottom depth for each collection record. Although diet samples in the CCTD were not sampled evenly across habitat types, and we did not have sufficient data available to compare the actual depth of predator capture; we examined predator foraging habitat trends by comparing the number of collection locations that captured predators that had consumed mesopelagic prey (Figure 4 inset) and the composition of predator taxa that had consumed mesopelagic prey by habitat type (Figure 5). All quantitative analyses were conducted using the R programming language (R Core Team, 2022) in Rstudio (RStudio Team, 2022).

Prey length can be an important determinant of predation susceptibility. Most mesopelagic fish lengths were measured as standard length (SL) values, but total length (TL), fork length (FL), and in some cases back calculated SL measurements were also available. We used SL or back calculated SL measurements to compare the length frequency distribution of mesopelagic fish prey between families and compared SL of mesopelagic fish to coastal pelagic fish prey. For those prey records that lacked SL information, but had FL or TL measurements, we converted to SL using length to length conversion values available from fishbase.org. In total, we had length information for 3,267 mesopelagic fish prey, which were plotted for those mesopelagic fish families with at least 10 length records available (Figure 6A). We also compared the length frequency distribution of mesopelagic fishes with that of coastal pelagic prey for those predator species that consumed mesopelagic fishes within the database, to assess whether mesopelagic fishes had overlapping or distinct length distributions to coastal pelagic fishes (Figure 6B).

1.4 Results

The FO analysis revealed mesopelagic fishes to be important prey for multiple phyla of higher trophic level predators. For 11 predator taxa, greater than 25% of all diet samples contained mesopelagic fish prey. Although there was variability in the total number of samples examined, we classify a FO value greater than 25% as an "important" prey item. For four dolphin species, Northern right whale dolphin *Lissodelphis borealis*, short-beaked common dolphin *Delphinus delphis delphis*, Pacific white-sided dolphin *Lagenorhynchus obliquidens*, and long-beaked common dolphin *Delphinus delphis bairdii*, 89, 86, 48, and 29% of samples, respectively, contained mesopelagic fish prey. Pelagic squids also appear to rely on mesopelagic fishes as prey, with four of the five squid taxa in the database containing percentages of mesopelagic fish in diet samples greater than 25%: Armhook squid Gonatidae spp., (75%) Cock-eyed squid Histioteuthis spp. (55%), Humboldt squid *Dosidicus gigas* (52%), and Hooked squid Onychoteuthidae spp. (38%). Additionally, Silvergray rockfish *Sebastes brevispinis* (52%), Bigeye thresher shark *Alopias superciliosus* (51%), and Broadbill swordfish *Xiphias gladius* (50%) all had a prevalence of mesopelagic fishes of 50% of samples or greater (Figure 1B and Supplementary Table S2). Just below our 25% criteria, Albacore *Thunnus alalunga* (19%) and Canary Rockfish *Sebastes pinniger* (19%) had a relatively high frequency of mesopelagic prey in their diet samples followed by the Sandpaper skate *Bathyraja kincaidii*, Pacific Ocean perch *Sebastes alutus* and Bluefin Tuna *Thunnus orientalis*, which each had a percent FO of 16% followed by Northern fur seal *Callorhinus ursinus*, 15% FO.

In addition, 36 total predator taxa in the CCTD database had a minimum of one record of a mesopelagic fish in their diet. This included six of the seven marine mammal species, 19 bony fishes including: swordfish, tuna, and salmon species, seven elasmobranchs and four of the five squid taxa, indicating that mesopelagic fish may be an occasional prey source for an even greater diversity of predators in the California Current. When we compare the contribution of mesopelagic fish with that of coastal pelagic fish species in the diet of predators, there were 21 taxa for which mesopelagic fishes were more frequently encountered in the diet than all coastal pelagic fish species combined and included: Northern right whale dolphin *Lissodelphis borealis*, short-beaked common dolphin *Delphinus delphis*, Armhook squid Gonatidae, Cock-eyed squid Histioteuthidae, Humboldt squid *Dosidicus gigas*, Silvergray rockfish *Sebastes brevispinis*, Bigeye thresher shark *Alopias superciliosus*, Broadbill swordfish *Xiphias gladius*, Pacific white-sided dolphin *Lagenorphynchus obliquidens*, and others; see Supplementary Table S3 for full list.

Myctophids were the most common family of prey, eaten by the greatest diversity of predator taxa, 32 in total (Figure 3), although we are not able to resolve whether this is a result of their abundance within the mesopelagic zone or predator selectivity. Myctophids comprised the top 8 most frequently encountered prey items according to the highest resolution taxon categories, and when aggregated by family, Myctophids were the dominant mesopelagic prey (Figure 3), occurring in the diets of 2,621 unique predators and not considering the actual count of individuals per predator or multiple species of Myctophid per diet sample. It was not possible to identify all Myctophids to species, such that 939 of a total of 4,372 Myctophid records were only identified to family. Of those Myctophids that were identified to 15 species, the following occurred in the greatest number of unique diet samples (Figure 2C): Northern lampfish *Stenobrachius leucopsarus* (~20%), Bigfin lanternfish *Symbolophorus californiensis* (16%), Blue lanternfish *Tarletonbeania crenularis* (15%), California headlightfish *Diaphus theta* (13%), Dogtooth lampfish *Ceratoscopelus townsendi* (10%), Broadfin lampfish *Lampanyctus ritteri* (9%), Mexican lampfish *Triphoturus mexicanus* (9%), Sunbeam lampfish *Lampadena urophaos* (5%), and California flashlightfish *Protomyctophum crockeri* (3%). The remaining taxa comprising less than 1% of the identified Myctophid samples.

While Myctophids had the greatest number of predator species and FO, likely attributable to their abundance, our work also highlights the prevalence of additional mesopelagic fish families (Figure 3): Paralepididae (Barracudina) occurred in 526 individual diet samples from 12 predator taxa, followed by Bathylagidae (Deep-sea smelts), 482 individual samples from 14 predator taxa, Microstomatidae (Pencil smelts), 147 samples from 12 predator taxa, Melamphaidae (Ridgehead), 66 samples from five predator taxa, Scopelarchidae (Pearleye), 66 samples from four predator taxa and Stomiidae (Dragonfishes), 52 samples from seven predator taxa. The remaining families represented less than 1% of the total number of diet samples. While some predator taxa consumed a limited number of mesopelagic fish taxa, other predator species consumed a wide diversity of mesopelagic taxa. Of the predators in our database, Humboldt squid *Dosidicus gigas* consumed the greatest number of mesopelagic taxa (30), followed by California Sea lion *Zalophus californianus* and short-beaked common dolphin *Delphinus delphis delphis* (22 taxa each), Pacific hake *Merluccius productus* (21), Northern right whale dolphin *Lissodelphis borealis* (19), and Sablefish *Anoplopoma fimbria*, Albacore *Thunnus alalunga* and Bluefin tuna *Thunnus orientalis* (13 each), (see Supplementary Table S4 for complete list), indicating that while Myctophids were the dominant mesopelagic fish prey encountered, additional mesopelagic fish families were also represented in predator diets.

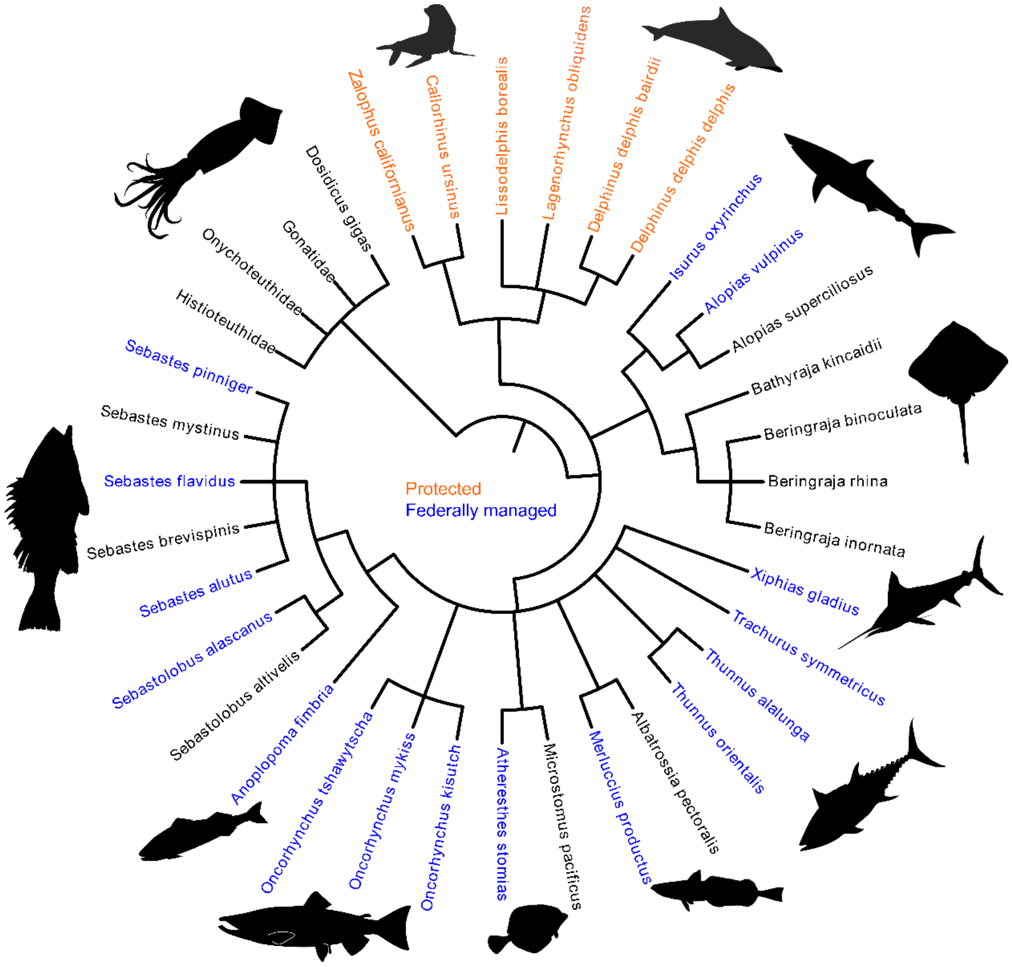
Mesopelagic predator collection records occurred over a similar geographic extent as those of all predator collections, ranging from British Columbia south to Baja and out into the North Pacific Gyre (see Figure 4). The proportion of collection records with predators that had consumed mesopelagic prey was greatest in deep waters, 40% (bottom depths > 1000 m), followed by 29% for slope collections (bottom depths of 200–1000 m). These values were similar to the 36% observed from scat sample records collected onshore at marine mammal colonies. Contrastingly, but not surprising, given the deeper distribution of mesopelagic fishes, was the relatively small percentage (2%) of predator collection records that had consumed mesopelagic fish from bottom depths associated with the shelf (0–200 m); see Figure 4 inset.

The species composition of mesopelagic predators varied across habitats. The collection location of predators that had consumed mesopelagic fish was greater in deep habitat (bottom depths > 1000 m) for short-beaked common dolphin *Delphinus delphis delphis*, cock-eyed squid Histioteuthidae, Shortfin mako shark *Isurus oxyrinchus*, Northern right whale dolphin *Lissodelphis borealis*, Longspine thornyhead *Sebastolobus altivelis*, Albacore *Thunnus alalunga*, Pacific bluefin tuna *Thunnus orientalis*, and Broadbill swordfish *Xiphias gladius* (for those taxa with at least 10 diet samples collected, see Figure 5). This contrasted to predator taxa whose greatest number of collections containing mesopelagic fish prey occurred over the slope (bottoms depths from 200 to 1000 m): Bigeye thresher shark *Alopias superciliosus*, Common thresher shark *Alopias vulpinus*, Sablefish *Anoplopoma fimbria*, Sandpaper skate *Bathyraja kincaidii*, Humboldt squid *Dosidicus gigas*, and Pacific hake *Merluccius productus*. Longnose Skate *Beringraja rhina*, Chinook Salmon *Oncorhynchus tshawytscha*, Pacific Ocean perch *Sebastes alutus*, Silvergray Rockfish *Sebastes brevispinis*, and Canary Rockfish *Sebastes pinniger* were unique in having the greatest number of collections with mesopelagic prey occur over shelf depths (bottom depths from 0 to 200 m), shallower than the distribution of most mesopelagic fish species.

The comparison of length frequencies between mesopelagic and coastal pelagic fish prey revealed substantial overlap but with a mesopelagic fish length peak occurring at shorter lengths than coastal pelagic prey (Figure 6B); mesopelagic fish lengths were centered around ~50 mm (5 cm), while coastal pelagic species around ~125 mm (12.5 cm). In general, the range of length values for coastal pelagic and mesopelagic fishes were similar (11–466 mm for mesopelagic fish and 2–505 mm for coastal pelagic fish), but most mesopelagic fishes that were consumed by predators in our database were smaller than coastal pelagic fish species. When we compared length frequencies by mesopelagic fish family (for those families with at least 10 length samples available) (Figure 6A), there were disparities among families, with fishes from Bathylagidae and Myctophidae peaking around 50 mm (5 cm), and Microstomatidae, Paralepidiade, and Tetragonuridae peaking at greater lengths: ~175 mm (17.5 cm) for Microstomatidae/Paralepidade and ~300 mm (30 cm) for Tetragonuridae, indicating that distinct mesopelagic fish families cannot be easily categorized into one size class. For a full breakdown of mean SL per taxa, see Supplementary Table S5.

1.5 Figures

A


Protected
Federally managed
Zalophus californianus
Callorhinus ursinus
Lissodelphis borealis
Lagenorhynchus obliquidens
Delphinus delphis bairdii
Delphinus delphis delphis
Isurus oxyrinchus
Alopias vulpinus
Alopias superciliosus
Bathyraja kincaidii
Beringraja binoculata
Beringraja rhina
Beringraja inornata
Xiphias gladius
Trachurus symmetricus
Thunnus alalunga
Thunnus orientalis
Albatrossia pectoralis
Merluccius productus
Microstomus pacificus
Atheresthes stomias
Oncorhynchus kisutch
Oncorhynchus mykiss
Oncorhynchus tshawytscha
Anoplopoma fimbria
Sebastolobus altivelis
Sebastolobus alascanus
Sebastes alutus
Sebastes brevispinis
Sebastes flavidus
Sebastes mystinus
Sebastes pinniger
Histioteuthidae
Onychoteuthidae
Gonatidae
Dosidicus gigas

B

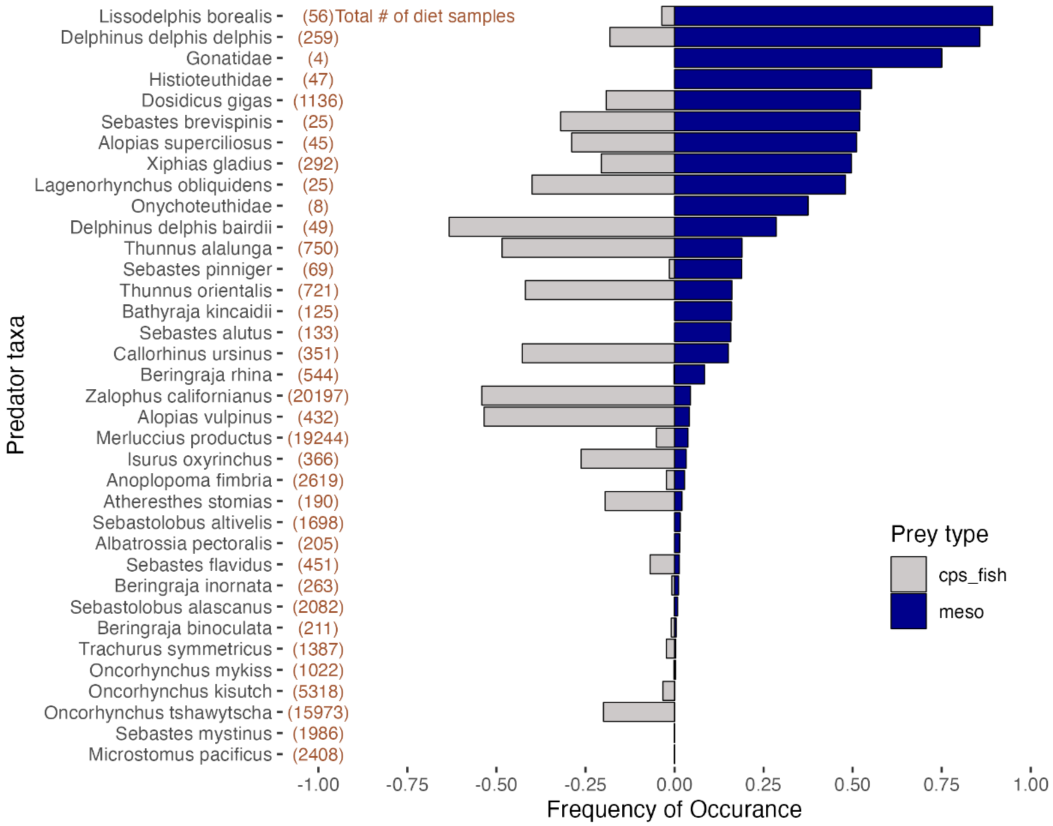


Figure 1 (A) Phylogeny of predator taxa that consumed a minimum of one mesopelagic fish prey. In total 36 predator taxa had mesopelagic fishes in their diet samples, equivalent to ~25% of all predator taxa within the California Current Trophic Database (CCTD). Of those predator species, 16 are federally managed or under international agreement (shown in blue), and six are protected marine mammal species (orange) or in the case of specific Salmonid stock/species both federally managed and protected. (B) FO of mesopelagic (blue) and coastal pelagic (gray) fish prey. The top 11 predator taxa had FO values greater than 0.25 (or 25% of all individuals within these taxa had consumed mesopelagic prey), indicating mesopelagic fish may be especially important for these predator taxa.

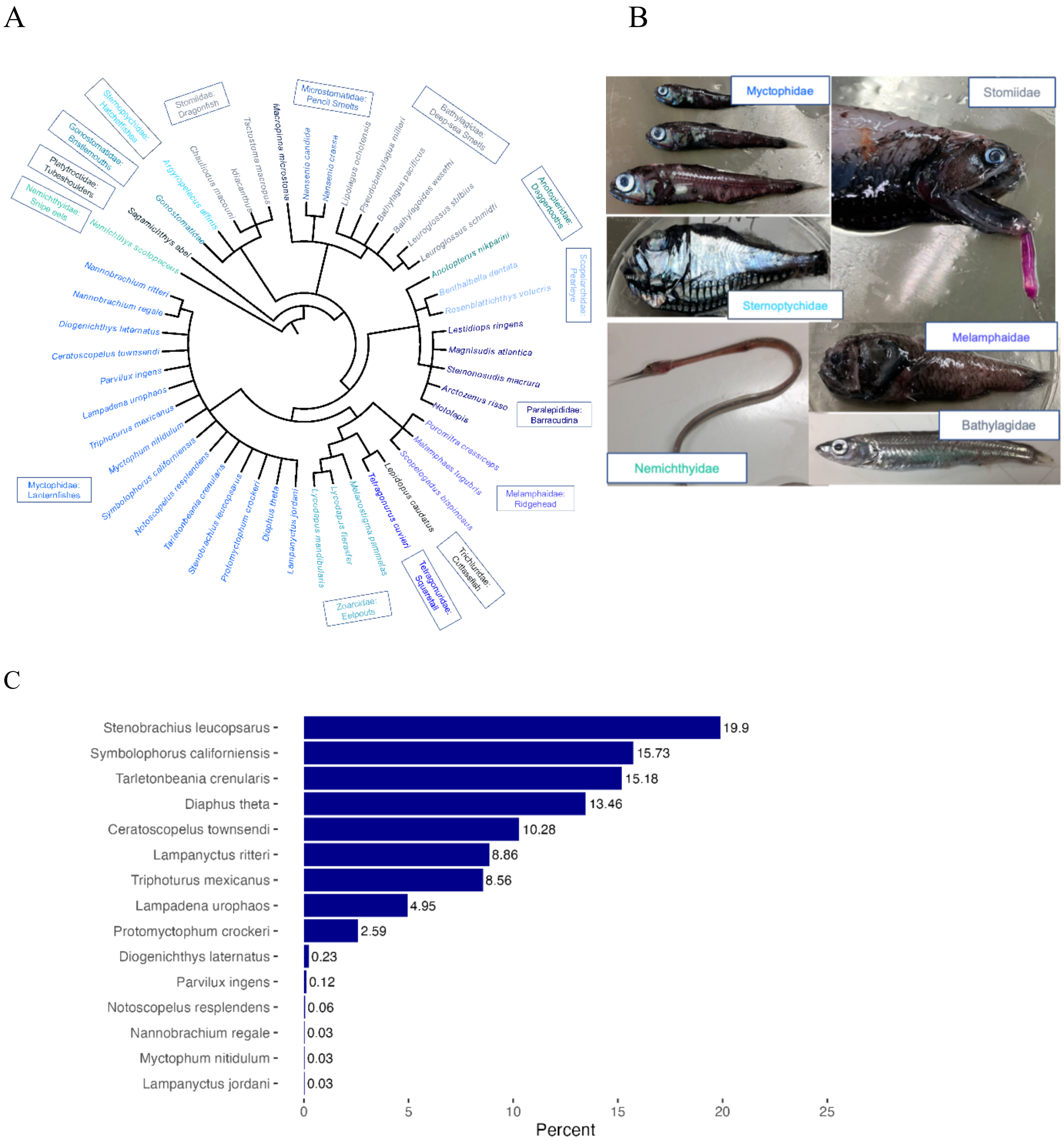


Figure 2 (A) Phylogeny representing the diversity of mesopelagic fish prey found in predator diet samples. (B) Pictures of representative families of mesopelagic families. (C) Of those fishes from the Myctophidae family that were identified to species, the most abundant Myctophid species as percent of total identified Myctophids.

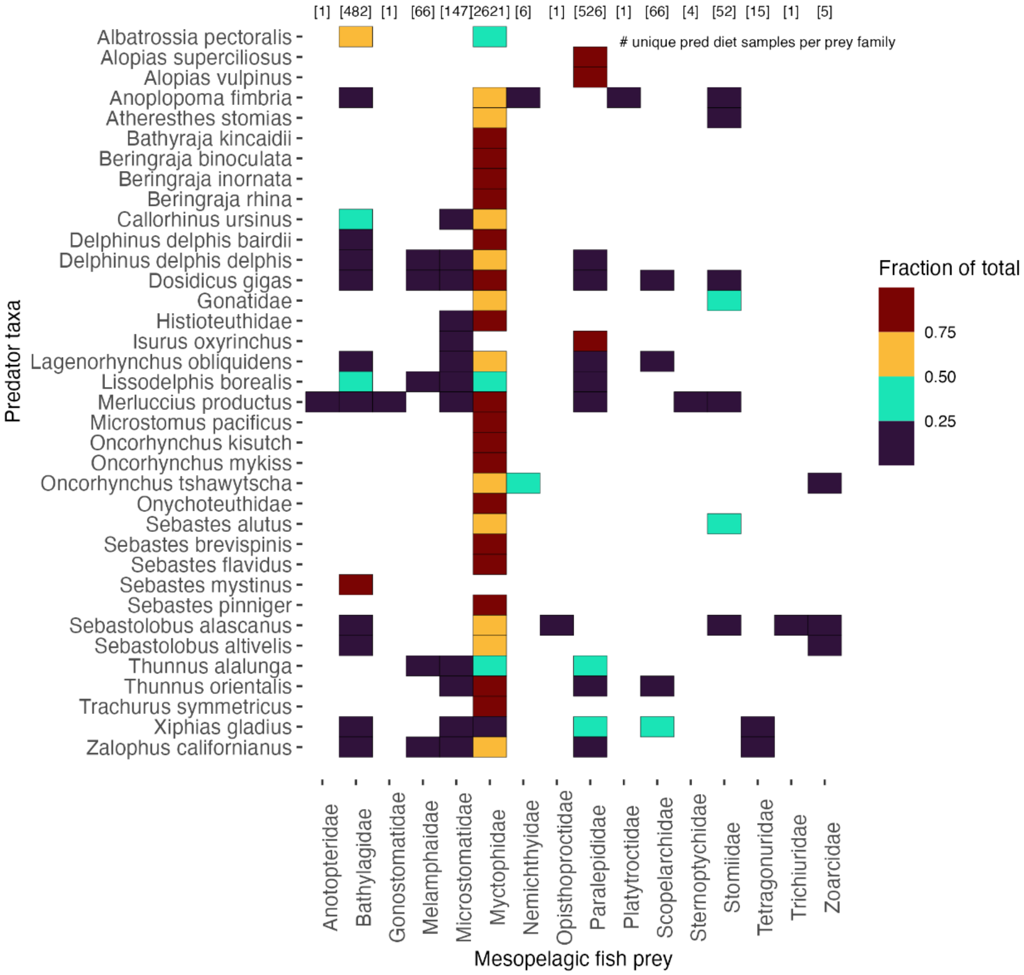


Figure 3 Diversity of mesopelagic fish prey consumed by predators within the CCTD depicted as the proportion of mesopelagic prey consumed for a given predator taxa. Myctophids had the greatest number of predators (32), followed by Bathylagids (14), Paralepididae and Microstomatidae (12 each), Melamphidae (5), Scopelarchidae (Pearleye) (4), and Stomiidae (7). Myctophids were also consumed by the greatest number of unique predators (2,621) followed by Paralepididae (526) and Bathylagidae (482) among others.

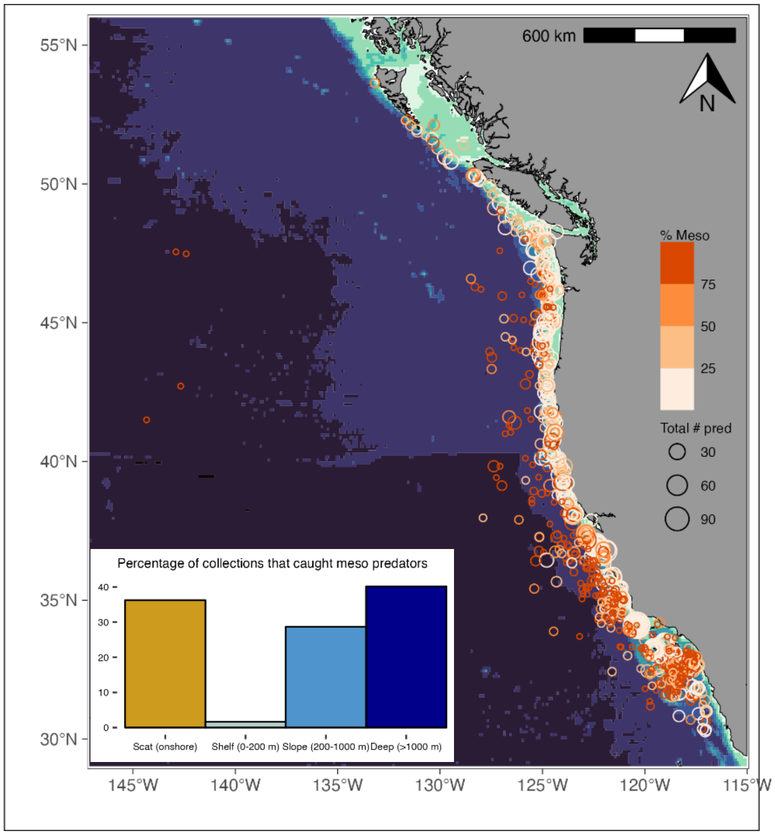


Figure 4 Map describing the location where predator collections occurred. Circle size corresponds to the number of predators captured at a given location while color describes the proportion of those predators that had consumed mesopelagic prey. Figure 4 inset: Depth distribution of predator collections that had consumed mesopelagic prey. Depths correspond to bottom depths.

