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Life in the Midwater: The Ecology of Deep Pelagic Animals

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Abstract

The water column of the deep ocean is dark, cold, low in food, and under
crushing pressures, yet it is full of diverse life. Due to its enormous volume,
this mesopelagic zone is home to some of the most abundant animals on
the planet. Rather than struggling to survive, they thrive—owing to a broad
set of adaptations for feeding, behavior, and physiology. Our understanding
of these adaptations is constrained by the tools available for exploring the
deep sea, but this tool kit is expanding along with technological advances.
Each time we apply a new method to the depths, we gain surprising insights
about genetics, ecology, behavior, physiology, diversity, and the dynamics
of change. These discoveries show structure within the seemingly uniform
habitat, limits to the seemingly inexhaustible resources, and vulnerability in
the seemingly impervious environment. To understand midwater ecology,
we need to reimagine the rules that govern terrestrial ecosystems. By spend-
ing more time at depth—with whatever tools are available—we can fill the
knowledge gaps and better link ecology to the environment throughout the
water column.

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1. GOALS OF THIS REVIEW

This review is aimed at readers knowledgeable about the marine environment but less familiar with the deep ocean. The term deep sea is often used as though it were synonymous with the deep seafloor, and indeed there are entire books about deep-sea biology that exclusively discuss the benthos. The truth is that the inconvenient 4-km-tall column of water separating the surface from the seafloor literally *is* the deep sea. It is a habitat that is an order of magnitude more voluminous than any other habitat on the planet, including the shallow ocean and all terrestrial habitats combined. It is simultaneously hard to access and directly linked to our daily lives. It is vast and cold, yet full of exotic-seeming life forms. Two of the major impediments to better understanding deep water-column ecosystems are related to perception: The inhabitants are often portrayed as grotesque and scary, usually based on images of badly damaged specimens, and the sheer size and remoteness of the domain may give the impression that it is impervious and has low societal value. Our secret objective is getting more people to appreciate this environment and to be motivated to protect those who live there.

Given its scale, the deep sea cannot be explained in any one paper or book, although there are many good volumes on the subject (e.g., Herring 2001, Priede 2017, Torres & Bailey 2022). For each of the sections below, there could be (and in many cases have been) dedicated reviews written. We try to draw from the rich history of research to give some insight into the ecology of the inhabitants and processes of the deep water column. Many of our examples are drawn from the eastern North Pacific, which has long been a focus area, although the general patterns apply throughout the deep ocean.

The deep water column is known by many names: the midwater, the mesopelagic zone, and the twilight zone. Pelagic means "of the open sea," and meso means "in the middle"—not as shallow as the upper epipelagic, but not as deep as the bathypelagic (and beyond). As explained below, the boundaries delineating the regions of the ocean—especially the lower bound of the mesopelagic—are largely human constructs of convenience. Organisms freely migrate right past our divisible-by-100 dashed lines on a chart. In this review, therefore, we focus on waters beyond 200 m but as deep as 4,000 m. Although knowledge gaps persist, there is sufficient research to be able to recognize trends and patterns. There is so much yet to learn and discover, but what we already know is plenty to evoke wonder at how life has proliferated in the deep ocean.