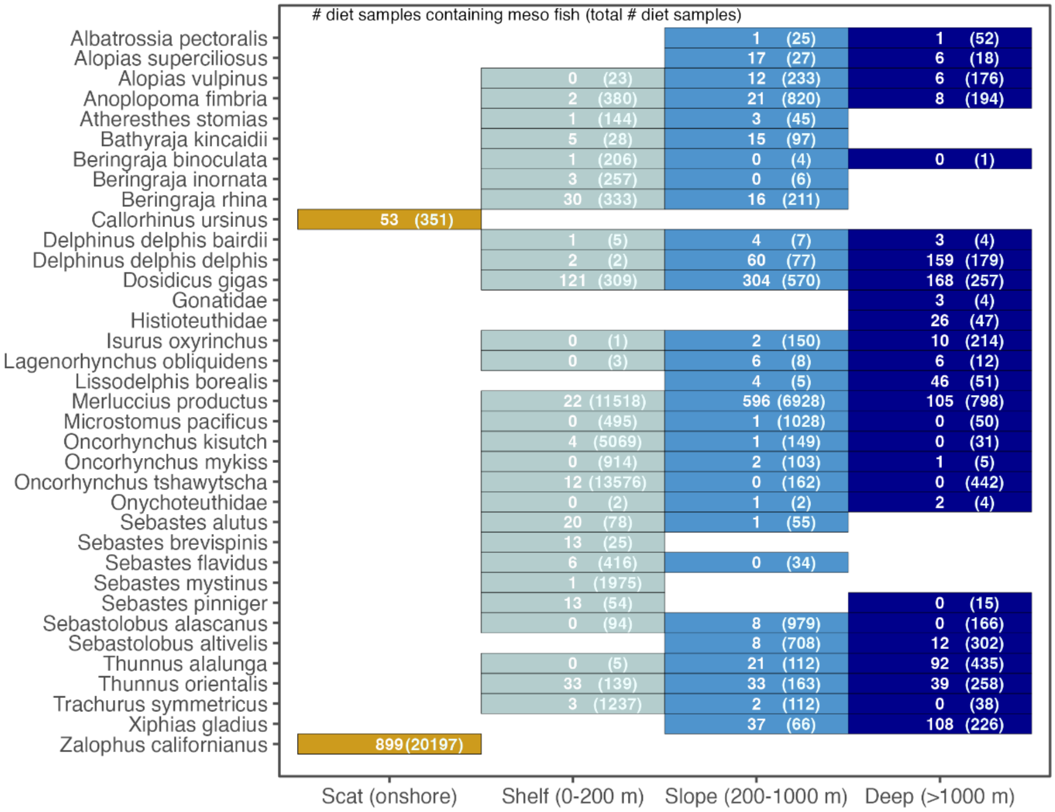


Figure 5 Comparison of predator composition (for those predator taxa that consumed mesopelagic fish in our database), across habitat types defined by bottom depth. For each habitat type, the total number of diet samples that contained mesopelagic fish prey and the total number of diet samples collected for that predator taxa (in parentheses) are displayed. Note that these values do not necessarily reflect the *total* number of diet samples collected, just those that had collection position information available in the database.

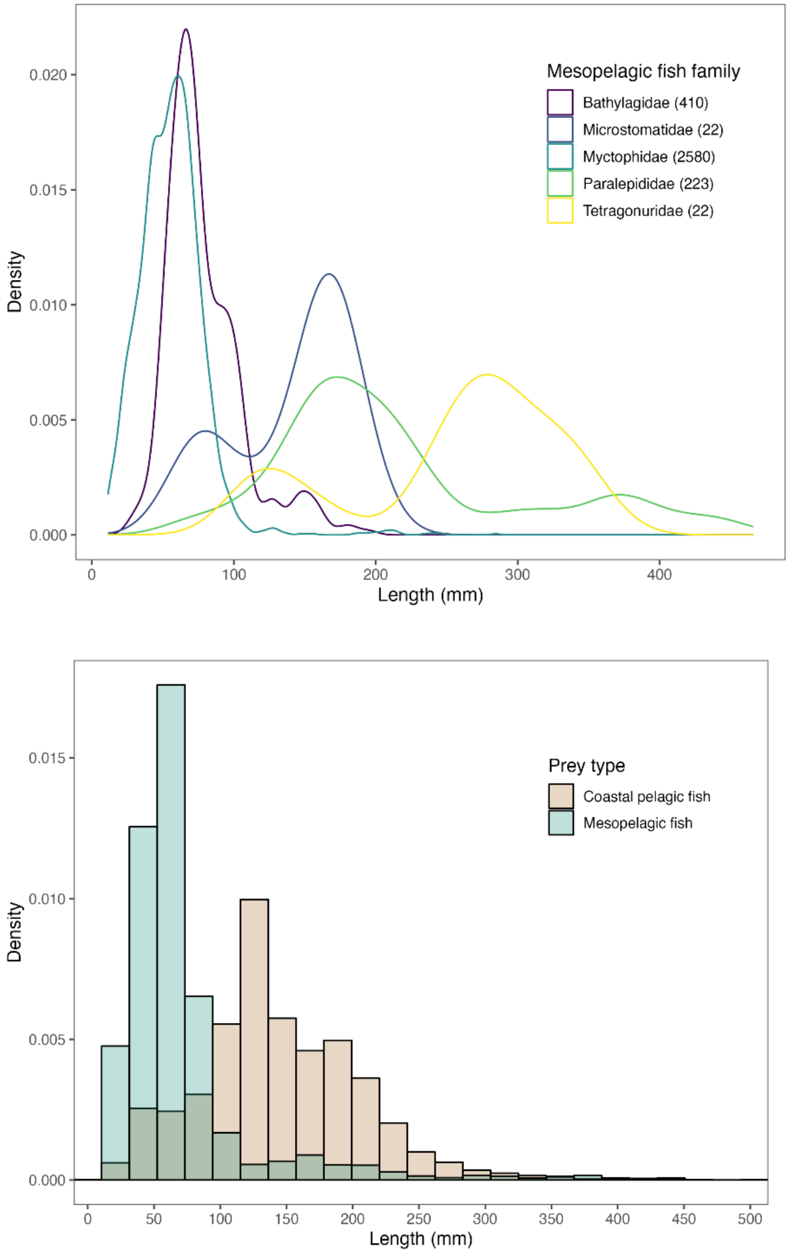


Figure 6 (A) Mesopelagic fish length values by family, for those families with at least 10 length measurements available. (B) A comparison of length frequencies for mesopelagic and coastal pelagic fish prey for those predator species that consumed mesopelagic prey. All length values are reported in mm from standard lengths and were either measured directly, back-calculated, or estimated from either TL or FL measurements.

1.6 Discussion

Our study represents an important step in the use of compiled diet data from numerous existing predator diet studies to evaluate the importance of mesopelagic fish as prey at the scale of a large marine ecosystem. In total, 25% of all 143 predator taxa in the CCTD consumed a minimum of one mesopelagic fish, including economically important fishery species such as bluefin tuna (16% of samples), albacore (19%), swordfish (50%), Humboldt squid (52%) and Pacific hake (4%). Mesopelagic fishes were also prevalent in the diet of marine mammals, occurring in four species greater than 25% of the time (Dolphins and Pinnipeds). For 11 of these predator taxa, mesopelagic fishes occurred in more than 25% of all individuals examined, and thus likely represent an important source of prey. The diversity of evolutionary and ecological niches represented among these 11 predator taxa [four pelagic squid, a shelf-edge associated rockfish, *Sebastes brevispinis*, two vertically migrating pelagic predators (the Bigeye thresher shark *Alopias superciliosus* and Broadbill swordfish *Xiphias gladius*), and four species of dolphins], suggest that mesopelagic fishes are important across a variety of trophic levels and habitats. The CCTD includes data for a limited number of predator species and does not currently account for many deep water predator species, especially mesopelagic dwelling predators, who are known to prey on mesopelagic fishes (Dufault et al., 2009; Choy et al., 2013). The CCTD does not yet include data from seabirds, which are also significant global predators of mesopelagic fishes (Watanuki and Thiebot, 2018), so our assessment is still incomplete for the California Current. Finally, although invertebrate prey were accounted for in the CCTD database and there is evidence that mesopelagic invertebrates (e.g., Gonatidae squid and Sergestidae shrimp) are important components of the forage base for higher trophic level predators in the California Current (Szoboszlai et al., 2015), we did not include them in our study. Thus, although our results demonstrate the value of mesopelagic fishes as prey to higher level predators, the true contribution of mesopelagic organisms to the ecosystem is likely underestimated.

Mesopelagic fishes inhabit daytime depths of ~200–1000 m, so we would expect predators of mesopelagic fish to forage over bottom depths at least this great. Indeed, we found the proportion of collection records with predators that had consumed mesopelagic prey to be greatest in deep waters; 40% in waters with bottom depths greater than 1000 m and 29% over the slope (bottom depths between 200 and 1000 m). As neritic prey decreases with increasing distance offshore, mesopelagic fishes may play an increasing role as prey to predators foraging further offshore. Of the 11 predator taxa with FO values of mesopelagic fish greater than 25% (i.e., those species for which we consider mesopelagic prey to be important), six of these 11 predator taxa were most often collected having consumed mesopelagic prey over deeper waters (bottom depths > 1000 m). This total increases to nine of the 11 predator taxa if we include predators that were most often collected with mesopelagic prey over the slope (bottom depth 200–1000 m). This contrasts to only one predator taxa, *Sebastes brevispinis*, that was captured exclusively over shelf depths, but still had a high incidence of mesopelagic prey. The 11th species, Pacific white-sided dolphin *Lagenorhynchus obliquidens* was collected with mesopelagic prey in similar proportions over the shelf and slope. Our comparison of predator taxa across collection habitats thus provides evidence that mesopelagic fishes are increasingly important as prey to predator taxa with increasing distance offshore.

Our results also revealed, however, that mesopelagic species were being consumed by predators collected onshore (in scat samples collected from marine mammal rookeries) and over the shelf (bottom depths 0–200 m). Nineteen predator taxa that had consumed mesopelagic prey were collected over shelf depths (Figure 5), which raises the question of how do inshore predators find mesopelagic prey? In the Main Hawaiian Islands, mesopelagic organisms can migrate up to 1.8-km onshore each night to feed (Benoit-Bird et al., 2001), during which time they are vulnerable to nocturnal, shallow predators. Predator taxa that were exclusively collected over shelf depths, indicating an unlikeliness to forage offshore in deep regions, such as three rockfish species in our analysis (Silvergray rockfish *Sebastes brevispinis*, Blue rockfish *Sebastes mystinus*, and Canary rockfish *Sebastes pinniger*), may be specifically targeting locations where mesopelagic fishes are transported. Yellowtail rockfish *Sebastes flavidus*, which were collected in both shelf and slope habitats, but that had only consumed mesopelagic fishes over shelf depths, for example, have been observed preying upon large numbers of Myctophid transported from adjacent submarine canyons (Pereyra et al., 1969). Submarine canyons are a common feature of the U.S. west coast shelfbreak where they facilitate the concentration and persistence of krill abundance hotspots (Santora et al., 2018). Myctophids, many of which prey upon krill, are known to aggregate along submarine canyon walls (Bosley et al., 2004). Research has shown that abrupt topographic features, including canyons, but also including banks, pinnacles, and other shelf features, can aggregate and trap mesopelagic zooplankton and fishes, making them more susceptible to predation (Isaacs and Schwartzlose, 1965; Genin et al., 1988; Genin, 2004) and provide opportunities for predators around these features to encounter mesopelagic prey. Predators collected over the shelf break such as Pacific hake *Merluccius productus* in our study (Figure 5), where there is a high diversity and abundance of mesopelagic fishes (Pearcy, 1964), may likewise be intercepting mesopelagic fishes trapped after getting transported during vertical migration from deeper depths, as was documented for European hake *Merluccius merluccius* residing along shelf breaks in the Western Mediterranean (Cartes et al., 2009). In the Southern Ocean, during high wind periods, Myctophids have been advected onto shelf regions where they are likewise consumed by land-based predators (Perissinotto and McQuaid, 1992). It is likely that a similar mechanism is responsible for conveying mesopelagic prey to shelf associated predators in our study, although more research in this area would be beneficial.

So far, we have discussed mechanisms whereby mesopelagic fish and predator interactions are facilitated by the daily vertical migration of mesopelagic fishes into the upper water column. Also referred to as “running the gauntlet” of predators (Robison et al., 2020), the daily movement of mesopelagic organisms into the upper water column over distances upwards of hundreds of meters is assumed to be a tradeoff between increased prey availability in surface waters and avoiding predation by visual predators during the day. While it is estimated globally that ~50% of mesopelagic organisms undergo vertical migration, up to 90% are estimated to migrate in the Eastern Pacific where our study takes place (Klevjer et al., 2016). Many species of Myctophids (Lanternfishes), the most frequently encountered mesopelagic prey in our study, migrate vertically (Watanabe et al., 1999; Brodeur and Yamamura, 2005), although there is considerable variability among species and life stages. For those groups of mesopelagic fishes that do not migrate vertically or for migrating species at mesopelagic depths during the daytime, there is still the risk of predation by deep-diving predator taxa. In the CCTD, we did not have sufficient data about the capture depth of predators to infer foraging depths, but for some predator taxa, we know that individuals forage consistently at mesopelagic depths. Broadbill swordfish *Xiphius gladius*, for example, which have a FO of mesopelagic fishes in their diet of ~50% are known to target deep-scattering layers when foraging (Dewar et al., 2011) and can dive to depths of up to 2878 m (fishbase.org). One limitation of our study is the bias within the CCTD toward nearshore and epipelagic predators (Figure 4), which likely leads to an underestimation of the role of non-migrating mesopelagic fishes in predator diets. For example, Gonostomatidae (Bristlemouths), considered one of the most abundant families of mesopelagic fishes in the world, were only represented in our database by a single predator record. While this could be attributed to the inherent difficulty in identification, due to the fragile nature of these fish, more likely Gonostomatidae play an increasingly important role as prey to deeper water predator communities that were not included in the diet database. Future work would benefit from the inclusion of diet data from deeper dwelling predatory species.

While Myctophids dominated the mesopelagic prey in our study in terms of FO and diversity of predators that consumed them, it was beyond the scope of this study to examine whether this was a function of predator selectivity or the abundance of Myctophids within the mesopelagic zone. Research indicates that Myctophids likely dominate the biomass of mesopelagic fishes within the Southern California Current (Davison et al., 2015), so their prevalence in the diets of predators in our study is likely due to this abundance more than any predator selectivity. While our results highlight the importance of Myctophids to predator diets, we additionally described 16 families of mesopelagic fishes encountered in predator diets, highlighting the diversity of species inhabiting mesopelagic depths and the need to account for the complexity of the mesopelagic community more appropriately when evaluating the role of mesopelagic fishes in the broader ecosystem. Previous work to characterize predator-prey interactions within the California Current, for example, have exclusively considered Myctophids (Szoboszlai et al., 2015), or Myctophids and Viperfish (Dufault et al., 2009) to describe mesopelagic forage. Likewise, ecosystem models for the California Current, which can be used to evaluate the dependence of top predator populations on their forage base (Smith et al., 2011), often include a single functional group to describe mesopelagic fishes (Field et al., 2006; Horne et al., 2010; Kaplan et al., 2013). As the 16 mesopelagic families in our study inhabitant distinct depths and likely respond to oceanographic variability in distinct ways, reducing this complexity to a single functional group could reduce our ability to interpret the impact of any changes to the mesopelagic zone on higher trophic level predators. Furthermore, for taxa with consistent diet data available over decadal timescales, it could be possible to identify shifts in the mesopelagic community in response to ocean climate variability and even develop a standardized mesopelagic indicator index for ecosystem assessment and function. There is considerable uncertainty in current ecosystem-based models regarding the effect of changing mesopelagic fish populations on higher trophic level predators. For example, when Kaplan et al. (2013) estimated the effect of reducing mesopelagic fish on Albacore populations using two different models, declining mesopelagic fish either had no effect or reduced Albacore populations by over 20% depending on the dependence of Albacore on mesopelagic fishes. By incorporating a diversity of mesopelagic fish species previously not considered and refining our understanding of the importance of mesopelagic prey to specific predator taxa, our study expands our collective understanding of trophic interactions between mesopelagic fishes and their predators, thereby supporting basic needs for the monitoring and modeling of ecosystem function now and into the future.

The U.S. National Marine Fisheries Service protects unfished forage fish along the U.S. West Coast, including mesopelagic fishes from the families:

Myctophidae, (Lanternfish) Bathylagidae (Deep- sea smelt), Paralepididae (Barracudina), and Gonostomatidae (Bristlemouths) (50 CFR §660.5-.6), members of which were found in the diets of predators in our study. Similar to a ban on fishing krill in federal waters [50 CFR §660.505(o)], this move recognizes the value of protecting a diverse forage base for higher trophic predators, specifically salmon, groundfish and highly migratory species. Our study provides evidence that this decision is justified, given the presence of mesopelagic fishes in the diets of each of these management units (salmon, groundfish, and highly migratory species). Our results further indicate that this action would protect a considerable amount of mesopelagic biomass, as 96.6% of all mesopelagic fish taxa counted from unique predator diet samples were from protected families. However, only ~56% of mesopelagic species identified in the database are from protected mesopelagic fish families, meaning there are many species still within the mesoepelagic zone that are not named for prohibitions on future fisheries. The families Microstomatidae, Melamphaidae, Scopelarchidae, and Stomiidae, for example, are not currently included in the ban, although they account for some of the most frequently encountered mesopelagic fish families after Myctophids, Paralepididae, and Bathylagidae. These species are protected, however, by a more general ban on the use of the type of net gear that would be needed to catch mesopelagic fish [50 CFR §600.725 (v)]. Furthermore, while National Marine Fisheries Service regulations safeguard mesopelagic fishes within federal waters (3- 200 nautical miles from shore), most mesopelagic habitat lies outside national jurisdiction in the high seas. Although these areas beyond national jurisdiction are overseen by the UN Convention on the Law of the Sea, currently there are inadequate provisions for governing potential emerging mesopelagic fisheries (Wright et al., 2020; Gjerde et al., 2021).

Our results demonstrate that the contribution of mesopelagic fishes to the diets of top predators is more diverse than what was previously known. Mesopelagic fishes are important prey to a diversity of higher trophic level predators, including 11 taxa, mostly caught over bottom depths > 200 m, which had mesopelagic fishes present in over 25% of all diet samples examined. Mesopelagic fishes were also found in diet samples of predator taxa collected over shallower depths (onshore to 200 m), highlighting the interconnectedness of mesopelagic fishes to nearshore and epipelagic habitats and predators. Changes in the availability of mesopelagic prey to higher trophic level predators, especially as a result of climate change, could have bioenergetic consequences, impacting economically valuable fisheries and protected species. Mesopelagic ecosystems are chronically under studied (St. John et al., 2016; Martin et al., 2020) and the response of mesopelagic fishes to oceanographic variability is still uncertain, especially for many less studied species and at different life stages [as most mesopelagic fishes inhabit epipelagic depths as larvae (Ahlstrom, 1969)]. Our study utilized a publicly available database to provide an ecosystem-level assessment of the importance of mesopelagic fishes to the predator community of the California Current and highlights the need to incorporate mesopelagic fishes into future management.

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1.1 Supplementary Information

Supplementary Table 1 A list of all mesopelagic prey taxa from the CCTD database with information on available depth distributions.

Family	*Scientific Name*	Common Name	Depth category	Min Depth	Max Depth	Ref	Comments
Anotopteridae	*Anotopterus nikparini*	North Pacific daggertooth	mesopelagic	0	2750	Miller & Lea 1972, Fishbase	usually 0-700m (Fishbase). Miller & Lea: only species in guide for Antopteridae family, *Anotopterus pharao* listed as "mesopelagic." Since *pharao* does not appear to be in the Pacific, likely *nikparini?* Either way, based on the "usual" depth distribution (0-700m), considering this spp to be mesopelagic.
Bathylagidae	*Bathylagidae*	Family: Deep-sea smelt	mesopelagic, upper bathypelagic			Priede 2017	Priede: "The Bathylagidae are planktivorous fishes of the mesopelagic or upper bathypelagic."
	Bathylagoides wesethi	Snubnose blacksmelt	mesopelagic	25	1130	fishbase	Miller & Lea 1972: "Mesopelagic, from approximately 130- 3281 ft."
	Bathylagus pacificus	Slender blacksmelt	mesopelagic	600	7700	fishbase	usually 600-800 (Fishbase). Miller & Lea: "Mesopelagic, 490 to over 3280 ft."
	Leuroglossus	Genus: Smoothtongue	mesopelagic, upper bathypelagic			Priede 2017	Priede: Because the family Bathylagidae described as "mesopelagic or upper bathypelagic," we use that broad description for this genus.
	Leuroglossus schmidti	Northern smoothtongue	mesopelagic, bathypelagic	394	1800	fishbase	
	Leuroglossus stilbius	California smoothtongue	mesopelagic	25	850	fishbase	Miller & Lea: "Mesopelagic, from near surface to 2264 ft. Abundant in offshore waters"

	Lipolagus ochotensis	Eared blacksmelt	mesopelagic, bathypelagic	930	6100	fishbase	
	Pseudobathylagus milleri	Stout blacksmelt	mesopelagic, bathypelagic	550	6600	fishbase	
Gonostomatidae	*Gonostomatidae*	Family: Bristlemouths	mesopelagic, bathypelagic			Eschmeyer 1983	Eschemeyer: "Found in deep midwaters of all temperate and tropical seas." Priede: "widespread occurrence down to an average maximum depth of over 2500m" also lists Cyclothone species depths between (300 - 2700m), so they cover mesopelagic depths and deeper
Melamphaidae	*Melamphaes*	Genus: Bigscales	mesopelagic, bathypelagic			Fishbase	Eschemeyer: Family Melamphaidae: "Adults are usually bathypelagic, young shallower." Miller & Lea: the two Melapmphaidae species listed were not from this family, but both mesopelagic. Because the one representative species from this genus in our database is Melamphaes lugubris with depth usually 200-500m in Fishbase, going with mesoepalgic + bathypelagic
	Melamphaes lugubris	Highsnout melamphid	mesopelagic	50	3400	fishbase	usually 200-500m (Fishbase)
	Poromitra crassiceps	Crested bigscale	mesopelagic, bathypelagic	164	2730	fishbase	usually 750-2730m (Fishbase)
	Scopelogadus bispinosus	Twospine bigscale	mesopelagic, bathypelagic	200	4000	fishbase	

Microstomatidae	*Nansenia*	Genus: Pencil smelts	mesopelagic			Priede 2017	Priede 2017: "Family: The Microstomatidae are slender-bodies silvery mesopelagic fishes" Based on literature reference: Poulsen 2015 Zootaxa "They are all small-mouthed elongated fishes separated primarily on continuous characters and usually found in the mesopelagic realm between 200 and 1000m". While it is possible that other depths occur, because of this general genus description and the evidence that both representative spp in the database are mesopelagic, I am going to identify as mesoepalgic here.
	Nansenia candida	Bluethroat argentine	mesopelagic, bathypelagic	83	1800	fishbase	
	Nansenia crassa	Stout argentine	mesopelagic	0	865	fishbase	Fishbase depth category originally listed as “benthopelagic” (which feels like a contradiction). But based on other species in this group and the general description of the family as “mesopelagic” in Priede, using category “mesopelagic” here.
Myctophidae	*Ceratoscopelus townsendi*	Dogtooth lampfish	mesopelagic	100	500	fishbase	
	Diaphus theta	California headlightfish	mesopelagic	10	3400	fishbase	usually 10-400m (Fishbase). Miller & Lea 1972: "Mesopelagic, surface to 2600 ft, usually below 600 ft"
	Diogenichthys laternatus	Diogenes lanternfish	mesopelagic, bathypelagic	0	2091	fishbase	
	Lampadena urophaos	Sunbeam lampfish	mesopelagic	50	1000	fishbase	Listed as "pelagic-oceanic" in fishbase but from the family Myctophidae and in mesopelagic depth range, so identifying as mesopelagic here
	Lampanyctus	Genus: Lanternfish	mesopelagic, bathypelagic			Miller & Lea 1972, Fishbase	The one representative species in Miller and Lea, Lampanyctus ritteri, described as “Mesopelagic, from 165 to 3600ft”, so includes mesopelagic, and because range of Lampanyctus jordani from Fishbase extends to 3400m, also including bathypelagic.

	Lampanyctus jordani	Brokenline lanternfish	mesopelagic, bathypelagic	588	3400	Fishbase	
	Lampanyctus ritteri	Broadfin lampfish	mesopelagic	20	1095	Fishbase	Miller & Lea: "Mesopelagic, from 165 to 3600 ft"
	Myctophidae	Family: Lanternfishes	mesopelagic, and bathypelagic			Priede 2017	Priede: "They are small fishes, mean maximum length 92cm and are dominant in epipelagic, mesopelagic and bathypelagic environments." Eschemeyer 1983 Family description: "Lanternfishes occur in all oceans. Nearly all of these are oceanic, living at moderate to deep depths during the day and migrating to or near surface at night."
	Myctophum nitidulum	Pearly lanternfish	mesopelagic, bathypelagic	412	1537	fishbase	
	Nannobrachium regale	Pinpoint lampfish	mesopelagic, bathypelagic	772	3400	fishbase	usually 500-?m (Fishbase)
	Notoscopelus resplendens	Patchwork lampfish	mesopelagic, bathypelagic	777	2121	fishbase	
	Parvilux ingens	Giant lampfish	mesopelagic	100	500	fishbase	Listed as pelagic-oceanic in Fishbase .
	Protomyctophum	Genus: Lanternfishes	mesopelagic			Priede 2017	Priede defines the family Myctophidae as "epipelagic, mesopelagic and bathypelagic." This genus is mentioned: "...three species to the Pacific Ocean. P. thompsoni and P. crockeri in the North Pacific and P.beckeri in the East Central Pacific. P Crockeri is a dominant species at the surface at night where it occurs in the Pacific Ocean." The one spp from Protomyctophum in Miller and Lea "Mesopelagic, to 1640 ft, rarely at surface" so choosing mesopelagic based on representative species.
	Protomyctophum crockeri	California flashlightfish	mesopelagic	100	500	fishbase	listed as pelagic-oceanic in fishbase, but Myctophid and depth range mesopelagic. From Miller and Lea "Mesopelagic, to 1640ft, rarely at surface"

	Stenobrachius	Genus: Lanternfishes	mesopelagic, bathypelagic			Priede 2017	Based on family (Myctophidae) considered to be mesopelagic. From Priede: ("epipelagic, mesopelagic and bathypelagic"). The one spp from genus Stenobrachius in Miller and Lea: “Mesopelagic, from near surface to 9500 ft”
	Stenobrachius leucopsarus	Northern lampfish	mesopelagic, bathypelagic	31	3400	fishbase	usually 31-1189m (Fishbase)
	Symbolophorus californiensis	Bigfin lanternfish	mesopelagic, bathypelagic	557	1497	fishbase	
	Tarletonbeania crenularis	Blue lanternfish	mesopelagic	0	710	fishbase	Miller and Lea: “Mesopelagic, from surface at night to 2730 ft”
	Triphoturus mexicanus	Mexican lampfish	mesopelagic	46	933	Miller & Lea 1972	Miller and Lea: “Mesopelagic, 150 to below 3060 ft.” (converted to m for reference at left). Fishbase lists depth range: 25m to NA.
Nemichthyidae	*Nemichthyidae*	Family: Snipe eels	mesopelagic and bathypelagic			Priede 2017	Priede: "...highly specialized mesopelagic and bathypelagic eels (depths down to 4580m)" From Wikipedia: "Pelagic fishes found in every ocean, mostly at depths of 300-600m but sometimes as deep as 4000m." Eschemeyer: "Delicate deepsea eels…." This family defined very clearly as mesopelagic in the article: Miller et al 2014 " Vertical body orientation by a snipe eel..."
	Nemichthys scolopaceus	Slender snipe eel	mesopelagic, bathypelagic	100	4337	fishbase	usually 100-1000m. (Fishbase) Miller & Lea "Depth 300 to 6000 ft."
Opisthoproctidae	*Macropinna microstoma*	Barreleye	mesopelagic, bathypelagic	16	1267	fishbase	Eschemeyer: "Family: great depths in midwaters--usually deeper than 500ft (152 m)”. Barreleye Macropinna microstoma "a deep pelagic species; Bering Sea to Baja at about 325-2925 ft (99-891m)". Miller & Lea: "Depth 324-2940 ft"
Paralepididae	*Arctozenus risso*	Spotted barracudina	mesopelagic, bathypelagic	0	2200	fishbase	Priede: “Arctozenus risso..widespread circumglobal species.. generally found at 200-1000m and associated with continental, island and seamount slopes” From lit (Devine and Guelpen 2020), caught in midwater trawl and mention they inhabit the deep pelagic waters

	Lestidiops ringens	Slender barracudina	mesopelagic, bathypelagic	0	3290	fishbase	Miller & Lea: "Mesopelagic." Eschemeyer: “from near surface to bathypelagic depths”
	Magnisudis atlantica	Duckbill barracudina	mesopelagic, bathypelagic	0	4750	fishbase	Listed as pelagic-oceanic, but depth range more consistent with mesopelagic+ bathypelagic. Based on wide depth category from fishbase a little unclear, but Il'inskiy, Balanov, Ivanov (Rare mesopelagic fishes...) consider this spp mesopealgic and so I will here. https://www.infona.pl/resource/bwmeta1.element.elsevier-7b28d715-9664-3d7f-ae12-9de3f4f5d356
	Notolepis	Genus: Barracudinas	mesopelagic, bathypelagic			Harry 1953	From literature, it appears this is a poorly understood taxa, but work by Harry 1953 "Studies on the bathypelagic fishes of the family Paralepididae" collected specimens (ranging from juveniles to adults) off the coast of San Diego from ~ 98m to 2743m, so going to define as mesopeaglic and bathypelagic https://www.jstor.org/stable/4064473
	Paralepididae	Family: Barracudinas	mesopelagic, bathypelagic			Priede 2017	Priede: Family Paralepididae “…deep pelagic habitat (mean maximum depth 1322 m).” Eschemeyer: Family: Paralepididae "Barracudinas occur in all temperate and tropical seas, in midwater, occasionally at surface."
	Stemonosudis macrura	Stemonosudis macrura	mesopelagic	18	330	fishbase	
Platytroctidae	*Sagamichthys abei*	Shining tubeshoulder	mesopelagic, bathypelagic	37	1500	fishbase	
Scopelarchidae	*Benthalbella*	Genus: Pearleyes	mesopelagic	500	1000	Eschmeyer 1983	Eschmeyer: Benthalbella dentata description: ”Usually at 1640-3280 ft (500-1000m)” Since this is the one spp from this genus in our database, going to use same depth category, and since the family Scopelarchidae described as mesopelagic, consistent with description.

	Benthalbella dentata	Northern pearleye	mesopelagic	500	1000	Eshemeyer	usually 500-1000m (Fishbase). Miller &Lea: “Mesopelagic”
	Rosenblattichthys volucris	Chubby pearleye	mesopelagic			fishbase	Fishbase, Biology section: “a mesopelagic species.” Consistent with family description
	Scopelarchidae	Family: Pearleyes	mesopelagic			Eshemeyer 1983	Eshemeyer: “Family Scopelarchidae: Adults are presumed to be mostly mesopelagic and bathypelagic- most live at about 1640-3280ft (500-1000m), but some are found shallower and at night possibly range near the surface” Fishbase: "Adults usually found in depths of 500-1000m; larvae usually occuring in 100-200m"
Sternoptychidae	*Argyropelecus affinis*	Pacific hatchet fish	mesopelagic	1	3872	fishbase	usually 1-600m (Fishbase). Oceanodromous. From Miller &Lea: “Mesopelagic, normally from 330-2000 ft”
Stomiidae	*Chauliodontinae*	Subfamily: Barbeled dragonfishes	mesopelagic, bathypelagic			Priede 2017	Priede: Family Stomiidae: “mean maximum depth 2303m…inhabit the mesopelagic and bathypelagic zones of the oceans” Based on this more general description of the family, using mesopelagic and bathypelagic as there isn’t much information available for this specific Subfamily
	Chauliodus macouni	Pacific Viperfish	mesopelagic, bathypelagic	25	4390	fishbase	Miller &Lea: “Depth 240-5000 ft”
	Idiacanthus	Genus: Barbeled dragonfishes	mesopelagic, bathypelagic			Eschmeyer 1983	Eschemeyer: "Deepsea fishes-- near the surface to about 6562 ft (2000m)". Priede: "Males are bathypelagic, unable to feed and presumed to be short-lived, whereas the females are active predators making extensive vertical migrations in pursuit of prey."
	Stomiidae	Family: Barbeled dragonfishes	mesopelagic and bathypelagic			Priede 2017	Priede: Stomiidae "family of 287 species of specialized deep-sea predatory fishes, mean maximum length 18 cm, mean maximum depth 2303m that inhabit the mesopealgic and bathypelagic zones of the oceans"
	Tactostoma	Genus: Barbeled dragonfishes	mesopelagic, bathypelagic			fishbase	Miller & Lea One species listed in our area, Tactostoma Macropus “Depth 102 to 1800 ft”

	Tactostoma macropus	Longfin dragonfish	mesopelagic, bathypelagic	30	2000	fishbase	Miller & Lea: “Depth 102 to 1800 ft”
Tetragonuridae	*Tetragonurus cuvieri*	Smalleye squaretail	mesopelagic	1	800	Fishbase	Miller & Lea "Depth, surface to 120 ft, but usually in greater depths well offshore. " Janssen and Harbison 1981:"Young Tetragonurus live in the upper waters, whereas adults are mesopelagic or bathypelagic and migrate to the surface waters at night (Fitch, 1951, Grey 1955, Tononaka 1957, Ahlstrom 1969). Eschemeyer: "Oceanic fishes of tropical to temperate seas.”
Trichiuridae	*Lepidopus caudatus*	Silver scabbardfish	mesopelagic	42	620	fishbase	Usually 100-300m. Eastern Atlantic distribution? Robertson 1979 recorded them spawning off coast of New Zealand, so apparently also in Pacific? Fishbase benthopelagic: living near the bottom as well as in midwaters or near the surface" From Demestre et al 1993: "mesopelagic species; it occurs along the shelf and slope down to 450m in the Catalan Sea"
Zoarcidae	*Lycodapus fierasfer*	Blackmouth eelpout	mesopelagic, bathypelagic	50	2212	fishbase	Miller& Lea: " Depth 162 to 6486 ft" Based on study by Sinclair and Stabeno 2002 (Dee-sea Reesearch II) *Mesopelagic nekton and associated physics of the southeastern Bering Sea,* in which they did a series of trawls at mesopelagic depths and this spp was listed as catch at 1000m.
	Lycodapus mandibularis	Pallid eelpout	mesopelagic	100	1370	fishbase	Eschemeyer: "Habitat: midwater, from near surface at night to about 2625 ft (800m) during the day; sometimes captured in bottom trawls but definitely a pelagic species". Love 2011: "This is a midwater, mesopoelagic species found in 96-1237m. Some individuals migrate vertically into shallower waters at night. " Fishbase: “Occurs in midwater, from near surface at night to about 800m during the day” Miller & Lea “Depth 192 to 1758 ft”
	Melanostigma pammelas	Midwater eelpout	mesopelagic, bathypelagic	96	2195	Miller & Lea 1972	Fishbase: (450m-?) Usually 699-?m Eschemeyer: "Pelagic in deep coastal waters at 314-3937 ft (96-1200m) or deeper" Miller & Lea: “Depth 314 to 7200 ft. The only pelagic California eelpout”

Supplementary Table 2 Predator taxa that had a FO of mesopelagic fish 15% (0.15) or greater

Predator scientific name	Total # of diet samples	# samples with meso	FO meso
Lissodelphis borealis	56	50	0.89
Delphinus delphis delphis	259	222	0.86
Gonatidae	4	3	0.75
Histioteuthidae	47	26	0.55
Dosidicus gigas	1136	593	0.52
Sebastes brevispinis	25	13	0.52
Alopias superciliosus	45	23	0.51
Xiphias gladius	292	145	0.5
Lagenorhynchus obliquidens	25	12	0.48
Onychoteuthidae	8	3	0.38
Delphinus delphis bairdii	49	14	0.29
Sebastes pinniger	69	13	0.19
Thunnus alalunga	750	142	0.19
Bathyraja kincaidii	125	20	0.16
Sebastes alutus	133	21	0.16
Thunnus oreintalis	721	116	0.16
Callorhinus ursinus	351	53	0.15

Supplementary Table 3 Comparison of frequency of occurrence (FO) for mesopelagic fishes and CPS fishes, for taxa that had a greater FO of mesopelagic fish compared to CPS fish

Predator taxa	Total # diet samples	# meso samples	FO meso	# cps fish samples	FO cps fish
Lissodelphis borealis	56	50	0.893	2	0.036
Delphinus delphis delphis	259	222	0.857	47	0.181
Gonatidae	4	3	0.75	0	0
Histioteuthidae	47	26	0.553	0	0
Dosidicus gigas	1136	593	0.522	218	0.192
Sebastes brevispinis	25	13	0.52	8	0.32
Alopias superciliosus	45	23	0.511	13	0.289
Xiphias gladius	292	145	0.497	60	0.205
Lagenorhynchus obliquidens	25	12	0.48	10	0.4

Onychoteuthidae	8	3	0.375	0	0
Sebastes pinniger	69	13	0.188	1	0.014
Bathyraja kincaidii	125	20	0.16	0	0
Sebastes alutus	133	21	0.158	0	0
Beringraja rhina	544	46	0.085	1	0.002
Anoplopoma fimbria	2619	74	0.028	60	0.023
Sebastolobus altivelis	1698	27	0.016	0	0
Albatrossia pectoralis	205	3	0.015	0	0
Beringraja inornata	263	3	0.011	2	0.008
Sebastolobus alascanus	2082	18	0.009	1	0
Oncorhynchus mykiss	1022	3	0.003	2	0.002
Microstomus pacificus	2408	1	0	0	0

Supplementary Table 4 A breakdown of the mesopelagic fish taxa consumed by individual predator taxa

Predator scientific name (# of mesopelagic prey taxa**)**	**Prey scientific name**	**# unique predator samples per taxon**
Albatrossia pectoralis (2)	Bathylagidae	2
	Myctophidae	1
Alopias superciliosus (3)	Lestidiops ringens	1
	Magnisudis atlantica	12
	Paralepididae	11
Alopias vulpinus (2)	Magnisudis atlantica	16
	Paralepididae	2
Anoplopoma fimbria (13)	Bathylagidae	11
	Bathylagus pacificus	4
	Chauliodus macouni	10
	Lampanyctus ritteri	4
	Leuroglossus	1
	Leuroglossus schmidti	1
	Myctophidae	32
	Nemichthyidae	1
	Nemichthys scolopaceus	1
	Sagamichthys abei	1

	Stenobrachius leucopsarus	3
	Tactostoma macropus	2
	Tarletonbeania crenularis	5
Atheresthes stomias (2)	Chauliodus macouni	1
	Myctophidae	3
Bathyraja kincaidii (1)	Myctophidae	20
Beringraja binoculata (1)	Myctophidae	1
Beringraja inornate (1)	Myctophidae	3
Beringraja rhina (1)	Myctophidae	46
Callorhinus ursinus (6)	Leuroglossus schmidti	26
	Myctophidae	2
	Nansenia	1
	Stenobrachius leucopsarus	20
	Symbolophorus californiensis	22
	Tarletonbeania crenularis	17
Delphinus delphis bairdii (11)	Bathylagidae	1
	Ceratoscopelus townsendi	7
	Diaphus theta	6
	Lampadena urophaos	2
	Lampanyctus ritteri	5
	Leuroglossus schmidti	3
	Myctophidae	1
	Stenobrachius leucopsarus	2
	Symbolophorus californiensis	8
	Tarletonbeania crenularis	2
	Triphoturus mexicanus	6
Delphinus delphis delphis (22)	Arctozenus risso	2
	Bathylagidae	10
	Ceratoscopelus townsendi	158
	Diaphus theta	135
	Lampadena urophaos	102
	Lampanyctus ritteri	147
	Lestidiops ringens	26
	Leuroglossus schmidti	99
	Magnisudis atlantica	6
	Melamphaes lugubris	31
	Myctophidae	37

	Myctophum nitidulum	1
	Nansenia	35
	Nansenia candida	8
	Notoscopelus resplendens	2
	Parvilux ingens	3
	Protomyctophum crockeri	26
	Scopelogadus bispinosus	21
	Stenobrachius leucopsarus	123
	Symbolophorus californiensis	172
	Tarletonbeania crenularis	43
	Triphoturus mexicanus	145
Dosidicus gigas (30)	Arctozenus risso	18
	Bathylagidae	32
	Bathylagoides wesethi	3
	Bathylagus pacificus	2
	Benthalbella	1
	Benthalbella dentata	1
	Ceratoscopelus townsendi	22
	Diaphus theta	137
	Diogenichthys laternatus	8
	Lampadena urophaos	2
	Lampanyctus jordani	1
	Lampanyctus ritteri	68
	Lestidiops ringens	8
	Leuroglossus schmidti	12
	Lipolagus ochotensis	4
	Magnisudis atlantica	20
	Melamphaes	3
	Melamphaes lugubris	2
	Nannobrachium regale	1
	Nansenia	1
	Nansenia crassa	19
	Paralepididae	20
	Parvilux ingens	1
	Protomyctophum crockeri	43
	Pseudobathylagus milleri	1
	Stenobrachius leucopsarus	227

	Symbolophorus californiensis	26
	Tactostoma	14
	Tactostoma macropus	3
	Tarletonbeania crenularis	276
Gonatidae (2)	Myctophidae	2
	Stomiidae	1
Histioteuthidae (4)	Diaphus theta	3
	Myctophidae	24
	Nansenia candida	2
	Tarletonbeania crenularis	4
Isurus oxyrinchus (3)	Magnisudis atlantica	8
	Nansenia	1
	Paralepididae	3
Lagenorhynchus obliquidens (12)	Ceratoscopelus townsendi	5
	Diaphus theta	7
	Lampadena urophaos	2
	Lampanyctus ritteri	4
	Lestidiops ringens	1
	Leuroglossus schmidti	2
	Nansenia	1
	Rosenblattichthys volucris	1
	Stenobrachius leucopsarus	4
	Symbolophorus californiensis	9
	Tarletonbeania crenularis	3
	Triphoturus mexicanus	3
Lissodelphis borealis (19)	Arctozenus risso	5
	Ceratoscopelus townsendi	44
	Diaphus theta	46
	Lampadena urophaos	40
	Lampanyctus ritteri	41
	Lestidiops ringens	13
	Leuroglossus schmidti	37
	Magnisudis atlantica	13
	Melamphaes lugubris	6
	Myctophidae	10
	Nansenia	19
	Nansenia candida	3

	Notolepis	1
	Protomyctophum crockeri	5
	Scopelogadus bispinosus	11
	Stenobrachius leucopsarus	44
	Symbolophorus californiensis	43
	Tarletonbeania crenularis	27
	Triphoturus mexicanus	31
Merluccius productus (21)	Anotopterus nikparini	1
	Argyropelecus affinis	4
	Bathylagidae	14
	Bathylagus pacificus	1
	Chauliodontinae	1
	Diaphus theta	28
	Gonostomatidae	1
	Idiacanthus	1
	Lampanyctus	4
	Leuroglossus	1
	Leuroglossus schmidti	6
	Lipolagus ochotensis	4
	Myctophidae	587
	Nansenia candida	2
	Paralepididae	9
	Protomyctophum	2
	Stenobrachius	2
	Stenobrachius leucopsarus	56
	Symbolophorus californiensis	3
	Tactostoma macropus	8
	Tarletonbeania crenularis	27
Microstomus pacificus (1)	Myctophidae	1
Oncorhynchus kisutch (2)	Myctophidae	3
	Stenobrachius leucopsarus	2
Oncorhynchus mykiss (1)	Myctophidae	3
Oncorhynchus tshawytscha (5)	Melanostigma pammelas	1
	Myctophidae	6
	Nemichthyidae	4
	Stenobrachius leucopsarus	1
	Tarletonbeania crenularis	1

Onychoteuthidae (2)	Diaphus theta	2
	Myctophidae	2
Sebastes alutus (5)	Chauliodus macouni	10
	Myctophidae	15
	Stenobrachius leucopsarus	4
	Tactostoma macropus	4
	Tarletonbeania crenularis	4
Sebastes brevispinis (1)	Myctophidae	13
Sebastes flavidus (2)	Myctophidae	5
	Stenobrachius leucopsarus	1
Sebastes mystinus (1)	Lipolagus ochotensis	1
Sebastes pinniger (1)	Myctophidae	13
Sebastolobus alascanus (7)	Bathylagus pacificus	1
	Lepidopus caudatus	1
	Lycodapus fierasfer	2
	Macropinna microstoma	1
	Myctophidae	7
	Tactostoma macropus	1
	Tarletonbeania crenularis	5
Sebastolobus altivelis (4)	Bathylagidae	5
	Diaphus theta	1
	Lycodapus mandibularis	2
	Myctophidae	19
Thunnus alalunga (13)	Ceratoscopelus townsendi	1
	Diaphus theta	4
	Lampanyctus ritteri	3
	Lestidiops ringens	68
	Magnisudis atlantica	7
	Myctophidae	16
	Nansenia	8
	Poromitra crassiceps	1
	Protomyctophum crockeri	4
	Stenobrachius leucopsarus	12
	Symbolophorus californiensis	11
	Tarletonbeania crenularis	31
	Triphoturus mexicanus	8
Thunnus orientalis	Ceratoscopelus townsendi	41

(13)	Diaphus theta	39
	Lampanyctus ritteri	10
	Lestidiops ringens	8
	Magnisudis atlantica	1
	Myctophidae	1
	Nansenia	6
	Protomyctophum crockeri	6
	Rosenblattichthys volucris	1
	Stenobrachius leucopsarus	43
	Symbolophorus californiensis	15
	Tarletonbeania crenularis	1
	Triphoturus mexicanus	55
Trachurus symmetricus (1)	Myctophidae	5
Xiphias gladius (17)	Arctozenus risso	8
	Ceratoscopelus townsendi	1
	Diaphus theta	1
	Lampadena urophaos	18
	Lestidiops ringens	29
	Leuroglossus schmidti	3
	Magnisudis atlantica	84
	Nansenia	32
	Paralepididae	3
	Protomyctophum crockeri	1
	Rosenblattichthys volucris	49
	Scopelarchidae	20
	Stemonosudis macrura	4
	Stenobrachius leucopsarus	2
	Symbolophorus californiensis	5
	Tetragonurus cuvieri	2
	Triphoturus mexicanus	4
Zalophus californianus (22)	Arctozenus risso	14
	Bathylagidae	9
	Bathylagus pacificus	1
	Ceratoscopelus townsendi	74
	Diaphus theta	53
	Lampadena urophaos	4
	Lampanyctus ritteri	22

	Lestidiops ringens	77
	Leuroglossus	1
	Leuroglossus schmidti	37
	Leuroglossus stilbius	160
	Magnisudis atlantica	75
	Melamphaes lugubris	1
	Myctophidae	53
	Nansenia	1
	Nansenia crassa	8
	Protomyctophum crockeri	4
	Stenobrachius leucopsarus	139
	Symbolophorus californiensis	226
	Tarletonbeania crenularis	75
	Tetragonurus cuvieri	13
	Triphoturus mexicanus	42

Supplementary Table 5 List of the mean standard length and standard error for mesopelagic fish taxa available in the CCTD database. Standard length values were either measured directly, back calculated or converted from total length of Fork length measurements using available length conversions for available species in Fishbase).

Mesopelagic fish taxa	Mean SL (mm) ± se	n
Anotopterus nikparini	203	1
Arctozenus risso	294.43 ± 13.05	16
Argyropelecus affinis	55 ± 5	2
Bathylagidae	84.49 ± 7.72	29
Bathylagus pacificus	141.12 ± 5.31	4
Ceratoscopelus townsendi	52.3 ± 1.92	71
Chauliodus macouni	96± 30	2
Diaphus theta	57.51 ± 1.47	293
Diogenichthys laternatus	26.12 ± 2.56	8
Gonostomatidae	195	1
Idiacanthus	104	1
Lampadena urophaos	180.84 ± 34.62	6
Lampanyctus	63.04 ± 6.88	5
Lampanyctus ritteri	45.99 ± 1.51	128
Lestidiops ringens	183.94 ± 3.94	124

Leuroglossus	113 ± 47	2
Leuroglossus schmidti	97.76 ± 6.85	22
Leuroglossus stilbius	73.47 ± 1.03	342
Lipolagus ochotensis	154.47 ± 5.99	11
Magnisudis atlantica	282.18 ± 14.46	65
Myctophidae	60.81 ± 1.23	183
Nansenia candida	84.45	1
Nansenia crassa	144.57 ± 8.95	21
Paralepididae	147.27 ± 18.38	18
Protomyctophum	55.85 ± 0.95	2
Protomyctophum crockeri	22.87 ± 1.14	76
Stenobrachius	61.44 ± 4.16	5
Stenobrachius leucopsarus	49.14 ± 0.79	604
Symbolophorus californiensis	82.57 ± 1.85	273
Tactostoma macropus	177.67 ± 10.65	3
Tarletonbeania crenularis	58.53 ± 0.51	642
Tetragonurus cuvieri	255.08 ± 16.15	22
Triphoturus mexicanus	44.55 ± 0.31	284

Coastal Pelagic Fish taxa	Mean SL (mm) ± se	n
Atherinopsis californiensis	201.78 ± 12.13	11
Clupea pallasii pallasii	106.96 ± 2.25	495
Engraulis mordax	106.47 ± 0.32	10951
Sardinops sagax	164.82 ± 6.3	6172
Scomber japonicus	222.69 ± 1.04	2757
Trachurus symmetricus	165.12 ± 0.89	3813

Chapter 2
Vertical distribution of mesopelagic fishes deepens during marine heatwave in the California Current

2.1 Abstract

Marine heatwaves can impact the distribution and abundance of epipelagic organisms, but their effect on deep pelagic communities is unclear. Using fisheries acoustics data collected in the Central California current from 2013-2018, we found that during the warmest years of a large marine heatwave (2015-2016), the estimated center of mass depth of mesopelagic fishes deepened by up to 100 m compared to pre-heatwave conditions. Using a generalized additive model, we evaluated which biophysical factors may have driven these changes and found that light, dynamic height anomaly, and acoustic backscatter explained 81% of the variability in depth. We attribute the vertical shift by mesopelagic fishes into deeper waters to heatwave driven compression of upwelling habitat that indirectly increased the amount of light reaching mesopelagic depths. Our results suggest that mesopelagic fishes are interconnected with and thus sensitive to changes in near-surface oceanographic conditions, which could lead to cascading effects on vertical carbon export and the availability of mesopelagic fishes as prey for top predators under future climate conditions.

2.2 Introduction

Mesopelagic fishes represent the greatest biomass of vertebrates on earth, with estimates exceeding that of all global annual commercial fish landings (Irigoien *et al.*, 2014; FAO, 2022). Mesopelagic communities contribute to global carbon export and are important prey for economically valuable and protected species such as Swordfish *Xiphias gladius*, Albacore *Thunnus alalunga* and marine mammals (Brodeur and Yamamura, 2005; Iglesias *et al.*, 2023). Although the mesopelagic zone is defined as the depths of 200-1000 m, many organisms inhabiting mesopelagic depths are connected to surface processes through vertical movements into surface waters to feed. This interconnection means mesopelagic organisms are affected by anthropogenic activities that impact epipelagic habitats, such as habitat alteration, climate change and fisheries exploitation (Martin *et al.*, 2020; Bisson *et al.*, 2023). Despite increasing ocean surface temperatures (IPCC, 2019) and expanding oxygen minimum zones (Breitburg *et al.*, 2018), the long-term indirect effects of climate change on mesopelagic communities are poorly understood, but predicted to increase shoaling of the DSL by 2100 (Proud *et al.*, 2017), expand mesopelagic habitat (Netburn and Koslow, 2015), or shift mesopelagic fishes poleward (Liu *et al.*, 2023). Our study is the first to document changes in the vertical distribution of the mesopelagic community in response to a large heatwave event and as such, advances the identification of important current and future environmental drivers shaping mesopelagic habitat.

The largest recorded marine heatwave event to date in the northeast Pacific began in the California Current Ecosystem (hereafter CCE) as a result of increased sea level pressure in the North Pacific in 2013 (Bond *et al.*, 2015) and eventually led to anomalous, surface intensified warm water along the US west coast which persisted for several years (Di Lorenzo and Mantua, 2016). Although the heatwave was felt in various locations and intensities between ~2014-2016 (Leising *et al.*, 2015; Mcclatchie *et al.*, 2016; Wells *et al.*, 2017), its effects in the central California Current region (where our study takes place), were not observed until late summer of 2014, and were most severe during 2015-2016 (Gentemann *et al.*, 2017). As our data were collected in the late Spring of each year (see Methods), for the purposes of our analysis we consider 2015 and 2016 to be the years associated with the marine heatwave impacts. During this time, increased sea surface temperatures led to extensive ecological change in the epipelagic community (Cavole *et al.*, 2016). Although research describing changes in the distribution, diversity and abundance of epipelagic organisms abound, few detail how this heatwave event impacted the mesopelagic community.

In the southern CCE, the abundance of larval mesopelagic fishes with northern, cold-water affinities declined, while those with warm-water affinities increased (Nielsen *et al.*, 2021; Thompson *et al.*, 2022). However, the extent to which these responses reflect actual changes in abundance or distribution of the adult spawners, relative to changes in either spawning intensity or the advection patterns of larval mesopelagic fishes, is uncertain. Mid-water trawl data collected at night at 30 m headrope depth along the California Coast for adult Myctophids (family Myctophidae), a dominant family of mesopelagic fishes in the California Current (Davison *et al.*, 2015b), suggest declines in 2015, though not below mean levels (Sakuma *et al.*, 2016). In the northern California Current (Oregon and Washington), Brodeur *et al.* (2019) found that the response of myctophids to the heatwave was species specific, with both increases and decreases observed during this period. However, the surveys upon which these studies are based were not designed to specifically monitor mesopelagic populations, as trawls were conducted at 30 m headrope depth at night and thus inadequately sample mesopelagic depths and did not allow for an evaluation in changes in the depth of mesopelagic communities during this time.