2. PHYSICAL PROPERTIES OF THE WATER COLUMN

The column of water between the ocean's surface and the seafloor is a vast environment that presents unique challenges and opportunities to its inhabitants—and to those who wish to study them. By volume, it represents more than 90% of the available living space on the planet (**Figure 1a–c**). Traveling downward from the surface, organisms experience strong gradients in temperature, pressure, light, nutrients, and oxygen (**Figure 1d–g**). While pressure increases linearly with depth, temperature falls rapidly below the sunlit shallow waters and then gradually thereafter, to a minimum of approximately 1.5°C (**Figure 1d,e**). Oxygen falls off as you descend beyond the well-mixed surface waters, reaching a minimum at a depth of several hundred meters. This oxygen minimum zone (OMZ) is where respiration outpaces the residual oxygen from the surface (Breitburg et al. 2018, Childress & Seibel 1998). Surprisingly, beneath that hypoxic zone, oxygen levels actually increase in most regions, and at a depth of 2,000 m, the oxygen may be the same as it was at 100 m (**Figure 1f,g**). Most of this deep, oxygen-rich water has sunk directly from cold polar regions, where it circulates through the deep sea for nearly 1,000 years before eventually seeing the atmosphere again. This connectivity means that even the health of the deep sea is susceptible to warming of polar waters. Light also diminishes rapidly near the surface, with
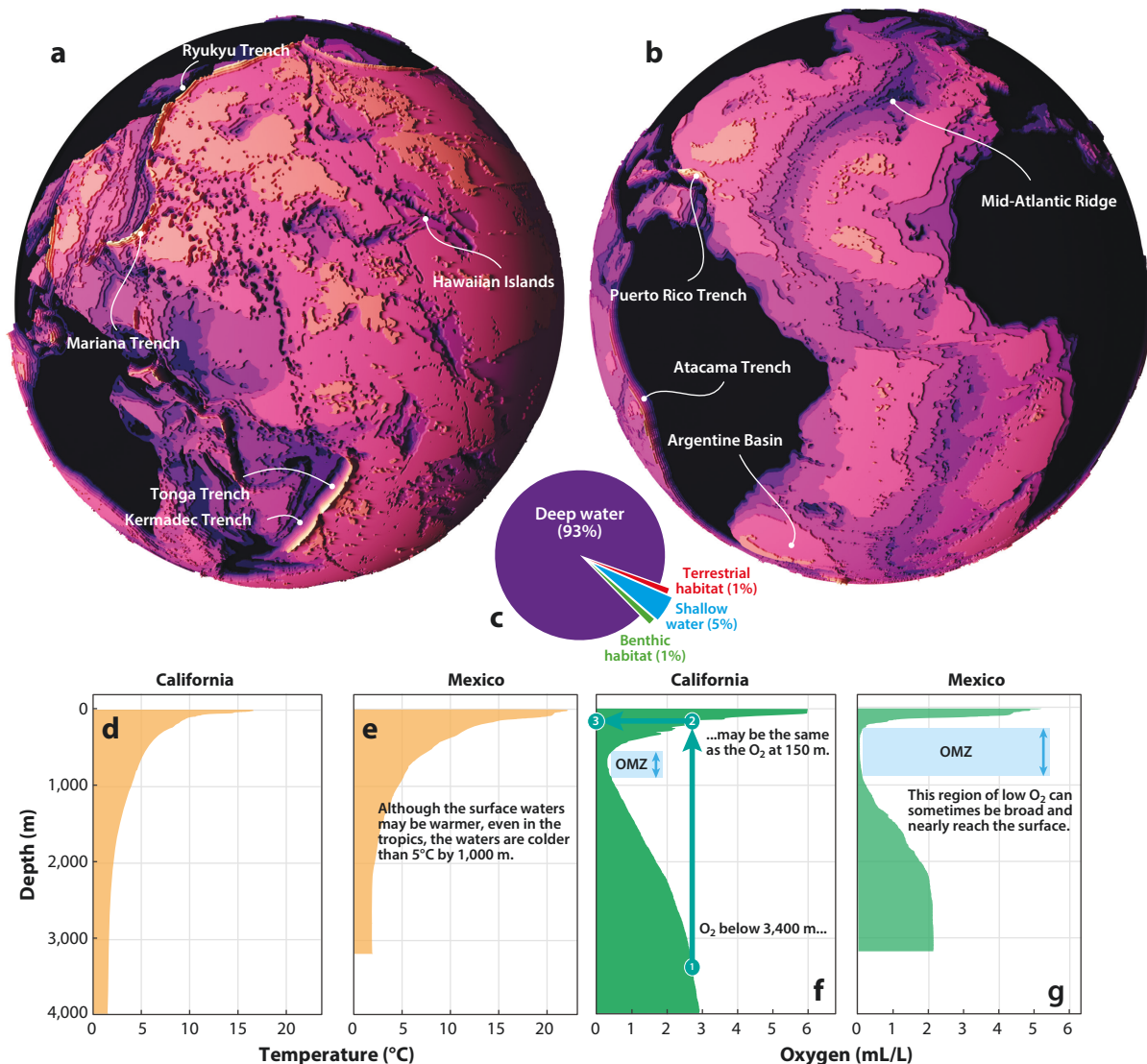
Figure 1

The deep midwater habitat. (*a,b*) Alternative views of the globe in which the deep ocean has been raised up above the surface to more effectively convey its vastness and volume. Land and waters shallower than 200 m are shown in black at zero elevation. Each layer is approximately 1,000 m of water depth, with hotter colors being deeper. The deepest trenches appear as sharp ridges, while islands, seamounts, and atolls appear as depressions. The Pacific Ocean (panel *a*) is bracketed by the world's deepest trenches, and the central basin is riddled with seamounts. The Atlantic Ocean (panel *b*) is fairly uniform, with a slight shallowing of the deepest waters along the Mid-Atlantic Ridge, where tectonic plates are diverging. (*c*) Percentage of living space on the planet by volume. Although the ocean is approximately 70% of the area of the planet, its average depth is 3,700 m. Assuming 100 m of living space above terrestrial habitats (1%) and 50 m of benthic habitat above the seafloor (1%) results in an estimate that 5% of the globe is shallow water and 93% of the available biovolume is in waters deeper than 200 m, shown in panels *a* and *b*. (*d–g*) Temperature and oxygen profiles from deep waters off California (panels *d* and *f*, respectively) and the Gulf of California, Mexico (panels *e* and *g*, respectively). The warm waters are restricted to the surface of the Gulf of California and decline exponentially to match the temperate offshore waters of the eastern Pacific. Oxygen does not decline to an extreme low in all regions, but where it does, there can be a mid-depth minimum, shown in the blue bars. The vertical extent of the oxygen minimum zone (OMZ) can stretch across almost 1,000 m of water column in productive areas with restricted circulation.