Deep-Scattering Layers (DSLs), so called because of their appearance when detected using active acoustics in deep water (Dietz, 1962), are dynamic in space and time, and responsive to variable oceanographic conditions (Boswell *et al.*, 2020). Quantifying changes in the vertical distribution of mesopelagic fishes is challenging via conventional trawl methods due to increased depths, variable diel vertical migration patterns (Catul *et al.*, 2011) and net avoidance (Kaartvedt *et al.*, 2012). Fisheries acoustics provide an alternative means of sampling mesopelagic fish with high spatial and temporal resolution, but are biased towards gas-bearing organisms. The global estimate of mesopelagic fish biomass, previously estimated from trawl data, for example, was revised upward by an order of magnitude following an acoustic estimate (Irigoien *et al.*, 2014). Acoustic surveys of the DSL have revealed the importance of numerous physical oceanographic conditions on DSL depth such as light (Benoit-Bird *et al.*, 2009; Røstad *et al.*, 2016; Aksnes *et al.*, 2017; Boswell *et al.*, 2020), oxygen (Bertrand *et al.*, 1999; Netburn and Koslow, 2015; Klevjer *et al.*, 2016), temperature (Fennell and Rose, 2015; Sutton *et al.*, 2017) and thermocline depth (Peña *et al.*, 2014; D'Elia *et al.*, 2016). However, it is less clear how the vertical distribution of mesopelagic fishes may be affected by a large-scale marine heatwave, when many of these environmental variables undergo simultaneous, and possibly compounding, changes.

To understand the potential impacts of future oceanographic variability on mesopelagic communities, there is a need to first quantify the response of mesopelagic fishes to present conditions, especially those associated with anomalous warming events, which are predicted to increase with climate change (Di Lorenzo and Mantua, 2016; Frölicher *et al.*, 2018). In this study, we utilize a dataset of continuous active sonar data collected in the late spring of 2013-2018 within the CCE to test the hypothesis that the large marine heatwave of 2015-2016 impacted the vertical distribution of mesopelagic fish. Using *in situ* hydrographic data and remotely sensed observations, we also quantify relationships between environmental variables and the depth of mesopelagic fishes to explain how oceanographic conditions in the upper ocean could indirectly shape the vertical distribution of deep pelagic communities below.

2.3 Methods

Study area and survey data

The Rockfish Recruitment and Ecosystem Assessment Survey (RREAS), conducted by the Southwest Fisheries Science Center (SWFSC) of the National Marine Fisheries Service, is an annual, late spring (i.e., May-June) survey that began in 1983 to monitor recruitment strength of rockfish and other groundfish in the CCE (Field *et al.*, 2021; Santora *et al.*, 2021). Continuous, multifrequency measurements of acoustic backscatter have been collected by the RREAS since 2000, although unprocessed data from 2000-2010 are no longer available. Our study focuses on 2013-2018 to demonstrate the impacts of the intense marine heatwave that affected the US west coast in relation to conditions preceding (2013, 2014), during (2015, 2016) and following (2017, 2018) the heatwave. Acoustics data were collected from two research vessels, the R/V *Ocean Starr* (2013-2015), and the NOAA Ship *Reuben Lasker* (2016-2018) with a Simrad EK60 echosounder (Kongsberg). The geographic scope was restricted to the "core" region of the survey (36.45 to 38.33°N) to ensure comparable sampling coverage between years (Fig. 1). Data from 2019 were omitted due to irregularities in acoustic sampling and in 2020 due to survey cancellation during the COVID-19 pandemic. Although four dedicated acoustic transects were opportunistically sampled, most acoustic data used in this analysis were collected while in transit between predetermined trawl or CTD stations.

Acoustic data collection and selection

Echosounder calibrations were conducted before and/or after each survey, using a 38.1 tungsten carbide calibration sphere (Foote et al., 1987; Demer et al., 2015). Underway, 38 kHz echosounder data were collected from the hull ~3.3 m (R/V *Ocean Starr)* or centreboard ~7 m (*Reuben Lasker)*, with a pulse duration of 1.024 ms and transmitted power of 2000 W, recorded to a max range of 750 m and a variable ping rate (set to maximum). To avoid overlap between the mesopelagic and epipelagic community during diel vertical migrations, we exclusively used daytime data, defined here as 2 hours before or after sunrise/sunset (Irigoien *et al.*, 2014). Daily sunrise and sunset times were calculated using the {suncalc} package (Thieurmel and Elmarhraoui, 2022) in R (R Core Team, 2023) with Rstudio (RStudio Team, 2023). Data collected when ship speeds fell below 5 knots were excluded to avoid noise. We define the mesopelagic zone as the portion of the water column between 175 m and 675 m, over bottom depths ≥725 m. The upper limit (175 m) was selected to omit weak fluid filled epipelagic scatters resonant at depths above 175 m (Davison *et al.*, 2015a) and to coincide with daytime mesopelagic fish depths in the CCE (Davison *et al.*, 2015a). The maximum depth (675 m) corresponds to 50 m above the minimum bottom depth of 725 m and incorporated the vast majority of backscatter from the main scattering layer (Fig 2), which was the focus of this study. In the CCE, there is occasionally a weaker, deeper scattering layer present below the main DSL, which we did not likely include, as the main scattering layer in our region is consistently above 600 m (Urmy *et al.*, 2012; Davison *et al.*, 2015; Netburn and Koslow, 2015).

Acoustic data processing

All data filtering and cleaning was conducted using Echoview (Echoview® version 10, 2022). The seabed was distinguished via best bottom candidate algorithms in Echoview or via 18 kHz automatic bottom detection when available (2016-2018) and were visually inspected for accuracy and manually edited where necessary. Acoustic backscatter between 0-10 m and within 10 m of the seabed were removed to avoid nearfield effects and interference caused by bottom topography, respectively. In regions of variable, complex bathymetry, such as steep canyons, we additionally removed bottom-associated noise (likely caused by side-lobe interference) extending beyond 10 m above the seafloor. To correct for the effect of variable oceanographic conditions on sound speed and sound absorption, we calculated daily sound speed profiles (using the {oce} package (Richards, 2022) "UNESCO" equation of (Fotonoff and Millard (1983)), and absorption coefficient values (calculated in Echoview using the Francois & Garrison (1882) equation), from available CTD measurements of salinity, temperature, and pressure, typically from 2-500m. As pH information was not available from *in situ* measurements, we used the default value of 8.0 as a reasonable approximation for absorption coefficient calculations (Foote *et al.*, 1987). False bottom regions were identified using an angular position algorithm developed by Blackwell *et al.* (2019) and manually removed. Impulse noise and attenuated signal (Ryan *et al.*, 2015), transient noise (Ryan *et al.*, 2015; Jech *et al.*, 2021) and background noise (De Robertis and Higginbottom, 2007) were removed using filters in Echoview. We were unable to account for transducer motion, as boat movement data were not collected at a sufficient sampling rate (Dunford, 2005; Ryan *et al.*, 2015; Jech *et al.*, 2021). Throughout processing, we referenced settings recommendations from (Ryan *et al.*, 2015; MESOPP, 2020; Haris *et al.*, 2021), adjusted to match our specific data. We gridded cleaned acoustic data into 100 m horizontal by 5 m vertical bins (Davison *et al.*, 2015a), and removed cells with greater than 50% of data removed during cleaning. Volume backscattering strength ($\mathrm{S_v}$) estimates were then exported from Echoview for further analysis.

Acoustic metrics

Deep-scattering layers are typically comprised of mixed assemblages of small organisms, generally referred to as micronekton (Brodeur and Yamamura, 2005), making it difficult to identify individuals acoustically from echosounders mounted on surface vessels. Acoustic backscatter, measured here as mean volume backscattering strength ($S_v\ or\ MVBS$), is a logarithmic measure of s_v (volume backscattering coefficient) defined as:

$$s_v = \sum \sigma_{bs}/V \qquad (1)$$

where V is volume and σ_{bs} is the volume backscattering cross-section (Maclennan *et al.*, 2002). Although we do not have reliable *in situ* biological samples necessary make any inferences about biomass, we consider mean volume-backscattering strength here as a proxy for acoustic density (Urmy *et al.*, 2012).The mean vertical position of mesopelagic fishes was estimated by calculating centre of mass depth (CM), the mean depth of acoustic backscatter, weighted by s_v (Urmy *et al.*, 2012):

$$CM = \frac{\int z\, s_v(z) dz}{\int s_v(z) dz} \quad (2)$$

where z is depth and $s_v(z)$ is the backscattering coefficient at depth z. Centre of mass depth is only one proxy for tracking DSL depth, and previous studies have identified upper and lower boundaries of the DSL (Netburn and Koslow, 2015) or calculated additional metrics such as evenness or aggregation (Urmy *et al.*, 2012). However, given our broad spatial domain and interest in resolving oceanographic processes occurring at the ~ 25 km scale, we chose centre of mass depth as a robust metric for characterizing the depth of the majority of backscatter, similar to previous studies (Klevjer *et al.*, 2016).

Assessment of spatial autocorrelation

Continuous acoustic sampling can result in spatial autocorrelation, violating the assumption of sample independence required for most statistical tests. Spatial autocorrelation was quantified by plotting correlograms for depth-integrated (175-675 m) mean volume backscattering strength ($mean\ S_v$), over distance sampling units (i.e. horizontal grid cell size) of 100 m using the {ncf} package (Bjornstad, 2022). To account for variations in vertical coverage, we excluded from the autocorrelation analysis locations with more than 25 (out of 100) missing vertical cells. Moran's *I* was calculated as a measure of the degree of correlation in S_v between points at increasing horizontal distances (lags). The distance at which data were no longer spatially autocorrelated was estimated as either the distance where p-value > 0.05, or Moran's *I* reached 0, whichever came first (Fig. 3). Distances were estimated for each year separately, and a mean and median distance calculated across all years (mean: 27 km, median of 24 km). Based on these values and results of a sensitivity analysis (Fig. S1), we selected a grid cell size of 25 km to avoid spatial autocorrelation. Prior to echo-integration, acoustic backscatter data were regridded using the {raster} package (Hijmans, 2023) without imposing a minimum number of vertical cells but ensuring adequate coverage by removing any regridded (25 x 25 km) cells with less than three (100 m) horizontal cells. The 25-km regridding distance is comparable to the Rossby radius of deformation (~20-30 km average for mid-latitudes in the eastern Pacific (Chelton *et al.*, 1998)), which is a natural physical length scale for coastal upwelling in the CCE and has been used previously to characterize acoustic backscatter in our region (Santora *et al.*, 2011).

Mesopelagic echo classification

There is strong evidence suggesting that 38 kHz acoustic backscatter in the mesopelagic zone is dominated by fishes (Kloser *et al.*, 2009; O'Driscoll *et al.*, 2009; Irigoien *et al.*, 2014; Proud *et al.*, 2017), especially in the California Current region (Koslow *et al.*, 2011; Davison *et al.*, 2015b). Hence, we exclusively utilized backscatter data collected at 38 kHz and applied a S_v sample threshold of -75 dB to discriminate fishes from fluid-filled scatters. Based on estimated target strengths (TS) measured by Davison et al. (2015a) from the CCE, we chose a TS value from California Smoothtongue (*Leuroglossus stilbius*), a common species of mesopelagic fish in the CCE lacking a swim bladder (-68.2 dB) and added -6 dB to account for fish not centred in the beam (Rudstam *et al.*, 2009). Target strength was then related to S_v via:

$$\mathrm{S_v} = \mathrm{TS} + 10\log_{10}(\mathrm{n}) \qquad (3)$$

where TS was our minimum target strength (-74.2 dB) and n represents the minimum target density (1 fish per 1 m^3 water) to give a threshold value of approximately ~ -75 dB. This value falls within the range of threshold values used to distinguish mesopelagic fishes from other forms of backscatter: -90 dB (Irigoien *et al.*, 2014; Klevjer *et al.*, 2016; Aksnes *et al.*, 2017), -65 dB (Escobar-Flores *et al.*, 2019) and -70 dB (Bertrand *et al.*, 1999). We did not have 18 kHz data available in 2013-2015, precluding the use of differential frequency responses to further resolve taxonomic groups (D'Elia *et al.*, 2016). Our analysis may also include backscatter from semi-pelagic species that aggregate over the shelf-slope boundary, such as Pacific Hake (*Merluccius productus*), which are not considered mesopelagic. We selected acoustic data from bottom depths ≥ 725 m and integrated to a maximum depth of 675 m to avoid backscatter directly above the bottom and at the shelf break, but this does not guarantee that all benthic/shelf associated fishes were excluded from our analysis. Without direct ground truth data available, our analysis also potentially includes siphonophores with gas inclusions (Davison *et al.*, 2015b; Proud *et al.*, 2019) and dense aggregations of weak-scatters such as zooplankton (Urmy *et al.*, 2012; Davison *et al.*, 2015b; Proud *et al.*, 2019). However, we assume here that the majority of backscatter between 175 – 675 m, with a sample threshold of -75 dB applied, comes from mesopelagic fishes.

Oceanographic data collection and processing

In situ oceanographic data were collected at sea with a calibrated Seabird Electronics SBE9-1050 (2016-2018) and SBE19plus (2013-2015) CTD profiler. Here, we restricted the CTD casts to those that extended to at least 500 m depth and were collected within the acoustic sampling region (Fig. 5). Oceanographic data from the down cast were averaged into 2 m depth bins during post-processing (Santora *et al.*, 2012). Temperature and salinity measurements were used to calculate density and derive a corresponding dynamic height referenced to 500 m depth. The quality of each cast was further verified by plotting oceanographic variables as a function of depth and visually inspecting individual profiles to remove portions of two casts where salinity and density were well outside their expected range, likely due to instrument error.

For each 25x25 km grid cell containing acoustic data, we extracted available CTD data for temperature, density, and dissolved oxygen at the following depths: 175 m (the upper edge of our mesopelagic region) and 500 m (the deepest CTD data available). Chlorophyll-*a* values were first smoothed using a running mean based on two adjacent 2-m depth bins to account for instrument variability, and then integrated over the upper 100 m of the water column. Dynamic height anomalies were calculated by subtracting the mean dynamic height at 500 m for all CTD casts in our study. We removed two dynamic height values that were greater than three standard deviations from the mean. When more than one CTD cast was available per grid cell, we calculated a mean value from all casts within that cell for a given survey year. If CTD data was unavailable for an acoustic cell, we omitted that cell from analysis, which reduced the overall number of cells from 122 containing acoustic data to 86 that included acoustic data and all oceanographic variables. Since *in situ* light estimates from a PAR sensor were only available for three of the six study years due to a malfunctioning sensor, satellite derived diffuse attenuation coefficients at 490 nm from Aqua MODIS were used as a proxy for light. We chose science quality, 8-day composite data at a resolution of 4 km, as daily composite data had gaps caused by variable cloud cover. Using the {rerddap} (Chamberlain, 2023) and {erddapXtracto} (Mendelssohn, 2022) packages, we extracted diffuse attenuation coefficients for the closest 8-day composite data in space and time to our acoustic tracks. The depth at which light reached 1% of surface irradiance (Z), which is typically considered the depth of the euphotic zone, was calculated as:

$$Z = \frac{-\ln({}^{E_z}/_{E_o})}{K490}, \qquad (4)$$

where E_z is irradiance at depth Z, E_o is the irradiance at the surface, and the 1% light level is given by ${}^{E_z}/_{E_o} = 0.01$. Z values were then averaged to obtain a mean value per 25 km grid cell.

Statistical analysis

Interannual comparison of centre of mass depth

Differences in centre of mass depth of mesopelagic fishes between years were examined using a non-parametric Kruskal-Wallis test with a pairwise Wilcox test and Bonferroni correction for multiple comparisons. The Kruskal-Wallis test, selected because of its robustness to the assumptions of normality and variance, uses ranks to tests the null hypothesis that biomass and centre of mass depth were identical across years. Here, we assume that acoustic estimates of backscatter were independent between years, given the dominant time scales of oceanographic variability in the region and the fluidity of mesopelagic communities between seasons (Urmy *et al.*, 2012). We also conducted a sensitivity analysis comparing our Kruskal-Wallis test results of interannual differences at multiple spatial scales: 1, 5, 10, 15, 20, and 25 km (Fig. S1). Although we were not able to randomize sampling due to the structured nature of the survey, we assume that there was no intentional bias in the acoustic data related to mesopelagic fish.

Linking centre of mass depth to environmental covariates

A generalized additive model (GAM) was used to quantify which environmental covariates explained observed variability in centre of mass depth. Prior to model fitting, we evaluated collinearity amongst oceanographic covariates and removed those that were highly correlated (correlation coefficient >0.7, as recommended by (Dormann *et al.*, 2013) (Fig S2). Using the {mgcv} package (Wood, 2023), we then fit a GAM with centre of mass depth as the response variable and temperature (at 175 m and 500 m depth), oxygen (at 175 m and 500 m depth), chlorophyll-*a* (integrated over 0-100 m depth), dynamic height anomalies, MVBS (as a proxy for acoustic density), and *Z* (euphotic depth) as environmental covariates. This full model was fit with a Gaussian distribution using the Restricted Maximum Likelihood (REML) method. We used a knots value (*k*) of 10 for the number of basis functions per smooth and verified that this was an appropriate value in {mgcv}. After running the full model, we evaluated pairwise concurvity, a non-linear measure akin to collinearity that occurs when two smooth terms approximate each other. We removed those terms with "worst" values greater than 0.8. Model fit was evaluated and considered appropriate for our data using both the {mgcv} and {gratia} (Simpson, 2023) packages (Fig. S3). In addition to MVBS, our final model included temperature and oxygen at 175 m, oxygen at 500 m, chlorophyl integrated over the upper 100 m, dynamic height anomalies and euphotic depth (Z). We chose not to include year or geographic location (latitude, longitude) so that all model variance explained could be attributed to oceanographic variables. While year was not included in our final model, we nevertheless examined variability of oceanographic conditions amongst years to characterize interannual changes in the environment (Fig. S4).

2.4 Results

Changes in mesopelagic patch size

The spatial autocorrelation analysis indicated strong spatial structuring of the mesopelagic acoustic signal. The distance at which we could assume spatial independence varied among years (Fig. 3) but was twice as great in 2016 as any other year (~57 km in 2016 compared to ~9 km in 2013, 29 km in 2014, 19 km in 2015, 23 km in 2017 and 26 km in 2018). An alternative view of these spatial autocorrelation distances is as the "patch size" of mesopelagic fishes. In this interpretation, 2016 had the largest patch size of mesopelagic fishes ~57 km across. The mean distance of spatial independence across all years was ~ 27 km, with a median value of ~24 km. The sensitivity analysis, which compared centre of mass depth across years at multiple horizontal grid resolutions (1, 5, 10, 15, 20 and 25 km), revealed consistent statistical results for interannual centre of mass comparisons for grid cell sizes from 10 km to 20 km (see Fig. S1).

Oceanographic variability

In total, we quantified 3,483 km of acoustic data (Table 1) and 191 CTD casts of oceanographic data. The number of CTD casts varied from 13 in 2017 to 51 in 2015 (Fig. 3). Inter-annual variability of regional upwelling conditions was apparent from our hydrographic sampling before and after the marine heatwave. Specifically, median values of dynamic height anomalies were greatest in 2016 (median of 0.05) and lowest in 2013 (-0.06), indicating stronger upwelling during 2013 and weaker upwelling during 2015, 2016 and 2017 (median: -0.01, 0.05 and -0.01 respectively) (Fig. S4). The depth of the euphotic zone, Z, inferred from satellite derived diffuse attenuation coefficients (Kd 490) was deepest in 2015 and 2016 (median values of 57.23 m and 54.08, respectively), compared to the shallowest recorded euphotic zone depth in 2013 (median value of 21.59 m), a difference of ~30 m (Fig. S4). Median annual temperature at 175 m varied by less than 1.2 °C over our study period with a range of values from 7.8 to 8 .9 ºC, indicating that warming at the surface during the heatwave was not necessarily reflected at mesopelagic depths (Fig. S4). Finally, median dissolved oxygen values appeared to be higher in 2015 and 2016 (2.09 ml/l in 2015 and 2.03 ml/l in 2016) compared to the other years of our study, which ranged from 1.71 ml/l in 2013 to 1.85 ml/l in 2017 (Fig. S4).

Changes in vertical distribution

The Kruskal-Wallis analysis comparing acoustically estimated centre of mass depth identified a statistically significant deepening of the median depth of mesopelagic fishes during the marine heatwave (2015 and 2016) compared to other years (Fig. 4). The shallowest centre of mass depth occurred in 2013 (256 m), a year associated with anomalously strong upwelling conditions and preceding heatwave conditions. The marine heatwave years (2015 and 2016) exhibited significantly deeper centre of mass values (368 m and 364 m) than pre (2013-2014) and post (2017-2018) heatwave conditions and were over 100 m deeper than in 2013. Overall, the centre of mass depth exhibited a parabolic behaviour over our study years (Fig. 4a), starting relatively shallow in 2013, deepening significantly during the marine heatwave (2015-2016) and eventually shoaling following the heatwave, although the centre of mass depth in 2018 (322 m) had not returned to the shallow levels observed in 2013 (256 m). If we examine these results across the full distribution of centre of mass depth values (Fig. 4b), 2013 stands apart as having a shallower peak distribution, while 2015 and 2016 exhibit a clear shift to greater deepening and narrowing in the range of centres of mass.

Environmental drivers of depth distribution

The fitted GAM with oceanographic covariates explained 81.4% of the deviance in centre of mass depth, reaching model convergence after 12 iterations. Euphotic depth Z (i.e., depth at which light reaches ~1% of its surface intensity) ($p< 0.001$, edf: 1.1), dynamic height anomaly ($p<0.001$, edf: 3.1) and mean volume backscatter (MVBS) ($p< 0.001$, edf: 1.9) were all significant covariates explaining variability in centre of mass depth (Fig. 6). Light (Z) exhibited a positive, approximately linear relationship with centre of mass depth, with centre of mass depth deepening with increasing light. Centre of mass depth increased (i.e., was deeper) with increasing dynamic height anomalies when dynamic height values were negative (i.e. when there was stronger upwelling, the DSL was shallower). For positive dynamic height values (indicative of weaker upwelling), the centre of mass depth was stable regardless of additional increases. As acoustic backscatter increased, so did the centre of mass depth, up to a MVBS value of ~ -68 dB, at which point the centre of mass depth levelled-off and even became slightly shallower with further increases. Dissolved oxygen at 175 m and 500 m, temperature at 175 m, and chlorophyll-*a* in the upper 100 m did not have a significant effect on centre of mass depth.

2.5 Figures

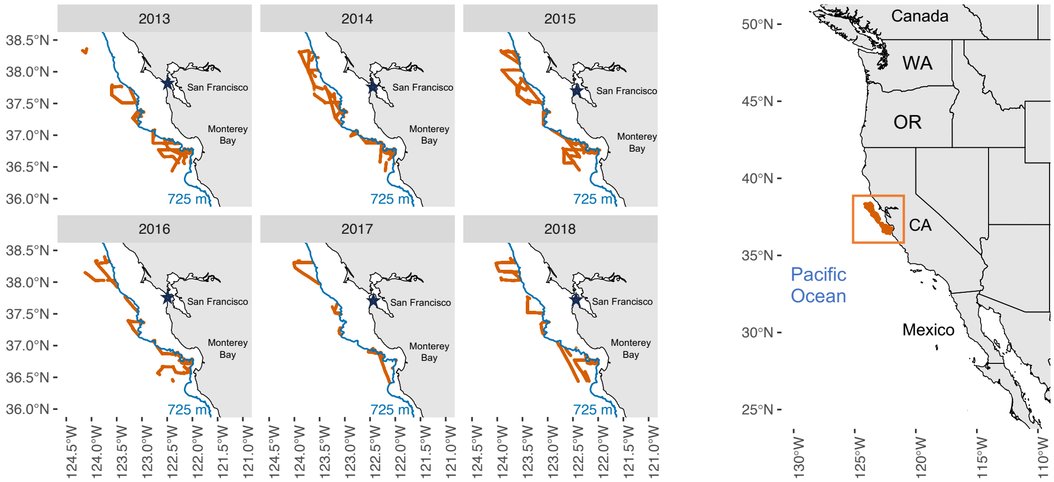

Figure 1 The spatial extent of processed acoustics data collected as part of the NOAA Rockfish Recruitment and Ecosystem Assessment Survey. We selected daytime acoustics data collected from waters with bottom depths deeper than 725 m (blue line), and ship speed greater than 5 knots.

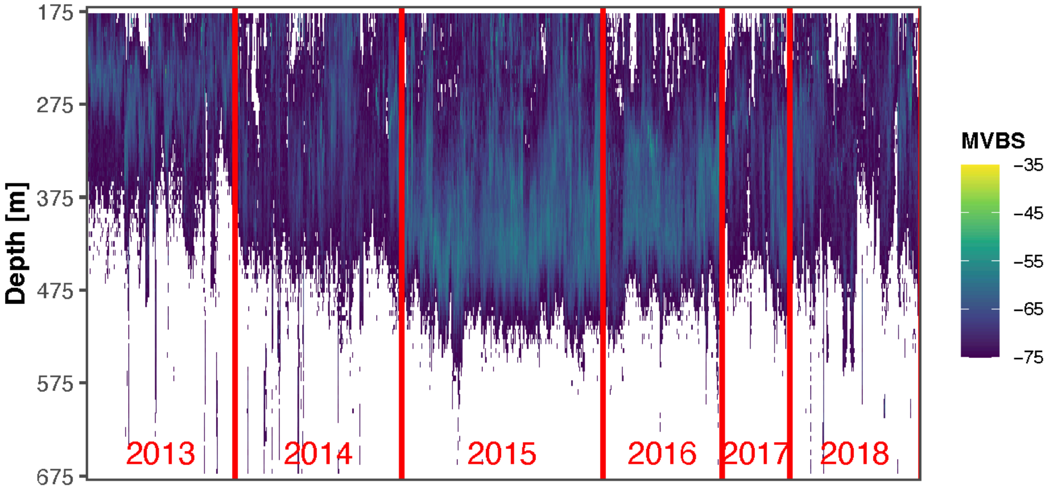

Figure 2 Acoustic backscatter measured as mean volume backscattering strength (MVBS, Sv [dB re 1 m^{-1}]) for the period from 2013-2018. These data have been cleaned and averaged into 100 m horizontal by 5 m vertical bins

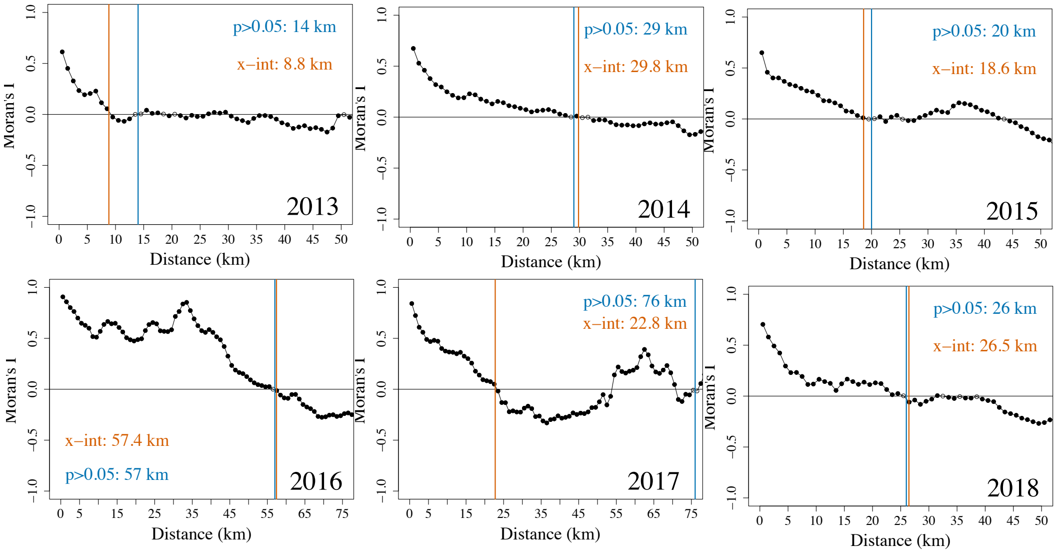

Figure 3 Correlograms representing spatial correlation in acoustic backscatter by distance (lag), represented on the x-axis. Spatial independence is estimated as either the distance at which Moran's *I* =0 (orange line), or the distance at which the p-value was no longer significant (blue line), whichever distance occurred first. Note that the distance scale for 2016 and 2017 was extended to 75 km.

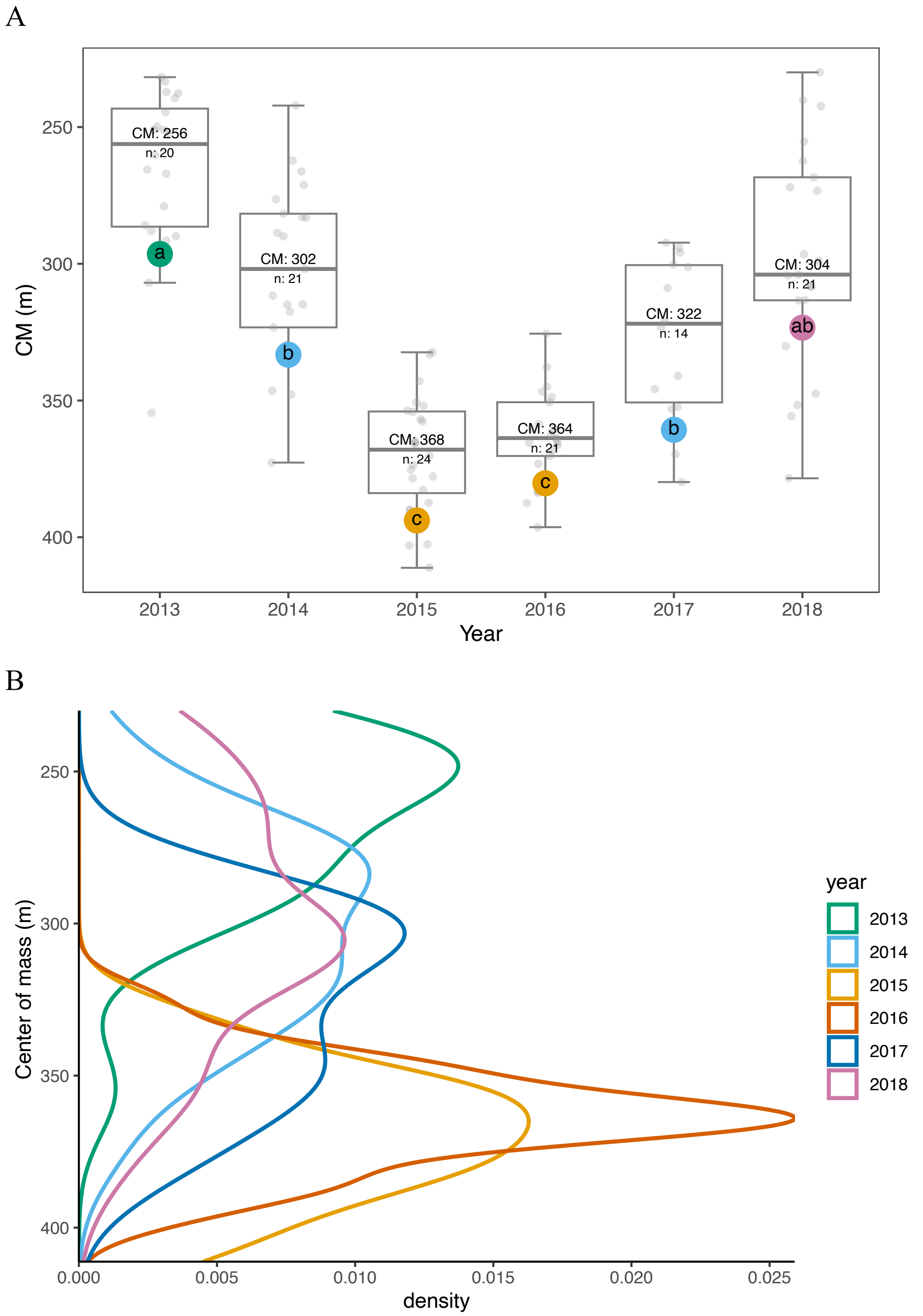

Figure 4 Annual estimates of the center of mass depth [m] for mesopelagic fishes estimated from acoustic backscatter. Colors (and letters in figure a) denote statistically significant groups determined from Kruskall-Wallis test with multiple comparisons (A) or the distribution of center of mass values between years (B).

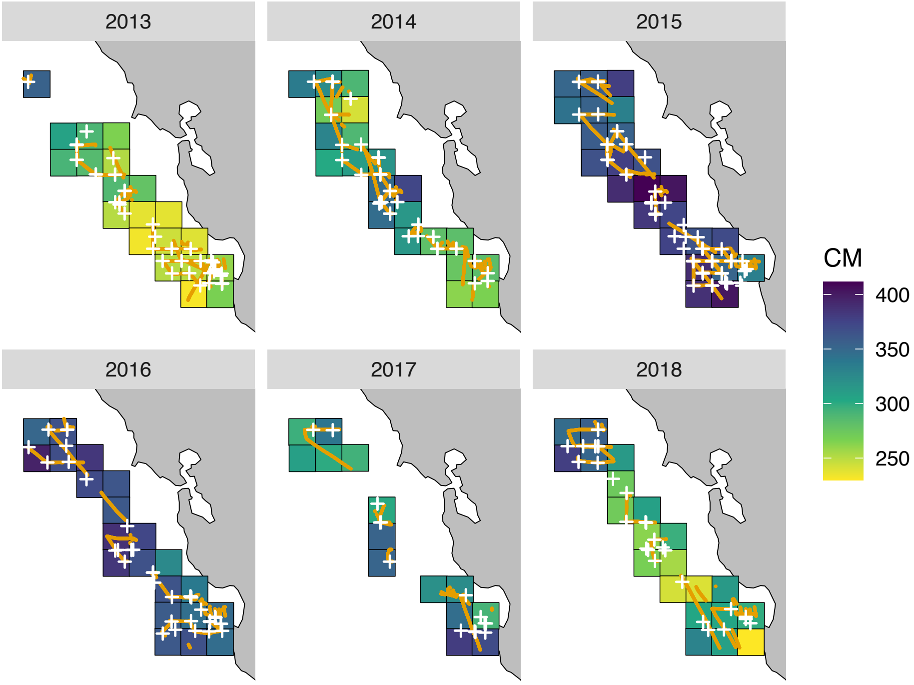

Figure 5 25x25 km grid cells containing both acoustics data and all oceanographic variables. Cells are colored by the mean center of mass depth [m] of mesopelagic fishes estimated from acoustic backscatter, and the white pluses represent the location of oceanographic sampling abord the Rockfish Recruitment and Ecosystem Assessment.

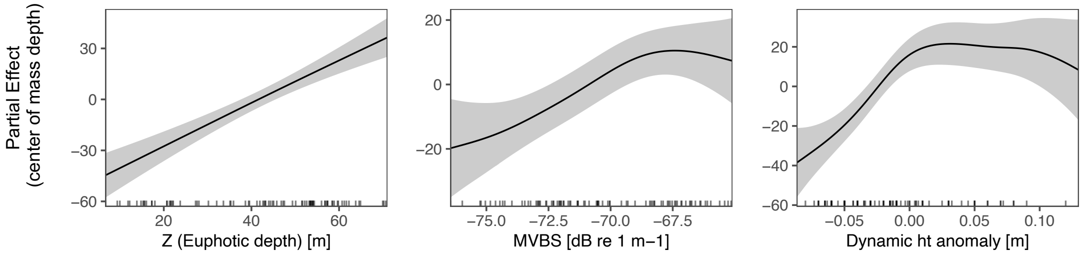

Figure 6 Generalized additive model (GAM) plots depicting the partial effect of each significant covariate (x-axis) on center of mass depth (y-axis). Shaded regions represent confidence bands for smooths 2 standard errors on either side of the smooth, including uncertainty in the global mean.

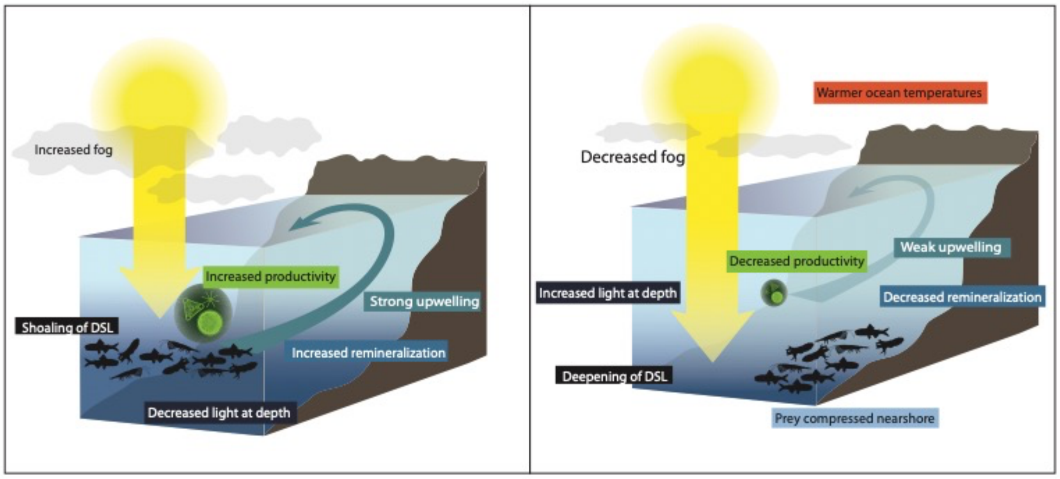

Figure 7 A depiction of the mechanism for the observed shift of mesopelagic fishes deeper during 2013-2018. A compression of upwelling habitat nearshore during the marine heatwave (2015-2016) led to decreases in primary productivity and boundary layer clouds. These factors increased the amount of light that reached mesopelagic depths and mesopelagic fishes responded by shifting deeper into the water column.

Table 1 Summary of acoustics data by year. Mean bottom depth below our sampled water column was estimated from {marmap}(Pante and Simon-Bouhet, 2013). Dates for acoustics and CTD data represent the range of values included in our analysis from start date to end date.

Year	**Distance sampled [km]**	**Number of days sampled**	**Mean bottom depth [m]**	**Acoustics date range [day/month]**	**CTD date range [day/month]**
2013	621	13	1716	10/5 – 1/6	10/5 – 28/5
2014	697	18	1623	3/5 – 8/6	3/5 – 8/6
2015	839	14	1899	2/5 – 13/6	7/5 – 14/6
2016	496	14	1677	28/4 – 3/6	27/4 – 4/6
2017	283	10	1637	28/4 – 6/6	28/4 – 5/6
2018	546	15	1803	14/5 – 20/6	14/5 – 20/6

2.6 Discussion

Connection between near-surface oceanic conditions and mesopelagic communities

Mesopelagic ecosystems are commonly defined by their distance and distinctness from the upper ocean, but our work demonstrates that anomalous and extreme events affecting the upper ocean can impact the vertical daytime distribution of fishes inhabiting mesopelagic depths. During 2015-2016, when a surface intensified marine heatwave impacted the central California current ecosystem, the centre of mass depth of mesopelagic fishes deepened from ~62-112 m and ~42-54 m compared to pre (2013-2014) and post (2017-2018) heatwave conditions. When compared to a strong upwelling year (2013), centre of mass depth was over 100 m deeper during the heatwave (2015-2016). While most of the warming associated with the marine heatwave was restricted to the upper 50 m of the water column (Zaba and Rudnick, 2016; Santora *et al.*, 2017), some heat diffused vertically below the mixed layer where it persisted, even after surface temperatures normalized (Jackson *et al.*, 2018; Scannell *et al.*, 2020). The range of temperatures recorded at 175 m from CTD measurements however, varied by less than 1.2 °C across all years (2013-2018) and did not exhibit a marked warming during the heatwave (Figure S4), indicating that temperature did not increase appreciable at mesopelagic depths during 2015-2016. Mesopelagic fishes tolerate a wide range of temperatures as they undergo nightly migration into shallower, warmer depths, which may justify why temperature at 175 m did not explain a significant portion of centre of mass depth variability. Instead, our results suggest that indirect changes in near-surface conditions that impacted the amount of light reaching mesopelagic depths was the likely cause of the shift in vertical distribution observed in our study.

The vertical distribution of mesopelagic communities is driven by conflicting needs to feed in productive near-surface waters and to avoid visual predators (Longhurst, 1976; Robison *et al.*, 2020). Christiansen *et al.* (2021) demonstrated that predator interactions increase with increasing light, and when confronted with predators, mesopelagic fishes descend deeper into the water column. Globally, Aksnes *et al.* (2017) have shown that DSL depth varies across basins based on changes in light penetration, which supports conclusions by Røstad *et al.* (2016) that there is an optimal light level that mesopelagic communities are selecting for. Light was predicted to exert a greater effect on vertical distribution than temperature in Norwegian Fjords (Langbehn *et al.*, 2019), and mesopelagic communities are even sensitive to short-term changes in light, such as those observed during a passing storm (Kaartvedt *et al.*, 2017). Results from our generalized additive model (GAM) indicate that light had an approximately linear relationship with centre of mass depth, with centre of mass depth increasing with increasing light. This result is consistent with previous work demonstrating that light absorbance can affect the vertical distribution of mesopelagic fishes (Aksnes *et al.*, 2004). The centre of mass depth of mesopelagic communities in the Gulf of Mexico was likewise associated with light intensity as well as mesoscale oceanographic features (Boswell *et al.*, 2020), indicating that mesopelagic communities respond to changing oceanographic conditions. However, few long-term studies of mesopelagic communities exist, making it difficult to link changing near-surface conditions to changes in mesopelagic communities.

During 2015-2016, upwelling habitat along the central California coast was largely confined nearshore (Santora *et al.*, 2020; Schroeder *et al.*, 2022) and the thermocline and nutricline shifted deeper (Zaba and Rudnick, 2016), leading to declines in phytoplankton biomass (Peña *et al.*, 2019). This decrease in phytoplankton biomass, not clearly observed from our CTD measurements, but visible in satellite data over the extent of our acoustics tracks (Fig S4), likely allowed more light to penetrate deeper into the water column. We postulate here that mesopelagic fishes responded to this increase in light intensity by moving deeper to evade visual predators (Fig 7). Evidence for this mechanism comes from our finding that centre of mass depth was associated with dynamic height anomalies, a proxy for coastal upwelling intensity. Moreover, euphotic depth (Z) was deepest in 2015 and 2016 (over 30 m deeper than in 2013), indicating that the amount of light attenuated by phytoplankton in the water column declined during the heatwave, which allowed for more light to penetrate to mesopelagic depths. Although we did not measure light intensity directly at mesopelagic depths, which limits our ability to make comparisons across ecosystems (Aksnes *et al.*, 2017), our proxy for euphotic zone depth (Z) derived from Kd490 (8-day diffuse attenuation coefficient at 490 nm from the Aqua MODIS satellite), allowed us to adequately cover the location of our acoustic tracks and infer relative changes in light experienced at mesopelagic depths. In the future, *in* *situ* measurements of light at mesopelagic depths would allow for more quantitative assessment of the specific light intensities being selected for.

In addition to decreased light attenuation by phytoplankton during the heatwave, there is also evidence supporting a reduction of clouds in the marine layer. Marine layer clouds form as result of differential temperatures between cool, upwelled surface waters and the atmosphere (Tont, 1975). Thus, a reduction of upwelling strength could additionally contribute to increased solar radiation reaching the ocean's surface during the heatwave (Myers *et al.*, 2018; Schmeisser *et al.*, 2019). A combined reduction of phytoplankton biomass and marine layer clouds during the peak of the heatwave for the central California coast in 2015-2016 could thus have led to a compounding effect on light levels at mesopelagic depths. Although light conditions were inferred from 8-day composites of satellite data averaged over 25 km, our results nonetheless provide strong evidence that light intensity in the water column, which increased during the heatwave, affected the vertical distribution of mesopelagic fish. This finding establishes a mechanistic framework for future investigations relating changes in near-surface warming and primary production, to the vertical distribution of mesopelagic fishes while also highlighting the need to maintain and or establish greater monitoring at mesopelagic depths. Utilization of regional ocean models to characterize the biophysical conditions of mesopelagic habitats and additional deployments of advanced monitoring technologies such as gliders, cameras and eDNA may offer an opportunity to fill some of these monitoring needs.

Although we focus here on the vertical distribution of mesopelagic communities, acoustic backscatter (measured as MVBS) was a significant covariate explaining centre of mass depth and there was a noted increase in MVBS during 2015 and 2016 (Fig 2 and S4). This was accompanied by an increase in patch size based on Moran's I, reaching almost 60 km in 2016 (Fig 3). Although increasing backscatter can, in some cases, indicate increasing biomass (MacLennan and Simmonds, 1992), we were not able to distinguish between uncertainties associated with resonance effects (which can increase acoustic backscatter as a function of increasing pressure at depth Godø *et al.*, 2009; Davison *et al.*, 2015; Kloser *et al.*, 2016; Proud *et al.*, 2019) and changes in the species and length composition of the mesopelagic communities ensonified. For example, some of the most common mesopelagic fishes in the California Current possess gas bladders when young that regress with fat as the fish ages, leading to a counterintuitive decreases in backscatter with increasing size (Davison *et al.*, 2015). Without knowing the species composition or length distribution of the mesopelagic fish community, we are therefore unable to determine whether changes in acoustic backscatter can be attributed to increasing abundance or changes in the length or species distribution of the mesopelagic community. Of the limited catch data collected concurrently on the RREAS during 2013-2018, there was not an increase in mesopelagic fish during 2015-2016. A likely explanation is that trawling was restricted to the upper water column (between 30-45 m), thus inadequately sampling biomass of non-vertically migrating mesopelagic fishes. Furthermore, mesopelagic fishes have patchy distributions in space and time and are often composed of distinct aggregations of individual taxa (Benoit-Bird *et al.*, 2017), the intricacies of which are difficult to capture with discrete trawl samples. Hence, we cannot make definitive conclusions about overall biomass changes during the heatwave relative to other years, but recognize that his would be a valuable avenue for future research.

There is however some empirical evidence that previous increases in mesopelagic fish abundance in the CCE were linked to warmer ocean temperatures (Thompson *et al.*, 2014; Ralston *et al.*, 2015), as changes in advection likely contributed to a conveyance of oceanic species shoreward (Santora *et al.*, 2017). Some larval mesopelagic fishes with more warm water affinities increased in abundance three-fold during the heatwave in southern California (Thompson *et al.*, 2022). It is thus possible that better foraging conditions or warmer temperatures contributed to increased reproductive effort or shifts in the timing of spawning during this time, although it could also indicate changes in the horizontal distribution of mesopelagic taxa during the heatwave. As most of these studies occurred above mesopelagic depths (<200 m), our work also accentuates the need for long-term monitoring programs dedicated to documenting changes in the species composition, abundance and demographics of mesopelagic communities. Such efforts would help resolve whether changes in acoustic backscatter can be attributed to changes in absolute abundance or related to resonance effects or community demographic changes.

Broader ecosystem impacts

Mesopelagic fishes are important prey for a diversity of predators within the California Current, including economically valuable and protected species (Iglesias *et al.*, 2023). Recent findings suggest that Albacore foraging within the California Current specifically target shallow mesopelagic scattering layers to reduce energetic costs (Arostegui *et al.*, 2023). During the 2015-2016 marine heatwave, Northern Elephant seals (*Mirounga angustirostris)*, who rely on mesopelagic fishes as critical prey (Goetsch *et al.*, 2018), spent more time foraging at deeper depths (Holser, 2023), consistent with our result of a deeper distribution of mesopelagic fishes during this time. Increased vertical movement of both mesopelagic fishes and their predators likely exact a higher energetic cost, but the link between changing distributions of mesopelagic fishes and their higher trophic level predators have been limited by inadequate data on the distribution of mesopelagic prey and incomplete incorporation of mesopelagic taxa in ecosystem-based modelling efforts. Additional research exploring the trophic connections between mesopelagic fish and their higher trophic level predators would allow us to better evaluate and predict the effect of changing ocean conditions on the distribution of top predator populations.

Mesopelagic communities in an uncertain, but warmer future

Our study demonstrates that mesopelagic fishes inhabiting daytime depths between 175-675 m are impacted by surface intensified marine heatwave events. Although this study focuses on a single marine heatwave event in the California

Current that peaked in 2015-2016, our findings have broader implications for the impact of changing surface processes on global mesopelagic populations. Proud et al. (2017) predict a mean shoaling of the global mesopelagic zone and an associated increase in the biomass of mesopelagic organisms by 2100. As temperatures continue to warm and the frequency and severity of marine heatwaves is projected to increase (Frölicher *et al.*, 2018), mesopelagic fishes may play an increasingly important role as prey in the broader pelagic ecosystem. Few long-term deep pelagic monitoring programs exist, making it difficult to evaluate the response of mesopelagic fishes to changing ocean conditions. Our multi-year study highlights how using data collected during an ecosystem assessment survey (albeit one not specifically designed to monitor the mesopelagic) can nonetheless inform our understanding of mesopelagic communities and their habitat. A shallower or deeper mesopelagic community could have implications for carbon export and the availability of mesopelagic prey to higher trophic level predators. The interconnectedness of mesopelagic organisms to epipelagic processes provides evidence that mesopelagic ecosystems are susceptible to anthropogenic changes in surface waters and as it pertains to the largest biomass of fishes on earth, this finding could have cascading effects across both deep pelagic and epipelagic ecosystems.

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2.9 Supplementary Information

Figure S1 Sensitivity analysis comparing results of an interannual comparison of centre of mass depth [m] using a Kruskal-Wallis test with multiple comparisons at different regridding cell sizes (1, 5, 10, 15, 20 and 25 km)

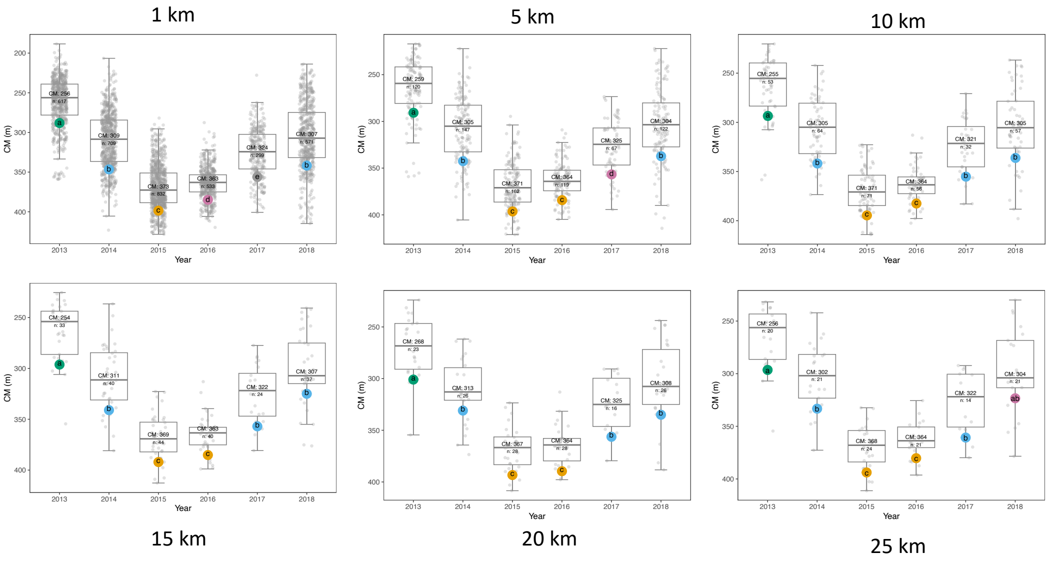


Figure S2 Pairs plot which evaluates collinearity amongst oceanographic covariates. We removed terms that were correlation with correlation coefficient values >0.7.

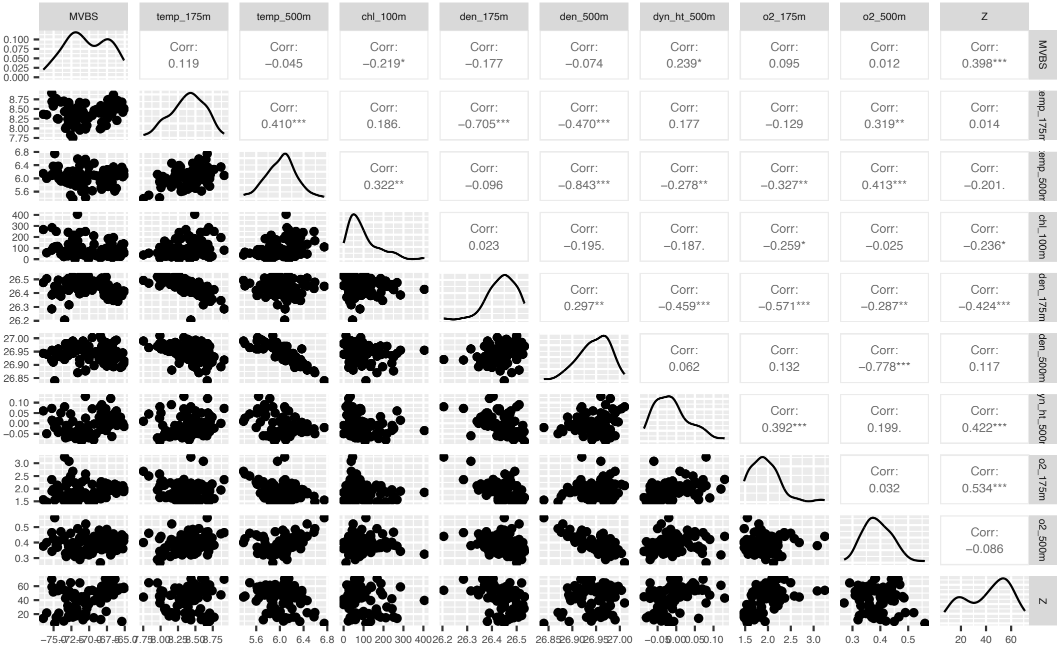


Figure S3 Model evaluation of the final generalized additive model (GAM) with center of mass depth as the response variable and oxygen and temperature at 175 m, oxygen at 500 m, dynamic height anomalies, chlorophyll in the upper 100 m, euphotic depth and mean backscatter (MVBS) as covariates.

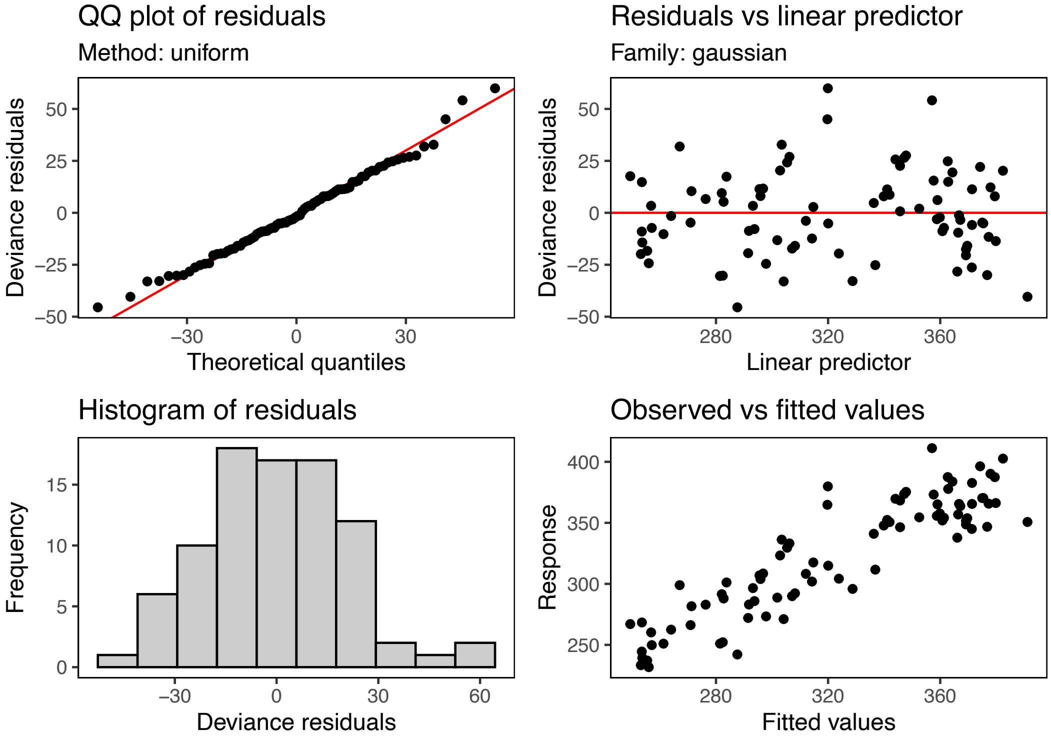
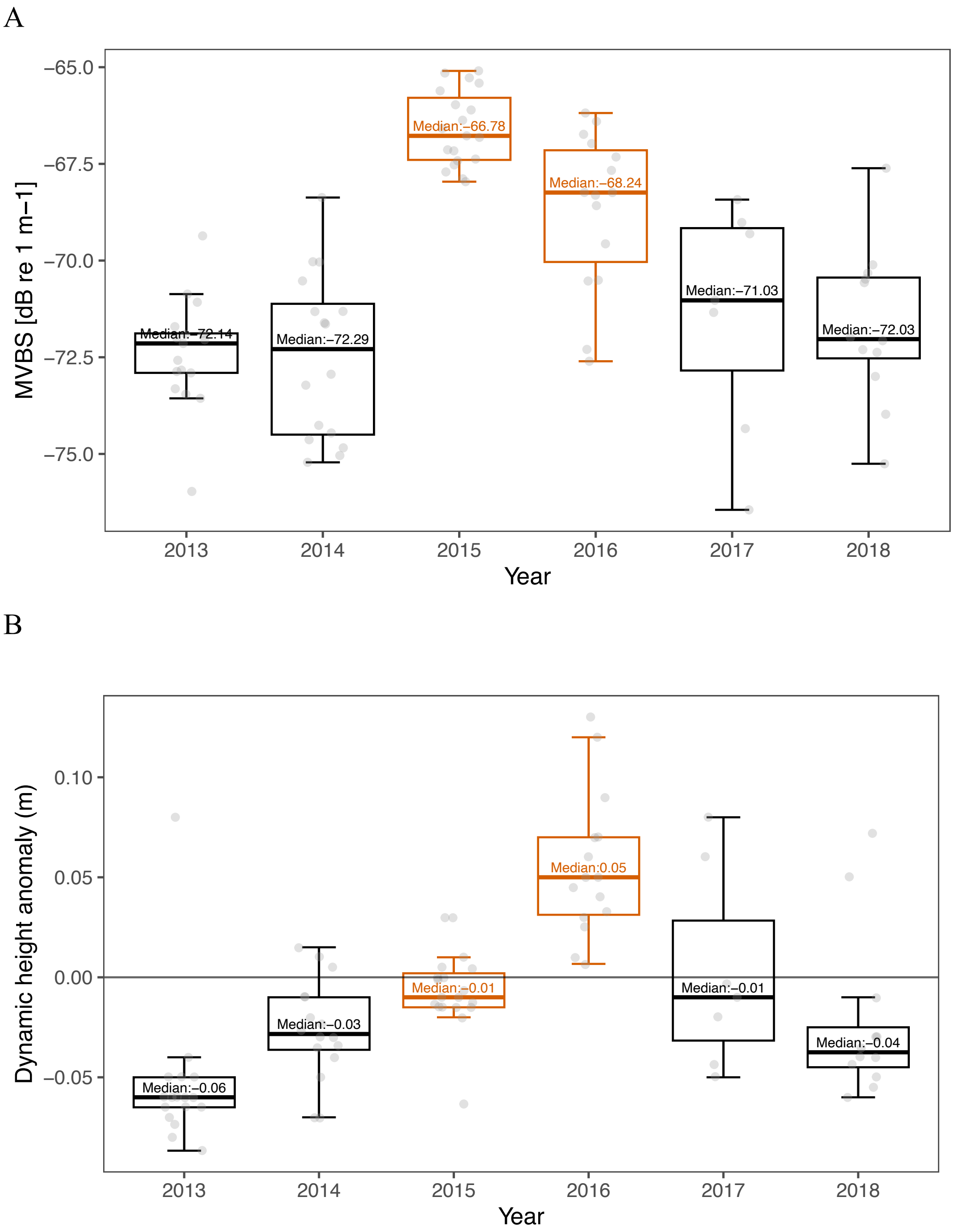
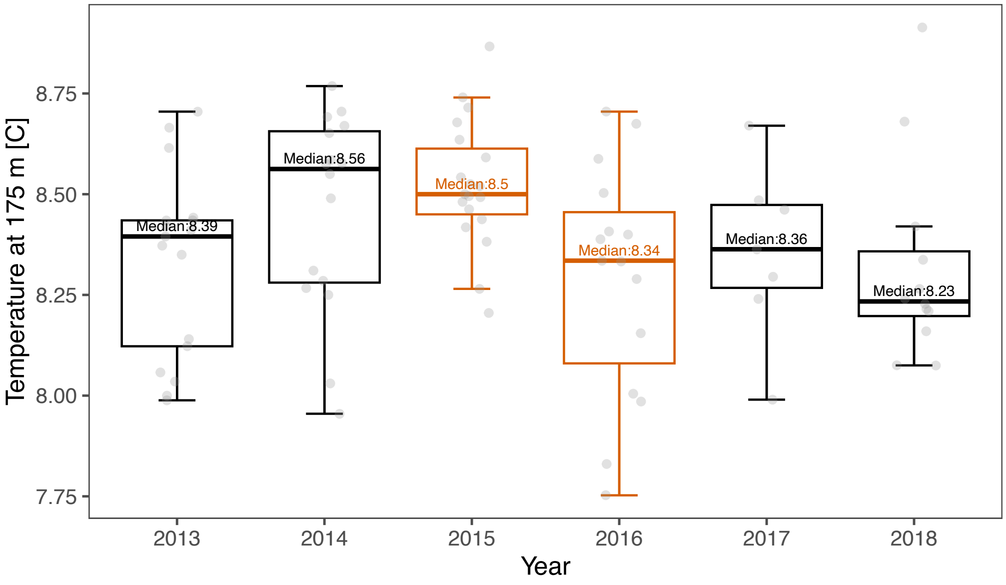


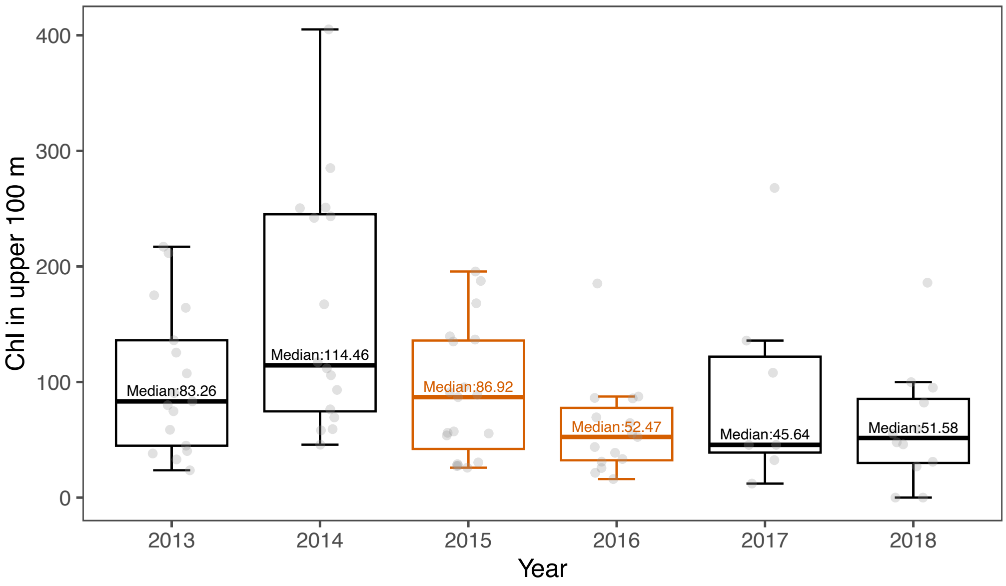
Figure S4 Interannual differences in acoustic backscatter (A) and oceanographic conditions measured from ship-board CTD measurements for dynamic height (B), temperature at 175 m (C) chlorophyll integrated in the upper 100 m (D) dissolved oxygen at 175 m (E) and temperature in the upper 10 m (F). Euphotic depth (Z) was estimated from Kd490 values from the Aqua MODIS satellite (G)



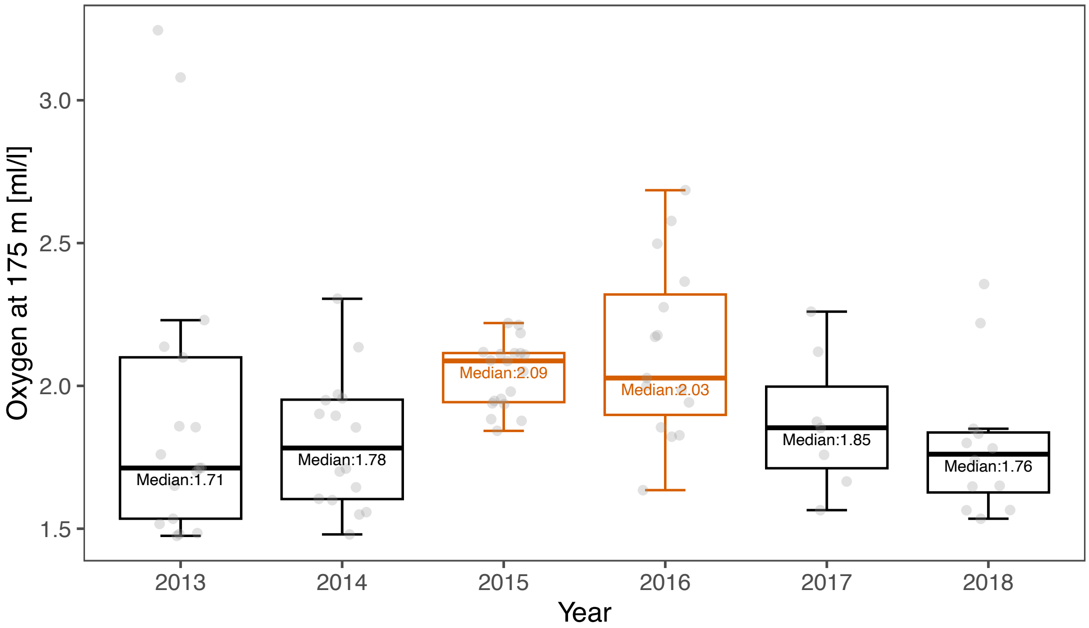
C


Temperature at 175 m [C]
8.75
8.50
8.25
8.00
7.75
Median:8.39
Median:8.56
Median:8.5
Median:8.34
Median:8.36
Median:8.23
2013
2014
2015
2016
2017
2018
Year

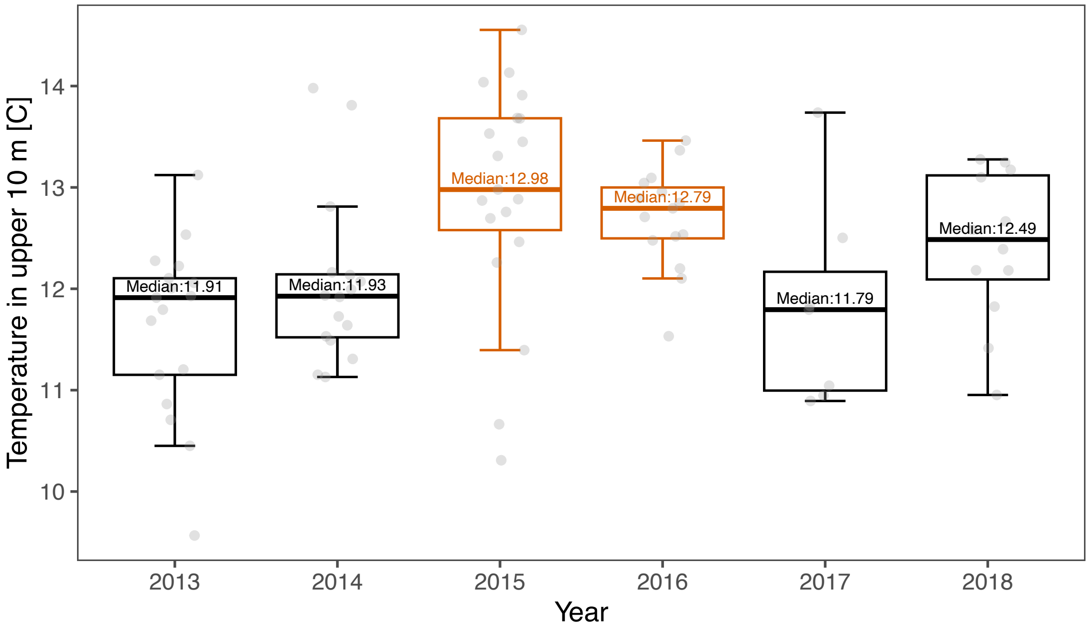
D


Chl in upper 100 m
400
300
200
100
0
Median:83.26
Median:114.46
Median:86.92
Median:52.47
Median:45.64
Median:51.58
2013
2014
2015
2016
2017
2018
Year

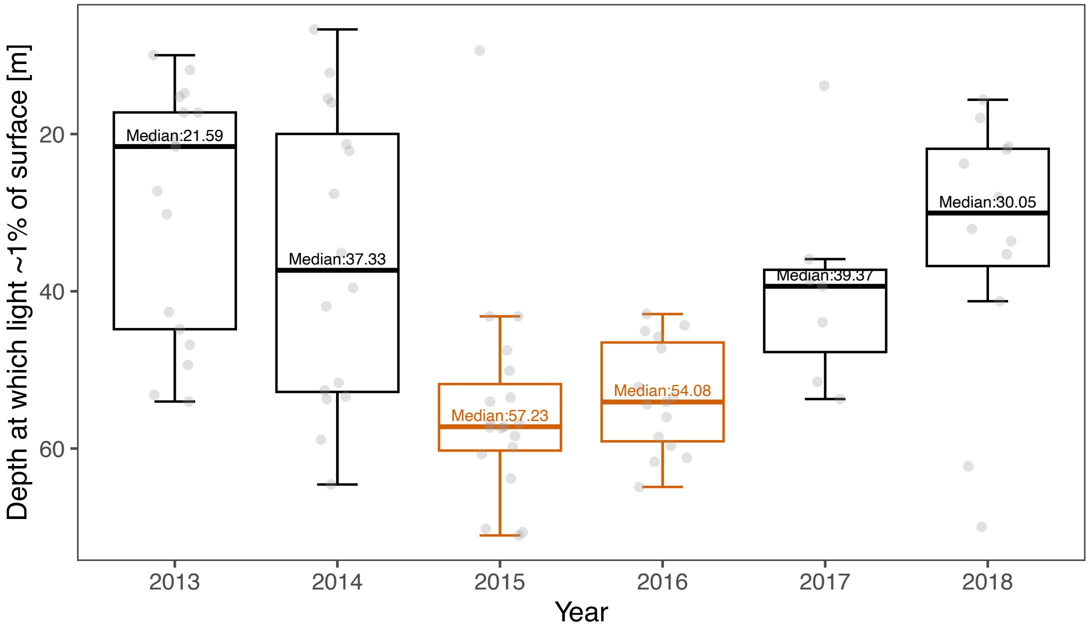
E


Oxygen at 175 m [ml/l]
3.0
2.5
2.0
1.5
Median:1.71
Median:1.78
Median:2.09
Median:2.03
Median:1.85
Median:1.76
2013
2014
2015
2016
2017
2018
Year

F


Temperature in upper 10 m [C]
14
13
12
11
10
Median:11.91
Median:11.93
Median:12.98
Median:12.79
Median:11.79
Median:12.49
2013
2014
2015
2016
2017
2018
Year

G


Depth at which light ~1% of surface [m]
20
40
60
Median:21.59
Median:37.33
Median:57.23
Median:54.08
Median:39.37
Median:30.05
2013
2014
2015
2016
2017
2018
Year

Chapter 3

Projected 21st century vertical compression of mesopelagic habitat in the California Current

3.1 Abstract

Despite its separation from the oceans' surface, deep pelagic ocean habitats are nonetheless impacted by the effects of climate change. Using an ensemble of downscaled climate projections under the RCP8.5 scenario, we evaluated 21st century changes in the vertical extent of mesopelagic habitat for the central California Current region. The model projections suggest a significant loss of mesopelagic habitat by the end of the 21st century (2070-2100) relative to present-day conditions (2000-2030). While the vertical extent of mesopelagic habitat declined ~58% (~45 m), the response was spatially variable, with predicted losses exceeding 50 m in the northern, offshore regions of our study domain and along the slope. Most of this change was driven by a shoaling of the lower limit of the mesopelagic zone, defined here as the hypoxic boundary (i.e., dissolved oxygen concentration of 60 $mmol/m^3$). Dissolved oxygen concentrations at 330 m (historical hypoxic depth) were projected to decrease by $\sim 10\ mmol/m^3$, exposing organisms inhabiting these depths to hypoxic conditions as early as the mid-21st century. In the projections, this oxygen decrease is associated with a 1.1°C increase in temperature at 200 m and a deepening of the 26.5 kg/m^3 isopycnal by more than 50 m. Differences amongst ensemble members, selected to represent the range of warming rates under the RCP8.5 scenario, were related to

differences in the oxygen content of water entering the southern boundary of our domain and highlight the potential importance of equatorial dynamics in shaping oxygen content at mesopelagic depths in the California Current. Overall, our results indicate that although the deep pelagic ocean represents some of the greatest volume of habitat on earth, the portion that is livable for higher organisms is expected to compress by the end of the century as a result of climate change.

3.2 Introduction

The deep pelagic ocean comprises up to 90% of the habitable volume of earth (Haddock and Choy, 2024). The upper portion of the deep pelagic ocean, the mesopelagic zone, occurs at depths between 200-1000 m and is home to a diverse assemblage of life, whose vertical movements connect the surface ocean to the deep sea. Unlike other marine habitats delineated by physical structures (corals, seafloor, coastline, etc.), mesopelagic habitats are defined exclusively by dynamical oceanographic conditions and processes. Although the mesopelagic zone is vast, a changing climate may limit the amount of this habitat that can support life. Deoxygenation is predicted to cause a global shoaling of mesopelagic habitats with associated losses in biodiversity (Stramma et al., 2010; Proud et al., 2017). Deep pelagic communities are diverse (Webb et al., 2010) and critical for ecosystem function- providing prey for higher trophic level predators (Iglesias et al., 2023) and facilitating carbon export (Irigoien et al., 2014), so any changes that limit their vertical extent in the water column could have cascading effects on the greater ocean ecosystem. Despite this significance, the deep pelagic ocean remains one of the least understood ecosystems on earth (Webb et al., 2010; St. John et al., 2016).

The diverse assemblage of organisms inhabiting mesopelagic depths, referred to collectively as the Deep Scattering Layer (hereafter "DSL), was originally identified by the strong acoustic backscatter reflected from organisms inhabiting the water column (Burd and Lee, 1951). While numerous oceanographic conditions influence the horizontal distribution of the DSL community globally (Sutton et al., 2017), light is important in limiting the upper vertical extent of the DSL (Røstad et al., 2016; Aksnes et al., 2017; Langbehn et al., 2019), as organisms attempt to evade visual predators (Longhurst, 1976). The lower boundary of the DSL, has been attributed to physiological limitations related to dissolved oxygen (Bertrand et al., 2010; Peña et al., 2014; Duncan et al., 2024). Within the California Current, the upper and lower boundaries of the DSL have been likewise connected to light and dissolved oxygen (Netburn and Koslow, 2015), but a lack of long-term mesopelagic studies have limited the inference that can be made about the direct and indirect effects of climate change related changes in light and oxygen on the distribution of mesopelagic communities. However, decreases in the abundance of mesopelagic fishes in southern California have been linked to declining oxygen (Koslow et al., 2011) and mesopelagic fishes have been shown to respond to marine heatwaves by changing their vertical distribution (Iglesias et al *in revision*), which suggests that mesopelagic communities are likely to be impacted by oceanographic changes associated with anthropogenic climate change.

The California Current Ecosystem (CCE), a productive eastern boundary region driven by seasonal upwelling (Checkley and Barth, 2009), is also the northward extension of a large oxygen minimum zone (OMZ) spanning most of the Eastern Pacific and which contributes to some of the shallowest observed distributions of mesopelagic communities globally (Klevjer et al., 2016). Hypoxic depths of 400 m are typical for the California Current, where hypoxic depth is defined as $60\ \mu mol/L \approx 60\ \mu mol/kg$ (Keeling et al., 2010). Hypoxic boundary depths can vary seasonally in response to coastal upwelling (Connolly et al., 2010), leading to increasingly hypoxic conditions on shallow shelf regions of the Northern California Current (Chan et al., 2008; Barth et al., 2024). Globally, continued expansion of OMZs since the mid 20th century has been linked to warming ocean temperatures (which controls oxygen saturation), stratification (which limits mixing), and changes in circulation (which influence source water and ventilation rates) (Keeling et al., 2010; Breitburg et al., 2018). Declining oxygen and the expansion of OMZs can have profound impacts on biological communities (Gilly et al., 2013), including habitat compression and biodiversity loss (Stramma et al., 2010). During 1984-2006, oxygen declined by 21% at 300 m depth in southern California, while the hypoxic boundary shoaled by up to 90 m (Bograd et al., 2008). Seasonal shoaling of the oxycline associated with coastal upwelling can limit the vertical extent and abundance of mesopelagic organisms in the California Current (Urmy and Horne, 2016), such as the observed shoaling of the lower boundary of the DSL during the late-winter and spring in Monterey Bay (Urmy et al., 2012).

Despite technological advances that have allowed for more continuous sampling of deep ocean environments, there remains limited observational data characterizing the mesopelagic zone (Levin et al., 2019). Further limiting the extent of observations in the deep ocean is the fact that satellite data cannot measure ocean state beyond the near-surface layers of the ocean. In the absence of *in situ* observations, regional ocean models are thus valuable to identify and predict physical and biogeochemical processes shaping the mesopelagic environment. Here, we use a combination of hindcast and downscaled regional climate projections from a coupled physical, biogeochemical ocean model (Kishi et al., 2007; Haidvogel et al., 2008) to provide the first assessment of spatial and temporal changes in the vertical extent of mesopelagic habitat in the central California Current by the end of the 21st century.

3.3 Methods

Coupled Physical-Biogeochemical Model

Physical properties of the regional circulation (temperature, salinity, ocean currents) are generated using an implementation of the Regional Ocean Modeling System (ROMS) (Shchepetkin and McWilliams, 2005; Haidvogel et al., 2008) for the California Current System with a horizontal resolution of 1/30° (~3 km) and 42 vertical terrain-following levels. Biogeochemical properties are generated using NEMUCSC, which is a customized version of the North Pacific Ecosystem Model for

Understanding Regional Oceanography (NEMURO) of (Kishi et al., 2007). NEMUCSC includes three limiting macronutrients (nitrate, ammonium, and silicic acid), two phytoplankton functional groups (nanophytoplankton and diatoms), three zooplankton size-classes (microzooplankton, copepods, and euphausiids), and three detritus pools (dissolved and particulate organic nitrogen and particulate silica). In its current version, NEMUCSC also simulates carbon and oxygen cycling following the formulations of (Hauri et al., 2012; Fennel et al., 2013) respectively.

Two different high resolution (1/30°) implementations of ROMS-NEMUCSC are considered here for analysis: a historical simulation encompassing the latitudes 30-48 °N for 1995-2020, and an ensemble of three downscaled climate projections encompassing the latitudes 32-44 °N for 2000-2100. For the historical simulation (hindcast), ROMS is forced at the surface with atmospheric fields from the ERA5 reanalysis and at the model open ocean boundaries by the GLORYS global reanalysis. NEMUCSC is similarly forced by daily averaged shortwave solar radiation from ERA5 and the GLORYS global hindcast for nutrients and dissolved oxygen at the open ocean boundaries. For the projections (forecast), we used a 1/30° model domain nested within the 1/10° downscaled regional climate projections of (Pozo Buil et al., 2021) for the broader California Current region. Briefly, the regional projections downscale three earth system model solutions representative of the physical and biogeochemical CMIP5 ensemble spread under the RCP8.5 high emissions scenario (GFDL-ESM2M(hereafter ROMS-GFDL) = low rate of warming; IPSLCM5 (ROMS-IPSL) = rate of warming close to ensemble mean; Hadley-GEM2-

E (ROMS-HAD) = high rate of warming. We then calculated the means for May-June to correspond with observation (RREAS) data, and to examine the seasonal period when the DSL is most likely to experience upwelling related shoaling (Urmy et al., 2012; Urmy and Horne, 2016). Additional details on the ROMS-NEMUCSC configuration and evaluation for the historical period can be found in (Fiechter et al., 2018, 2020; Cheresh and Fiechter, 2020; Cheresh et al., 2023). Further information on the ROMS-NEMUCSC configuration for the downscaled regional climate projections can be found in (Fiechter et al., 2021; Pozo Buil et al., 2021).

Evaluation of historical simulation (hindcast)

The ability of model fields to represent observed oceanographic conditions was evaluated using hydrographic data collected as part of the NOAA Southwest Fisheries Science Center, Rockfish Recruitment and Ecosystem Assessment Survey (RREAS). The RREAS occurs in the spring (May-June) of each year and collects *in situ* water column measurements down to 500 m at predetermined CTD locations (Santora et al., 2012, 2021). Temperature, density and chlorophyll observations were available from 1995 to present and dissolved oxygen concentrations from 2009 to present. No CTD data were available in 2011 and 2020 due to equipment issues and the COVID pandemic, respectively. Outliers in the CTD data were identified as temperature, dissolved oxygen or density observations greater than 3 standard deviations from the long-term mean and subsequently removed from analysis. Model chlorophyll was derived from simulated diatom and nanophytoplankton concentrations using a fixed C:N Redfield ratio and constant C:Chl ratio of 50 for diatoms and 100 for nanophytoplankton (Fiechter et al., 2018). To focus on the effect of chlorophyll on light attenuation in the upper water column, simulated and observed values were compared in terms of vertically integrated concentrations from the surface to 100 m depth. We also evaluated modeled and observed values of the 26.5 kg/m^3 isopycnal depth as an approximation for upwelling strength, as this isopycnal typically occurs at depths just below source waters for upwelling (Fiechter and Moore, 2024). We were unable to compare irradiance from simulated and observed values due to measurement discrepancies (total solar irradiance in the simulation (W/m^2) versus photosynthetically active radiation (PAR) at wavelengths between 400-700 nm for observations). Model-observation data agreement was quantified in terms of: (i) long-term means at specific depths (i.e., mean across all years) (Figure 2), (ii) temporal trends (i.e., slope of linear regression over time) (Figures 2, 3), (iii) bias (i.e., simulated minus observed long-term mean) (Figures 2, 3), (iv) interannual variability based on the ratio of simulated to observed standard deviation (Figure 2, 3), and (v) Pearson's correlation coefficients (Figures 2, 3).

Evaluation of downscaled projections (forecast)

Since earth system model solutions represent a free-running evolution of the climate system, they are only expected to reproduce past variability in a statistical sense (e.g., an earth system model will have El Niño events, but not necessarily during years when actual El Niño events were observed). Hence, due to the inherent lack of temporal correlation between the projections and observations, we took the approach here to first evaluate the historical simulation against in situ measurements (CTD casts) and then demonstrate that the downscaled climate projections have means and variability comparable to those of the historical simulation for their overlapping period (2000-2020). Given our focus on characterizing the future evolution of mesopelagic habitat, we compared the three climate projections (GFDL, IPSL, Hadley) to the historical simulation in terms of: (i) temperature at 200 m depth, (ii) depth of 26.5 kg/m^3 isopycnal, (iii) depth of 0.01035 W/m^2isolume (representative of mean historical (2000-2020) light intensity at 200 m over our study domain from the historical simulation), and (iv) depth of 60 $mmol/m^3$dissolved oxygen concentration (representative of hypoxic boundary) (Fig. 5). We chose a hypoxic boundary threshold of 60 $mmol/m^3$($\approx 60\ \mu mol/L \approx 60\ \mu M$), consistent with previous authors (Keeling et al., 2010; Deutsch et al., 2011; Köhn et al., 2022), similar to others (for example 63 $mmol/m^3$in Breitburg et al., 2018 and $\sim 60\ \mu mol/kg$ in (Bograd et al., 2008)), and physiologically limiting for many marine animals (Gray et al., 2002; Vaquer-Sunyer and Duarte, 2008). We did not include a metric for integrated chlorophyll here, as chlorophyll (integrated in the upper 100 m) and depth of the 0.01035 W/m^2isolume were highly correlated (R-squared above 0.90) in the historical simulation and in each downscaled projection. To facilitate comparison, all variables were spatially averaged over the same core RREAS region (Figure 1) used to evaluate the historical simulation against *in situ* observations.

Evaluating changes in the vertical extent of mesopelagic habitat

To quantify regional changes in the availability of vertical habitat for mesopelagic organisms, the analysis domain was expanded from that used for model evaluation (i.e., core RREAS area) to a broader region encompassing latitudes from Point Conception (34.5 °N) to Cape Mendocino (40 °N) and longitudinally from the 200 m isobath to 200 km offshore (Figure 1). A distance of 200 km offshore was chosen to span the core of the poleward flowing California Undercurrent (Ren et al., 2018). Four oceanographic quantities were calculated to characterize the mesopelagic zone and its variability in space and time: (i) temperature at 200 m was used as a proxy for temperature change at the upper limit of the mesopelagic zone in the central California Current (ii) depth of the 26.5 kg/m^3 isopycnal, as a proxy for changes in upwelling dynamics (iii) depth at which light intensity equaled mean hindcast estimates at 200 m from 2000-2020 over the expanded study area (0.01035 W/m^2), hereafter referred to as "isolume depth", and (iv) depth at which dissolved oxygen reached 60 $mmol/m^3$, representative of the hypoxic boundary. For each metric, we examined the ensemble mean and spread, calculated as the mean or standard deviation of the three ensemble members (ROMS-GFDL, ROMS-IPSL, and ROMS-Hadley) over our study domain (Figures 5, 6). Ensemble spread represents a measure of model uncertainty in our ability to predict the future evolution of mesopelagic habitat characteristics, given inherent variability in warming rates across different model projections under a fixed emission scenario. Since the vertical extent of mesopelagic organisms in the California Current has previously been linked to light

(Netburn and Koslow, 2015) and oxygen (Netburn and Koslow, 2015; Urmy and Horne, 2016), we define mesopelagic habitat here as the distance (in meters) between the isolume depth and the hypoxic boundary below (or bottom depth for those regions with bottom depths greater than 200 m, but that do not reach the 60 $mmol/m^3$ threshold) (Figure 6, 7). Although previous research has indicated that mesopelagic fish may be selecting for low oxygen (Netburn and Koslow, 2015), there is compelling evidence that it is light, often correlated with oxygen, driving the upper boundary of the DSL globally (Aksnes et al., 2017). We thus chose light as the variable shaping the upper distribution of the mesopelagic habitat, while recognizing that more research is needed to ascertain the specific factors affecting the upper limit of daytime mesopelagic community distributions.

3.4 Results

Model evaluation

The historical simulation (1995-2020) exhibited reasonable agreement with conditions observed *in situ* (CTD casts) at mesopelagic depths of ~ 150 to 300 m. While simulated temperature values underestimated observed means, biases were small (less than ~0.5 °C) and standard deviation ratios were between 0.75 and 1.5. Pearson's correlation coefficient values between modeled and observed temperatures ranged from ~0.40 to 0.63 and simulated and observed trends were in the same (positive) direction (Fig. 2). In contrast, simulated dissolved oxygen concentrations overestimated the observed means and variability at mesopelagic depths, with biases of ~6.6 to 9.1 $mmol/m^3$ for depths of 100-300 m, increasing to ~12.5 and 14.6 $mmol/m^3$ at 400 and 500 m depths. Standard deviation ratios were between 1 and 1.5 at mesopelagic depths (150-300 m) but increased to >2 at 400-500 m (Fig. 2). Correlations between simulated and observed dissolved oxygen concentrations in the mesopelagic zone were greatest (~0.8) for depths of ~ 150 to 300 m and decreased to ~0.52 and 0.06 at 400 and 500 m. Simulated values also correctly reproduced the large, positive trends observed in the upper part of the mesopelagic zone (100-300 m) over the period considered for model evaluation. Below 300 m, simulated and observed trends decreased rapidly, with simulated trends remaining positive and observed values switching slightly negative at 500 m.

For depth-integrated chlorophyll, both model and observations exhibited a declining trend over the period considered and simulated values reproduced observed interannual variability with a correlation of 0.46 (Fig. 3). However, the model underestimated the magnitude of the long-term mean (bias of -7.58 mg/m3) and year-to-year fluctuations (standard deviation ratio of 0.41). For the depth of the 26.5 kg/m^3 isopycnal, simulated and observed values indicated a similar positive (deepening) trend over the period considered and were correlated inter annually at 0.60. The model also adequately reproduced the long-term mean (bias of less than 5 m) and year-to-year fluctuations (standard deviation ratio of 1.14). For both variables, the simulated and observed long-term trend were small relative to the interannual variability, explaining only ~8% of the variance for chlorophyll and 12-15% of the variance for isopycnal depth.

A comparison of mesopelagic habitat metrics across the historical simulation and regional ocean models forced with downscaled climate projections over the RREAS region for 2000-2020 revealed means and interannual variability of comparable magnitudes. Considering that the projections are not expected to reproduce the exact timing of specific ocean conditions (e.g., ENSO events), their agreement with the historical simulation for 2000-2020 indicates consistent physical and biogeochemical dynamics (Fig. 5). Where there were significant differences between the mean of an ensemble member and the historical simulation (demarcated with an * in figure 4), biases were similar to or within one standard deviation of the mean of the historical simulation (i.e., bias of <0.20 °C vs. SD of 0.20 °C for temperature; bias of 10-12 m vs. SD of ~14 m for isopycnal depth; and bias of ~ -11 m vs. SD of ~14 m for isolume depth). Hence, we considered the downscaled projections adequate for examining future changes in mesopelagic habitat out to 2100.

Projected changes in oceanographic conditions of the mesopelagic zone

The ensemble of three downscaled climate projections (ROMS-GFDL, ROMS-IPSL and ROMS-HAD) for the central California Current suggests a warmer and less oxygenated mesopelagic zone by the end of the 21st century compared to present-day conditions. Temperature at the upper boundary of the mesopelagic zone (200 m depth), was projected to warm significantly (t-test $p<2.2e-16$) by an average of 1.1°C from a mean of ~7.8°C (2000-2030) to 8.9°C (2070-2100) and a trend of

0.02 [°C/year], while the depth of the 26.5 kg/m^3 isopycnal was projected to deepen by an average of 56 m (t-test, p-value<2.2e-16, 2000-2030 vs 2070-2100, Figure 5) with a trend of 0.81 [m/year]. In the coastal central California Region examined here, isopycnals typically tilt upward as you approach the coast, associated with the upwelling of deeper, denser waters to the surface, which fuel primary productivity. A deepening of the 26.5 kg/m^3 isopycnal, would thus indicate a reduction in isopycnal tilt related to weakened upwelling and/or a shallower depth of upwelling source waters. The depth of the hypoxic boundary (60 $mmol/m^3$) was projected to shoal by ~ 52 m from a mean of ~306 m in 2000-2030 to ~254 m for 2070-2100, with a minimum spatial mean value occuring as shallow as 226 m. The depth of the 0.01035 W/m^2 isolume deepened significantly between the start and end of the 21st century (t-test, p-value = 8.681e-06), but the magnitude of this change was small (~5 m, from ~199 m to 204 m) relative to those of the hypoxic boundary and 26.5 kg/m^3 isopycnal. A long-term increase of light intensity at depth (i.e., deeper isolume) is generally consistent with decreased upwelling (i.e. deepening isopycnal), which could reduce nutrient supply to the euphotic zone and subsequently decrease primary production (we observed a slight decrease in chlorophyll (linear trend: -0.01 [mg/m3/yr], r-squared: 0.688)).

Projected changes in vertical extent of mesopelagic habitat

A comparison of vertical mesopelagic habitat (distance from isolume depth to hypoxic boundary) available by the end of the 21st century (2070-2100 mean) relative to present-day conditions (2000-2030 mean) revealed a statistically significant decline by ~45 m (from ~107 m to ~62 m, t-test, p-value < 2.2e-16), comparable to ~58% decline in mesopelagic habitat (Fig. 6, lower left). Because the upper boundary (i.e., 0.01035 W/m^2 isolume depth), only deepened by ~5 m (Figure 5), the majority of this change was caused by the shoaling of the lower boundary (i.e., hypoxic depth or bottom depth for waters that did not reach hypoxic conditions). The period of steepest decline in mesopelagic habitat occurred from ~2045-2065 (Figure 6). The three ensemble members (ROMS-GFDL, ROMS-IPSL and ROMS-HAD) varied on either side of the ensemble mean until the middle of the century, but starting from ~2050 onward, both ROMS- IPSL and ROMS-GFDL predicted continued declines in habitat (to a mean of ~12 and 20 m vertical extent of mesopelagic habitat by 2070-2100), while ROMS- HAD projected *increases* (to a mean of ~154 m) by the end of the century. This bifurcation around the middle of the century contributed to increasing uncertainty (calculated as ensemble spread) in the latter half of the century. Dissolved oxygen concentrations at the mean depth of the historical hypoxic boundary depth (330 m), declined by 10 $mmol/m^3$ from a mean of ~61 $mmol/m^3$ for 2000-2030 to ~51 $mmol/m^3$ for 2070-2100 (Fig. 6, lower right), but the response varied by ensemble member. Whereas both ROMS-GFDL and ROMS-IPSL exhibited declining trends, ROMS-HAD predicted increases in oxygen at 330 m depth from ~2065 onwards.

During 2000-2030, the areas with the greatest vertical mesopelagic habitat extent (≥100 m) generally occurred along the slope and offshore to the north of ~37.5 °N and offshore of Monterey Bay (~36.5 to 37 °N). However, by 2070-2100, most of this habitat was vertically compressed, with only a very thin region of habitat left along the northern slope, greater than 100 m (Figure 6). The extent of mesopelagic habitat compression varied spatially, but the greatest loss occurred offshore in the region between San Francisco and Cape Mendocino (latitudes ~37.5 to 40 °N), a small patch offshore and to the south of Monterey Bay (~35.5 °N) and a thin band along the continental slope (Figure 6, upper panels). Although the overall trend was a decline in mesopelagic habitat, there was also a region in the southern end of our study region, just north of Point Conception (~34.5 to 36 °N), where there was limited change in mesopelagic habitat, and even some growth (by up to a max of 13 m) between the end and beginning of the 21st century. Spatial differences were apparent between the three ensemble members (Figure 7), with both ROMS-GFDL and ROMS-IPSL exhibiting coastwide decreases in mesopelagic habitat in 2070-2100 compared to 2000-2020. ROMS-HAD conversely, predicted increased oxygen in 2070-2100 compared to 2000-2030, and this effect was most pronounced in the southern range of our domain and intensified along the coast. Overall, the vertical extent of future mesopelagic habitat was significantly reduced (95% confidence level) compared to present-day values over most of the analysis domain, except for a narrow region north of Pt Conception near Santa Lucia Bank (~35 °N) and adjacent slope, where changes in habitat are projected to be small.

3.5 Figures

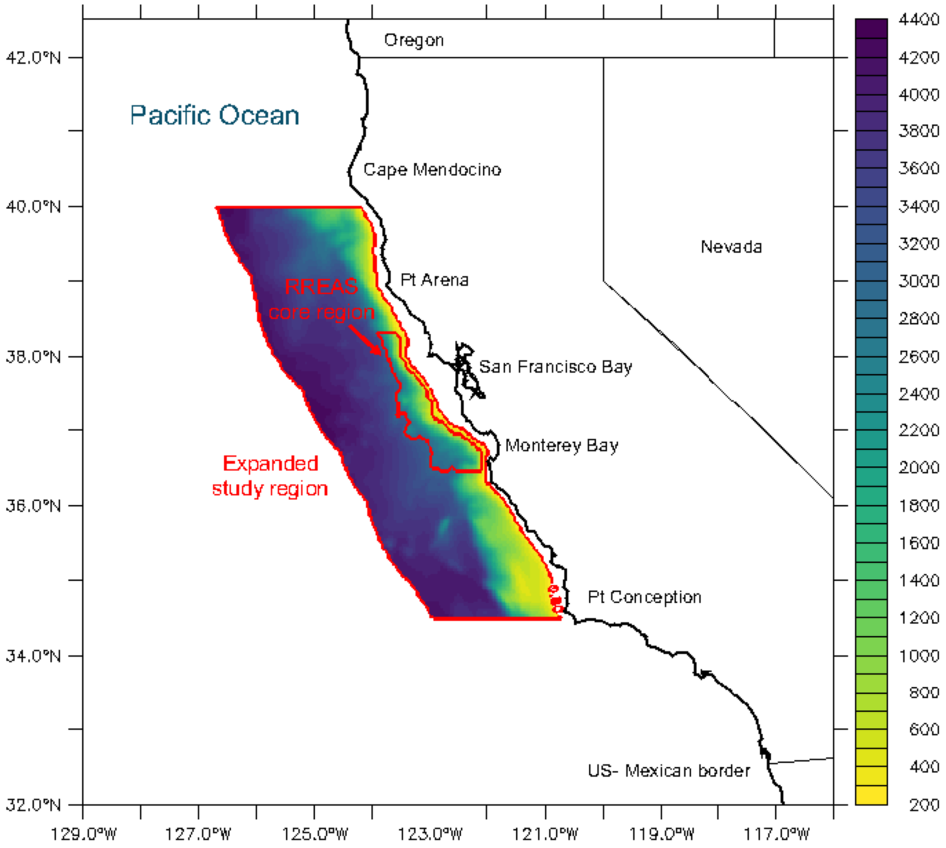


Figure 1 Location of Rockfish Recruitment and Ecosystem Assessment "core" Survey area (smaller red polygon) used to evaluate historical simulation against CTD observations and downscaled climate projection ensemble members (GFDL, IPSL, Hadley). The RREAS core region extends from 36.45 to 38.33 °N and from ~500 to 2500 m isobaths. Our expanded study domain (larger red polygod) extends to over the central California Current region, from Point Conception (34.5 °N) to Cape Mendocino (40 °N) and from the 200 m isobath to 200 km from the coast.

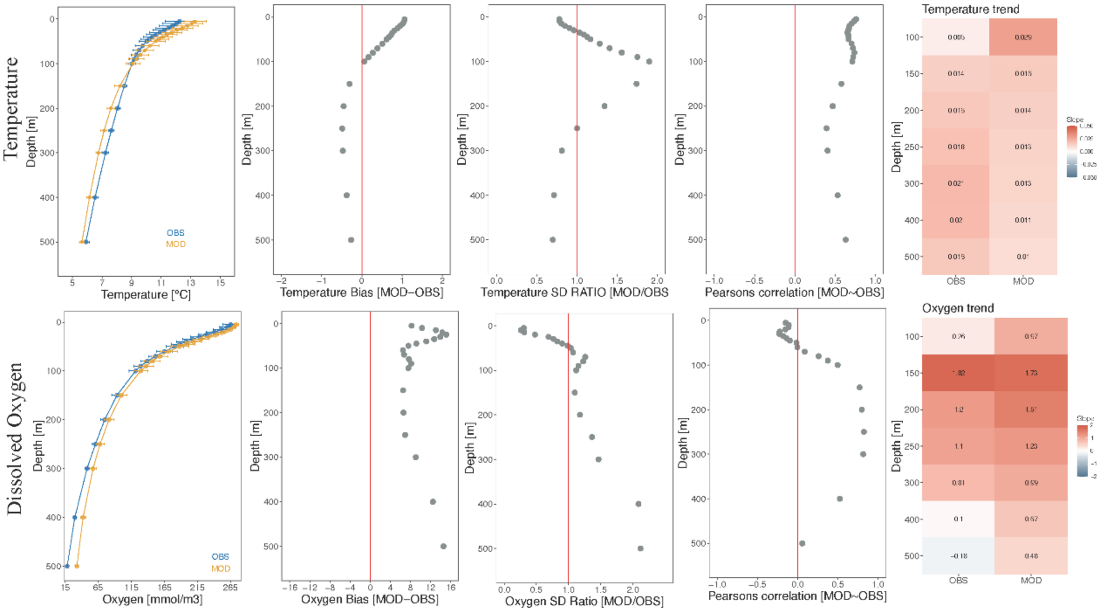


Figure 2 Comparison of historical simulated (MOD) and observed (OBS) temperature (upper panels) and dissolved oxygen (lower panels) as a function of depth. From left to right: long-term means, bias, standard deviation ratio, Pearson's correlation coefficient, and trend.

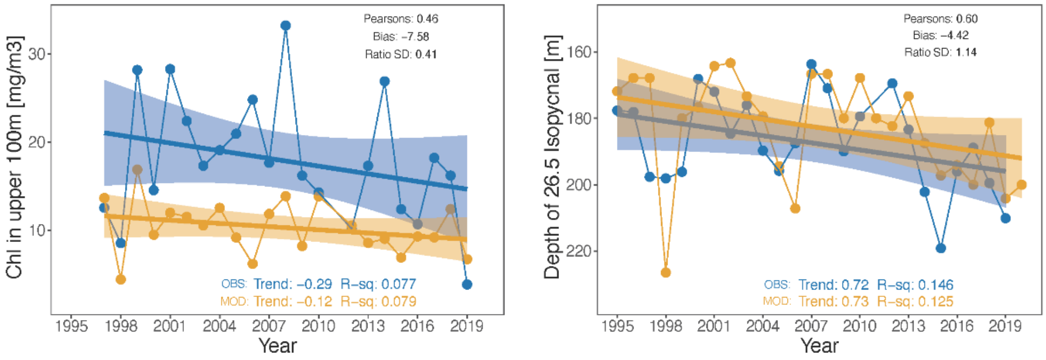


Figure 3 Comparison of historical simulated (MOD) and observed (OBS) depth-integrated (0-100 m) chlorophyll concentrations (left) and depth of 26.5 kg/m3 isopycnal (right). Corresponding values for the trend, Pearson's correlation coefficient, bias, and standard deviation ratio are indicated in each panel.

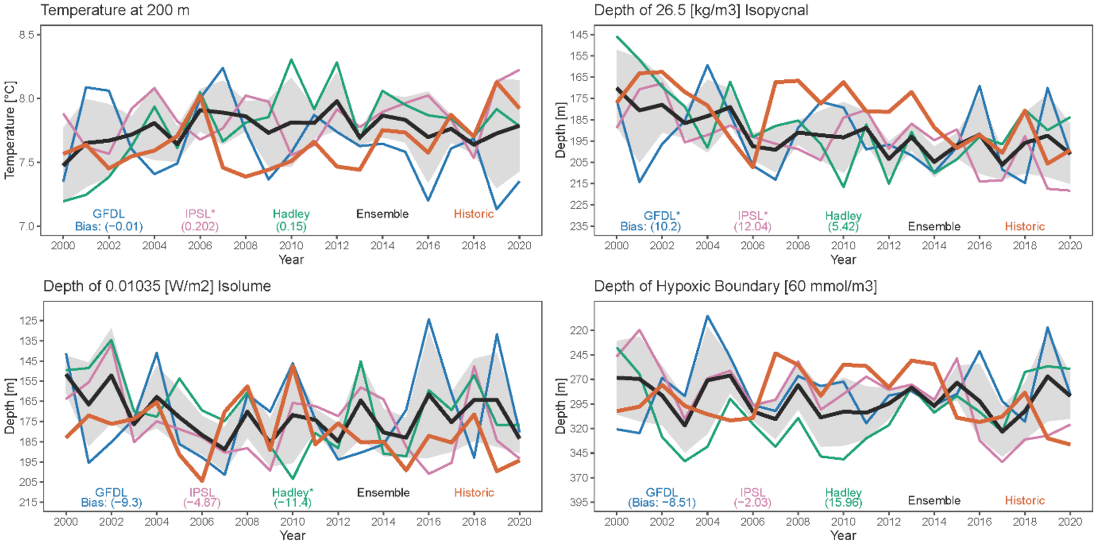


Figure 4 Comparison of historical simulation (orange) and downscaled climate projections (blue = GFDL, pink = IPSL, green = Hadley) for 2000-2020 in the core RREAS region. (Top left) Temperature at 200 m, (Top right) Depth of 26.5 kg/m^3 isopycnal, (Bottom left) Depth of 0.01035 W/m^2 isolume, (Bottom right) Depth of hypoxic boundary (60 $mmol/m^3$). In all panels, the black line represents the ensemble mean and gray shading the ensemble spread (standard deviation between the three ensemble members). Ensemble member means that varied significantly from the historical simulation means (determined from 2-tailed t-test, p-values <0.05) are demarcated with asterisk (*), and bias values are presented as the difference in means.

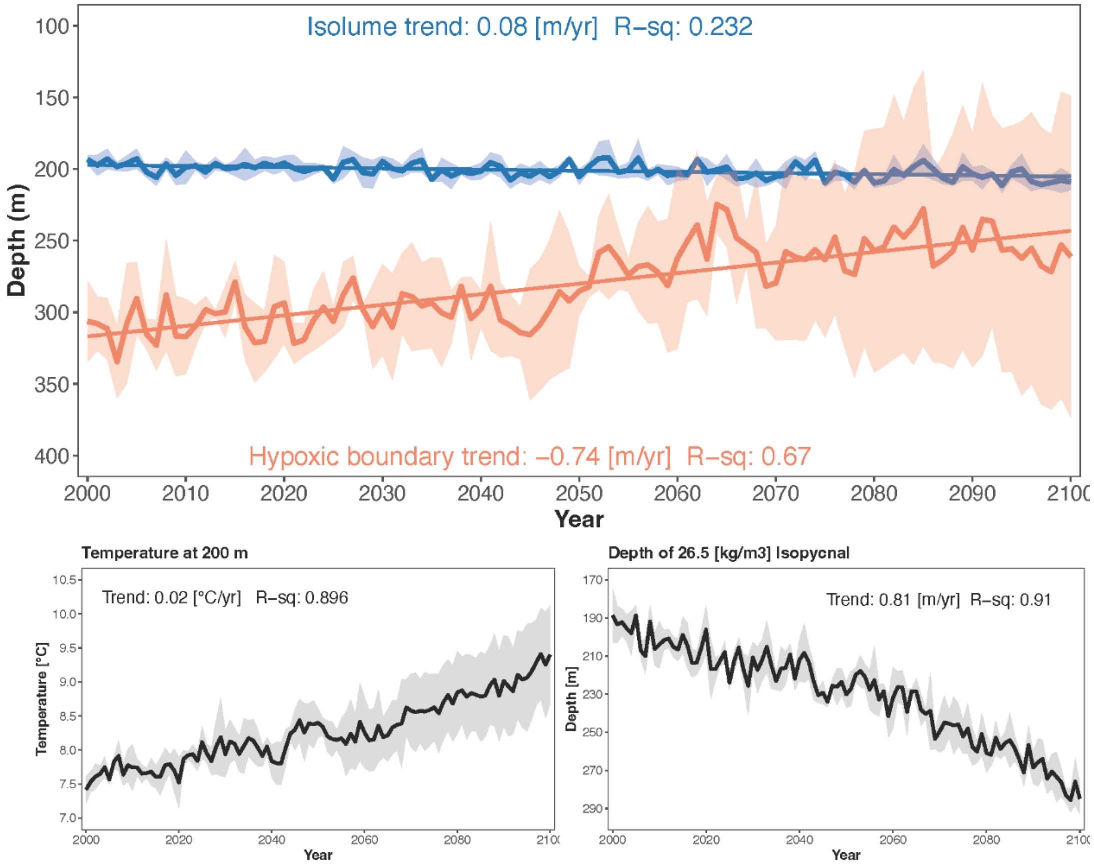


Figure 5 Changes in mesopelagic habitat properties during 21st century based on the ensemble mean and spread of three downscaled climate projections (GFDL, IPSL, and Hadly) in the central California Current (Top) Depth of the 0.07399 W/m^2 isolume (blue) and Depth of the 60 $mmol/m^3$ hypoxic boundary (orange). Shaded regions represent standard deviation between three ensemble members. (Below) Ensemble mean and spread of (Bottom left) Temperature at 150 m and (Bottom right) Depth of 26.5 60 kg/m^3isopycnal. Annual trends for each property are listed in their respective panels.

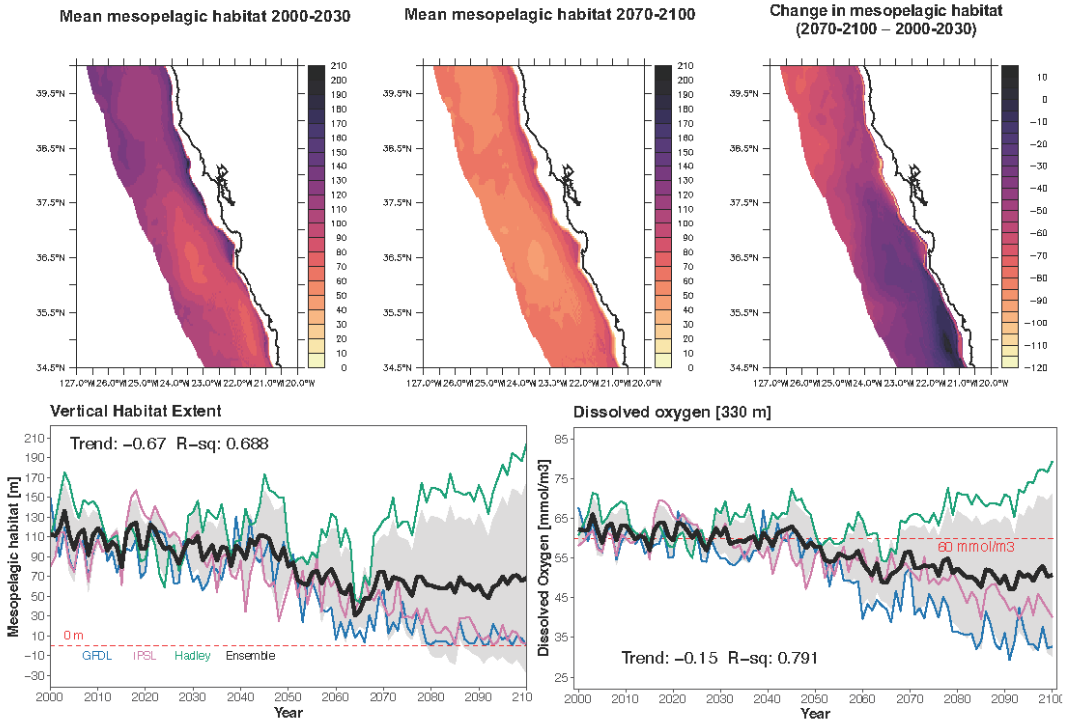


Figure 6 Projected 21st century change in vertical extent of mesopelagic habitat. Top: present-day (2000-2030 mean) habitat [m] (left), end-of-century (2070-2100 mean) habitat [m] (middle), and difference between present-day and end-of-century habitat [m] (right). Bottom: temporal variability of vertical mesopelagic habitat [m] and dissolved oxygen $[mmol/m^3]$ at 330 m (the mean (2000-2020) hypoxic depth from the historical simulation (right) averaged spatially over the domain. The black line represents the ensemble mean, the gray shading denotes the ensemble spread (standard deviation), and the individual ensemble members are shown in blue (ROMS-GFDL), pink (ROMS-IPSL), and green (ROMS-HAD).

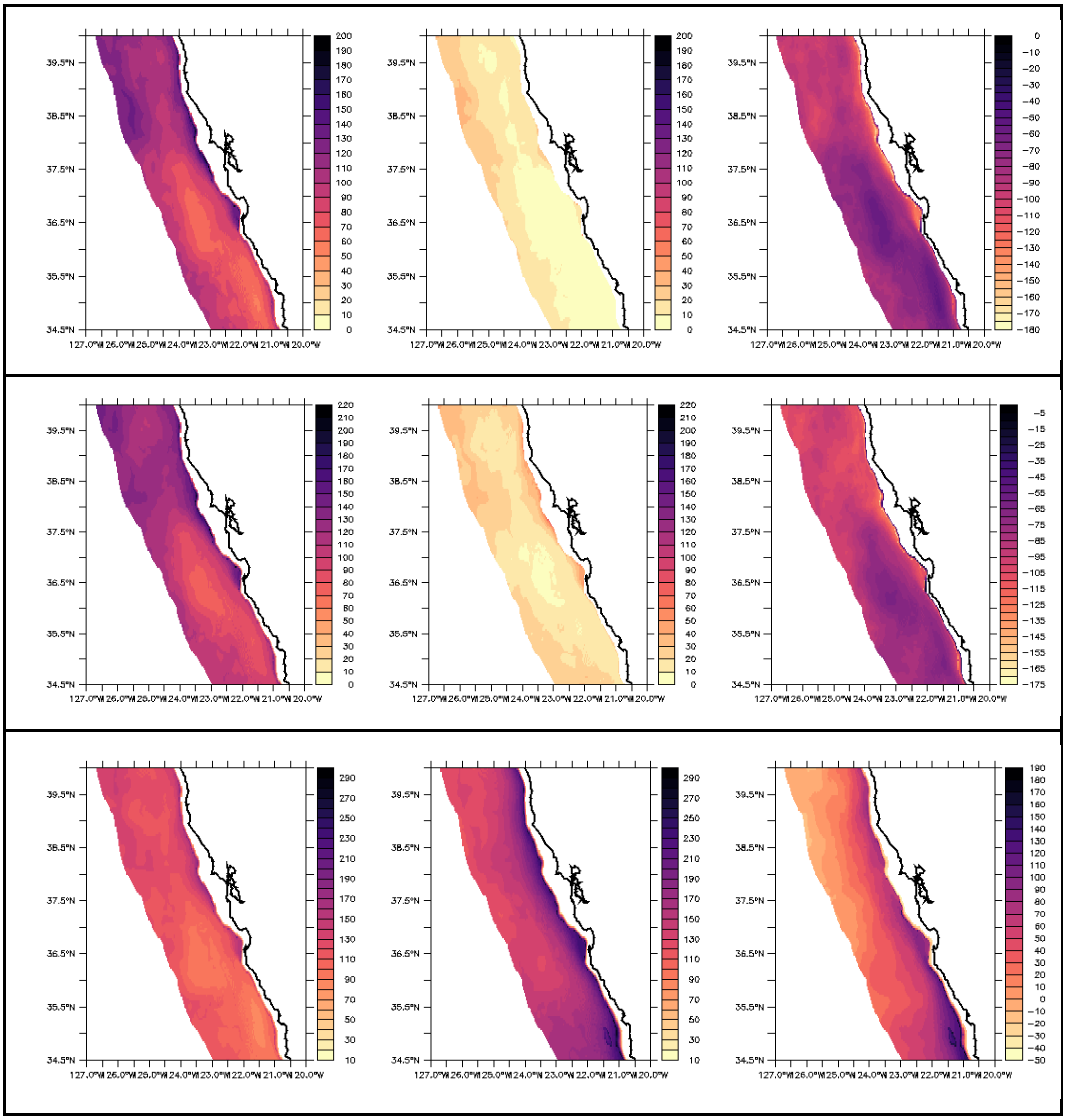


Figure 7 Projected 21st century change in vertical extent of mesopelagic habitat per ensemble member. Present-day (2000-2030 mean) habitat [m] (left), end-of-century (2070-2100 mean) habitat [m] (middle), and difference between present-day and end-of-century habitat [m] (right) for each ensemble member: ROMS-GFDL (top), ROMS-IPSL (middle), ROMS-HAD (bottom).

3.6 Discussion

The vertical compression of mesopelagic habitat by 58% (~45 m) projected in our study by the end of the 21st century exemplifies the interconnection between anthropogenic climate change and mesopelagic habitat extent. The ensemble of downscaled projections used here suggest with high certainty (low spread) that the upper boundary of the mesopelagic zone will deepen by up to 15 m (mean of~ 5 m). This result is consistent with a small decreasing trend observed in chlorophyll in the upper 100 m and a deepening of the 26.5 kg/m^3 isopycnal, related to reduced upwelling intensity and nutrient availability, which limits phytoplankton production and in turn increases the amount of light that can penetrate into the water column. In contrast, the lower boundary of the mesopelagic zone, defined by the depth at which dissolved oxygen concentrations reach near hypoxic levels, shoaled by ~50 m over the course of the 21st century. Hypoxic boundary uncertainty was relatively high however, as evidenced by the large spread across projected outcomes by 2100, ranging from an increase in mesopelagic habitat to its widespread disappearance from the central California Current region.

The upper boundary of the mesopelagic zone is bounded by light, which is important for mesopelagic organisms in providing cover from visual predators. While the depth of the isolume did not deepen considerably in our study, this was predicated on stable levels of primary production by the end of the century. However, there is considerable uncertainty in the ability of earth system models to project regional estimates of net primary productivity (Tagliabue et al., 2021) research has shown that increased stratification can lead to declines in chlorophyll by up to -3.0 mg/m^3 (Gómez-Ocampo et al., 2018). If future chlorophyll concentrations were to decline more significantly than our study projects, as has been suggested for other regions (Steinacher et al., 2010), then mesopelagic habitat would be further constricted in response to greater deepening of the upper boundary. Future work that explores other OMZs, such as the Humboldt current, which is both more productive and exhibits an even shallower hypoxic boundary, could provide valuable insights into how mesopelagic organisms in the California Current ecosystem may respond to future climate conditions.

Global warming contributes to deoxygenation by reducing the solubility of dissolved oxygen in seawater, increasing respiration (which consumes oxygen) and reducing exchange between the surface and deep ocean (Breitburg et al., 2018). Declines of 1-7% of dissolved oxygen are predicted for the next century and beyond (Keeling et al., 2010). Oxygen minimum zones, which typically occur at mesopelagic depths, have already expanded horizontally by millions of kilometers and are predicted to continue expanding (Stramma et al., 2010; Breitburg et al., 2018). Declining oxygen within the California current has been associated with surface stratification and advection (Bograd et al., 2008), changing water mass contributions (Bograd et al., 2015, 2019), decadal oscillation (PDO and NPGO) (Stramma et al., 2020), gyre-scale circulation (Pozo Buil and Di Lorenzo, 2017) and a combination of source water changes and remineralization (Ren et al., 2018). While our results indicate that the sholaing trend of the hypoxic boundary in the central California Current region will continue throughout the 21st century, they also suggest a possible decoupling between surface warming and oxygen at mesopelagic depths. Indeed, the downscaled projection with the highest rate of warming under RCP8.5 (Hadley) exhibits an increase in oxygen at 330 m depth, while the projection with the lowest rate of warming (GFDL) experiences the most severe reduction in dissolved oxygen.

Using the same downscaled climate projections we use to force our model, Pozo Buil et al. (2021) attribute differences in oxygen content among ensemble members to differences in Equatorial circulation. Specifically, the increase in oxygen at mesopelagic depth predicted by Hadley is associated with a strengthening of the Equatorial Undercurrent, which transports younger, more oxygenated waters eastward, while both GFDL and IPSL predict a weakening of the Equatorial Undercurrent over this time, which would mean greater influence of older, less oxygenated waters from the Eastern Pacific. Our results showed similar inconsistencies among model projections; ROMS-HAD showed coastwide increases in mesopelagic habitat (driven by increasing oxygen), which was intensified toward the southern border of our study domain and along the coast compared to both ROMS-GFDL and ROMS-HAD which predict coastwide declines in oxygen (Figure 7). Southern boundary waters in our domain are conveyed northward along the slope at depths between ~100-300 m by the poleward California Undercurrent (Hickey, 1979; Connolly et al., 2014; Evans et al., 2020). The link to northward advection of equatorial waters is also substantiated by the fact that the increase in mesopelagic habitat predicted here by ROMS-HAD is most noticeable near the southern border of our study domain and along the upper continental slope where the California Undercurrent circulation is expected to greatest. This result suggests that changes in the vertical extent of mesopelagic habitat in the California Current are likely to be determined by changes in circulation occurring at the equator.

While disagreement in deoxygenation trends among earth system models is a known challenge in projecting future climate conditions (Bahl et al., 2019), our approach based on three downscaled projections with different rates of warming for a given emissions scenario is useful for untangling the processes most likely associated with future changes in mesopelagic habitat. Despite the fact that RCP8.5 may represent an extreme warming pathway, our results suggest that the highest rate of warming does not necessarily produce the greatest habitat loss. Instead, a lower rate of warming, likely representative of a high warming case under the more moderate RCP4.5 emissions scenario, could lead to a much greater decline in future mesopelagic habitat when factoring in potential changes to basin-scale circulation, specifically equatorial circulation. As such, future research exploring the strength and water mass properties (both physical and biogeochemical) of the California Undercurrent, which feeds equatorial waters poleward along the US west coast at mesopelagic depths, may help narrow down the range of mesopelagic habitat futures in the southern and central regions of the California Current ecosystem.

A vertical compression of mesopelagic habitat by the end of the century was also predicted by (Proud et al., 2017), who used a biogeochemical model and the relationship between acoustic backscatter and primary production and wind stress to calculate a shoaling of the mean depth of the main DSL globally from 545 m to 510 m (a difference of ~35 m). The authors did not include oxygen as a parameter, nor did they examine the lower boundary of the main DSL specifically. Nevertheless, when compared to our predicted mean change in mesopelagic habitat (~45 m), this result indicates that the California Current may experience a faster decline (by ~40%) than the global average predicted by Proud et al. (2017). In contrast, (Netburn and Koslow, 2015) predicted an expansion of mesopelagic habitat by 2075 for the southern California Current region. By comparing shoaling rates for the upper DSL boundary (defined by light and oxygen) to shoaling at the lower DSL boundary (based just on oxygen), the authors concluded that the upper boundary would shoal faster than the lower boundary, and thereby expand the vertical extent of the DSL. One possible reason for the differences between their results and our own, which predict an overall decline in mesopelagic habitat is the authors assumed constant rates of change for oxygen (derived from the literature, such as Bograd et al. 2008 from 1984-2006), which does not adequately incorporate the effects of natural decadal variability on subsurface oxygen concentrations in the California Current (Pozo Buil and Di Lorenzo, 2017). Additionally, their inclusion of oxygen as an upper boundary to the DSL necessarily implied a faster rate of shoaling compared to our results based solely on isolume depth. While it is possible that mesopelagic organisms may select for low oxygen conditions, recent evidence from the central California Current region suggests that variation in light intensity is more likely controlling changes in DSL depth (Iglesias *in revision*).

Ecologically, periods of declining oxygen in the California Current have been attributed to reductions of mesopelagic fishes by up to 63% in southern California, such as 1951-2008 identified in (Koslow et al., 2011). The hypothesized mechanism for this decline was low oxygen conditions forcing mesopelagic fishes shallower into lighted waters, where they were consumed by visually oriented predators. Shoaling OMZs are already known to change predator prey interactions (Gilly et al., 2013) and the possible compression of habitat closer to the surface is likely to make it easier for deep-diving predators to target mesopelagic prey. However, a subsequent study found that the response of mesopelagic fishes to declining oxygen actually varied geographically, with warm-water, shallower OMZ adapted species actually increasing in abundance off Baja California, and in the southern portion of the California Current (Koslow et al., 2019). Indeed, some mesopelagic organisms can tolerate or even select for low oxygen conditions (Seibel, 2010; Bianchi et al., 2013; Netburn and Koslow, 2015), and it is possible that these populations may expand their latitudinal range with climate change. There is some evidence suggesting this may already be occurring in southern California, as (Thompson et al., 2022) documented a three fold increase in larval Mexican Lampfish *Triphoturus mexicanus,* a warm water affinity species, during a recent heatwave (2013-2016). Our results, which predict a vertical compression of mesopelagic habitat, highlight the need for long-term monitoring of adult mesopelagic fish communities to evaluate changes within these communities.

The global biogeography of mesopelagic ecosystems can be defined by temperature, salinity and dissolved oxygen (Sutton et al., 2017), which our research suggests are going to change significantly by the end of the century, and likely leading to a global homogenization of habitat, as predicted by (Proud et al., 2017). Genetic research on deep-pelagic fishes provides evidence that multiple instances of population expansion and contraction, likely related to changing ocean conditions, has occurred in the past (Weber et al., 2024). The effects of deoxygenation are not going to be felt equally across trophic groups, with crustaceans, for example, being recognized as particularly sensitive to low oxygen (Gray et al., 2002; Vaquer-Sunyer and Duarte, 2008), although there is evidence for low oxygen adaptation in some taxa(Childress and Seibel, 1998). In addition to the main scattering layer that was the focus of our study, there is often another scattering layer of mesopelagic organisms inhabiting deeper depths (~800 m globally, Proud et al. 2017). In the California Current region, this non-migratory layer occurs at ~500 m in the Monterey Bay for example. Remarkably, this community is present through most of the year, with a peak in fall, but entirely absent during the spring (Urmy and Horne, 2016) when upwelling is typically most intense in the Central California Current region. While our study did not specifically examine changes deeper in the water column, the projected decline in oxygen at 330 m depth will have an impact on these communities as well, especially since their seasonal absence indicates they are already likely inhabiting ocean conditions at the edge of their physiological limits.

Despite the importance of mesopelagic organisms to carbon export (Davison et al., 2013) and as prey to higher trophic level predators in the California Current ecosystem (Iglesias et al., 2023), there remains a lot to discover about the physical and biogeochemical processes shaping the mesopelagic zone these animals inhabit (Webb et al., 2010; St. John et al., 2016; Levin et al., 2019; Martin et al., 2020). Few long-term studies have examined changes in mesopelagic community structure through time or the response of mesopelagic communities to changing environmental conditions, so it is difficult to anticipate the true biological impacts of a vertically compressed mesopelagic habitat by the end of the 21st century. Although our study was restricted to May-June, the trends identified here for the depth of the hypoxic boundary are representative of changes in annual mean values and our results therefore extend beyond the upwelling season. Similarly, by downscaling earth system models that encapsulate variable rates of warming and different formulations of physical and biogeochemical processes, our study provided a more mechanistic understanding of the nature by which such futures are so uncertain, by highlighting the connectivity between deoxygenation trends along the California coast with changes in the strength of the Equatorial and California Undercurrents. Overall, our results suggest a future in which mesopelagic habitat is vertically compressed compared to historical levels and mesopelagic communities exposed to warmer, less oxygenated waters. Our study demonstrates the interconnection between anthropogenic emissions into the atmosphere and changes in the deep sea, highlighting the need to consider mesopelagic ecosystems when evaluating the impacts of climate change.

3.7 Acknowledgements

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Conclusions

The mesopelagic zone is often defined by its distance and distinctness from surface ecosystems. However, our results highlight the importance of the mesopelagic zone well beyond its commonly accepted depth range (200-1000 m). In chapter one, we show that mesopelagic fishes are consumed by predators residing outside of the mesopelagic zone. In chapter two, we provide a mechanism whereby changes in upper ocean conditions can affect the depth of the DSL. In chapter three, we provide evidence for a potential compression of mesopelagic habitat by the end of the century as the result of anthropogenic carbon emissions. Overall, these results demonstrate that the mesopelagic zone is ecologically and physically connected to processes occurring in the upper ocean and is deserving of greater consideration in future ocean policy. Below, we discuss the three questions this dissertation explored and the key results of our analysis that could help advance the field and could motivate future research and management directions.

Are mesopelagic fishes important prey for predators residing outside the mesopelagic zone?

Considerable research exists linking mesopelagic fishes to individual predator taxa (see (Brodeur and Yamamura, 2005 as an example within the California Current), but these studies typically focus on individual predator taxa, so prey importance is evaluated with respect to specific predator taxa. Our study significantly enhanced existing knowledge by focusing instead on the central role of mesopelagic fishes as prey to a diversity of predators occurring within the California Current. In particular, we were able to quantify the role of mesopelagic fishes as prey to predator taxa that were not specifically sampled with mesopelagic communities in mind, providing a quasi-random sampling of predators inhabiting the California Current Ecosystem. Of the 143 predator taxa included in the database, 25% of taxa had consumed at least one mesopelagic fish species, and of these predator taxa, 11 had mesopelagic fishes in over 25% of all diet samples. Of the species that consumed mesopelagic prey, economically important fishery species such as Swordfish (50% of diet samples), Bluefin Tuna (16%), Albacore (19%), Humboldt Squid (52%) and Pacific Hake (4%) were included, as were protected marine mammal species including 4 dolphins, who had mesopelagic fishes in greater than 25% of diet samples. Predator taxa that had consumed mesopelagic fish were collected across the California Current region, from shelf depths to offshore regions >1000 m deep. The proportion of mesopelagic prey generally increased in predators with increasing distance offshore (particularly around the slope margin and offshore).

The existence of mesopelagic fishes in the diets of predators inhabiting inshore shelf regions provides direct evidence that mesopelagic communities are interconnected to neighboring regions and is a rare example of energy transfer from the deep-sea to upper ocean habitats. For example, of the Sea Lion and Fur Seal scat sampled onshore at a breeding colony in Southern California, over 30% of predators sampled had consumed mesopelagic fishes. There were also instances of shelf associated predator species (i.e. predator taxa that were sampled over shelf depths) that had consumed mesopelagic fishes. Either these predator taxa spend time foraging in deeper habitats, forage nocturnally when mesopelagic prey are located at shallower depths, or took advantage of locations that entrapped or accumulated mesopelagic fishes, such as submarine canyons and other steep topography (Pereyra et al., 1969; Genin et al., 1988; Genin, 2004). Although the focused in this study was on mesopelagic fishes specifically, mesopelagic communities are comprised of a diverse assemblage of invertebrates that are just as likely to be important sources of prey and could be explored further in future investigations. In the Southern Ocean, Saunders et al., (2019) predicted that as global ocean temperatures continue to rise, small mesopelagic fishes may provide a needed alternative prey source as more traditional sources of prey, such as krill, decline. Future research that examines dynamics of the horizontal distribution of mesopelagic organisms (including horizontal nightly migration such as observed by (Benoit-Bird and Au, 2006)) and seasonal variability in distribution (such as the disappearance of a deeper-scattering layer during the Spring (Urmy et al., 2012)), could further inform our understanding of the needs of higher-trophic level predators in a changing ocean environment.

Are mesopelagic communities impacted by surface intensified marine heatwaves?

The large marine heatwave event that occurred off the US West coast in 2014-2016 (a.k.a “the blob”) led to well documented changes in the marine community of the California Current, from the base to the apex of the food web (for examples of ecological impacts, see Cavole et al., 2016; Jones et al., 2018; Brodeur et al., 2019;

Santora et al., 2020; Nielsen et al., 2021; Thompson et al., 2022; Free et al., 2023). Of the few studies to incorporate mesopelagic community changes in an assessment of impacts, mesopelagic observations came from either nighttime trawls above mesopelagic depths (ex. 30 m in (Sakuma et al., 2016; Brodeur et al., 2019), which captured strong vertical migrators, or larval data collected in the upper 200 m (Thompson et al., 2022). While these studies provide valuable insights into the vertically migrating and larval components of mesopelagic communities, they do not capture daytime distributions of adult mesopelagic communities. Our study specifically focused on mesopelagic depths by using continuous echosounder data. Comparing the depth of mesopelagic organisms to oceanographic conditions measured *in situ* via shipboard CTD casts, we were able to quantify how the vertical distribution of mesopelagic fishes changed in response to changing ocean conditions during the most severe years of the heatwave (2015-2016). Our finding that the depth of mesopelagic organisms increased by ~100 m during the most severe warming (2015-2016) compared to 2013 demonstrated that mesopelagic fishes are responsive to changes in ocean conditions near the surface. We hypothesized that during the marine heatwave, when upwelling habitat was compressed closer to shore (Santora et al., 2020; Schroeder et al., 2022), reductions of primary production led to an increase in light reaching mesopelagic depths, and mesopelagic organisms responded by descending deeper into the water column.

Light is an important variable structuring the depth of the Deep Scattering Layer (DSL), as mesopelagic organisms select for a specific light envelop that allows them to evade visual predators (Longhurst, 1976; Aksnes et al., 2017; Robison et al., 2020). However, light penetration is largely controlled by factors affecting the upper water column (such as nutrient availability), which in turn connects mesopelagic communities to surface processes. Shifts in the vertical distribution of mesopelagic fishes could have cascading consequences for carbon export dynamics and deep-diving predators that would need to traverse greater distances to access prey. Future research that examines the long-term effects of oceanographic conditions on the distribution and abundance of mesopelagic communities are needed to understand how anomalous events, such as heatwaves, predicted to increase with climate change (Frölicher et al., 2018), might continue to impact mesopelagic communities and, in turn, the rest of the California Current food web. Our finding that mesopelagic fishes descend deeper during a large marine heatwave is particularly concerning when viewed in combination with our conclusion from Chapter 3, that mesopelagic habitat is expected to shoal by the end of the 21st century.

How will the mesopelagic zone evolve in response to anthropogenic climate change?

While DSL depth has been linked to numerous oceanographic conditions, including dissolved oxygen (Bertrand et al., 2010; Netburn and Koslow, 2015; Klevjer et al., 2016; Urmy and Horne, 2016) and light (Benoit-Bird, 2009; Røstad et al., 2016; Aksnes et al., 2017), there is limited information available on the long-term effect of environmental changes on the mesopelagic ecosystem. Only a few studies have attempted to predict how global warming might impact the DSL, predicting either expansion (Netburn and Koslow, 2015), compression (Proud et al., 2017) or poleward (Liu et al., 2023) shifts. Our study, which used an ensemble of downscaled regional climate projections from a coupled physical-biogeochemical ocean model under the RCP8.5 high emissions scenario, projected a compression of mesopelagic habitat in the central California Current, caused by a shoaling of the hypoxic boundary by ~50 m. An unexpected outcome of our analysis was the identification of one of the largest sources of uncertainty in future mesopelagic habitat as changes in equatorial circulation propagated to the US West Coast via the California Undercurrent circulation (Pozo Buil et al., 2021). Our findings also suggest a complex relationship between surface warming and mesopelagic habitat loss, as the downscaled projection with the highest rate of warming exhibited the lower habitat compression (and even predicted expansion by the end of the century) due to remote advection of more oxygenated subsurface water masses into the central California Current region. While our research was focused on the California Current Ecosystem off the US West Coast, this result highlights an important aspect of the mesopelagic zone; just as the mesopelagic zone expands horizontally beyond any nations jurisdiction, so does the global ocean circulation influencing it. In other words, the future vertical extent of the mesopelagic zone along the US West Coast may depend on changes propagating from remote locations, such as the Equatorial Pacific region. Future work exploring the connections between the basin and regional scale processes that shape mesopelagic zone properties are timely, as mesopelagic communities are likely to experience the effects of anthropogenic climate change.

Future research and ocean policy directions

Few long-term mesopelagic datasets exist globally, making it difficult to determine the response to, and thus vulnerability of, mesopelagic organisms to existing and future oceanographic conditions. Deep-sea research is expensive, often requiring large vessels and specialized equipment. This cost contributes to geographical inequities in deep-sea science (Bell et al., 2023) and makes it difficult to draw comparisons across regions. While the focus of this dissertation was on waters within the California Current, most of the mesopelagic zone globally lays in areas beyond national jurisdiction. Currently, there are few existing policies which specifically include provisions for mesopelagic ecosystems (Wright et al., 2020; Gjerde et al., 2021), leaving mesopelagic communities particularly vulnerable to future threats of exploitation. For instance, the mesopelagic zone is threatened by possible exploitation for fisheries (Prellezo, 2019; Grimaldo et al., 2020; Standal and Grimaldo, 2020), the effects of potential deep sea mining operations (Drazen et al., 2020) and global climate change. However, mesopelagic fishes are not being considered for direct human consumption and instead would be used as fish meal, likely for the growing aquaculture industry. This, combined with the fact that mesopelagic science does not yet allow for making informed decisions about the impact of such extractive activities on mesopelagic communities, led a group of us from the JETZON (Joint Exploration of the Twilight ZONe) to argue for a precautionary approach to any exploitation (Bisson et al., 2023). At the international level, there is an opportunity to incorporate mesopelagic ecosystems into the implementation of a new UN treaty for sustainable use of the high seas (referred to as BBNJ or ABNJ agreement: Biodiversity/Areas Beyond National Jurisdiction), currently undergoing ratification. Closer to the California Current region, the US National Marine Fisheries Service protects unfished forage fish, including several mesopelagic taxa (i.e., families: Myctophidae (Lanternfish), Bathylagidae (Deep-sea smelts), Paralepididae (Barracudina) and Gonostomatidae (Bristlemouths)) in recognition of their role as prey to multiple components of the ecosystem (50 CFR §660.5-.6), which could serve as a model for other regions.

Mesopelagic ecosystems at a crossroads

Mesopelagic science is advancing quickly, and we now recognize the contributions of the mesopelagic zone to global biodiversity (Webb et al., 2010; Yang et al., 2024), biomass (Irigoien et al., 2014), and carbon export ((Davison et al., 2013)). Our work adds to this growing knowledge base by revealing how mesopelagic communities respond to changes in upper ocean conditions, such as those occurring during extreme marine heatwaves (Chapter 2), and how their vertical distribution could become compressed in a warmer, more stratified, and deoxygenated future (Chapter 3). Changes in habitat availability could in turn disrupt trophic connections between mesopelagic ecosystems and predators dwelling outside this zone (Chapter 1). Despite threats from industrial fishing, deep-sea mining and anthropogenic climate change, the ocean's mesopelagic zone persists in this moment as one of the largest unexploited (and awe-inspiring) habitats on earth. In recognition of the global role played by mesopelagic communities, we have the opportunity to ensure that mesopelagic populations continue to be a critical component of a functioning and healthy marine ecosystem by better incorporating and appreciating their role in future ocean policies.

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