half the light lost in the top few meters and 99% gone by approximately 100-m depth, dependent on the amount of biological and inorganic material in the water. At the bottom of the euphotic zone, light has dropped below the level where it can be used for photosynthesis. The exact depth of this boundary varies greatly in different regions of the ocean, and may be very shallow for polar regions in the winter or deep in clear tropical waters. Below that boundary, dim surface sunlight and moonlight are still usable by many organisms with sensitive, upward-looking eyes.

Despite these challenging gradients, deeper waters also offer unique opportunities that can enable long lives, large sizes, and the evolution of diverse body plans. The midwater habitat is extremely stable, and within depth zones, temperature fluctuations are in the single digits, changing only gradually. The three-dimensional space with no hard obstacles means that there are few places to hide, and threats can come from anywhere. However, the open space also means that visual interactions to find food or mates can happen over long distances. The three-dimensional volume also supports the growth and elaboration of fragile body parts for neutrally buoyant organisms, leading to animals that are tens of meters long but fall to bits when touched or exposed to bright lights. Cold temperatures and low metabolic rates lead to slow growth and maturation in long-lived organisms; deep-sea animals can be hundreds or even thousands of years old (e.g., Nielsen et al. 2016, Roark et al. 2009), and some of the most intriguing unresolved questions are the age, longevity, and growth rates in the mesopelagic.

While these conditions of low temperature, high pressure, darkness, and limited nutrients and oxygen are extreme from a human perspective, organisms living in those conditions would be shocked by the extremes that we face on land. Animals that have adapted to live in the deep are largely intolerant to small changes in their surrounding environment; they are often constrained within a narrow range of these parameters (Somero 2022, Wishner et al. 2018). As discussed in Sections 7 and 8, this means that small changes to their habitat can destabilize a species and provide challenges beyond what might be expected given the absolute size of the environmental change.

3. PATTERNS IN SPACE AND TIME

3.1. Vertical Zonation

The midwater is classically characterized according to distinct vertical layers or depth zones, with each depth stratum defined principally by the penetration of sunlight from surface waters (Angel 1993, Sutton 2013) and the associated communities of animals. The sunlit upper ocean is the epipelagic zone, generally 0–200 m, where daytime light levels are sufficient to support net primary production via photosynthesis. The mesopelagic zone, generally 200–1,000 m, begins where light levels are lower than what is required for photosynthesis and ends where visible light disappears completely. The mesopelagic is a dynamic and varied part of the water column, encompassing broad environmental ranges of temperature, light, and oxygen. Surface light provides cues in the deep sea (bright light in surface waters and dim light in the midwater) and is usable for navigating, discerning between day and night, finding prey, and avoiding predators. The bathypelagic zone generally encompasses depths greater than 1,000 m, to waters just above the seafloor, with a mean depth of approximately 3,700 m (Charette & Smith 2010). This zone is classically defined by the absence of measurable light and highly stable temperatures and salinities. Additional signposts are placed in the abyssopelagic and ultimately in the hadal zone, which represents the small fraction of the ocean lying in the deepest trenches.

Vertical zonation in the midwater is regionally specific, according to environmental properties that vary with geography and biogeochemistry (Reygondeau et al. 2018, Sutton et al. 2017). For example, the mesopelagic zone shifts seasonally with stark light regimes in polar regions, where entire seasons could be mostly lit or mostly dim throughout the water column. There are also

ocean regions with specialized mesopelagic ecosystem dynamics, like the Gulf of California, with deep basins and rapid vertical gradients (**Figure 1***e*,***g***), and the Red Sea, with clear, warm, oligotrophic (low productivity) waters above. In the North Atlantic, dense, oxygen-rich Arctic water sinks into the deep sea and flows toward Antarctica, circulating around the globe before being upwelled to the surface at least 600 years later (Toggweiler & Key 2003). The exact boundaries between zones are fluid and serve as a useful general framework for researchers. The vertical gradients in key environmental properties across the midwater environment ultimately result in somewhat stratified communities of animals, but the distributions may be based on a combination of these factors, along with other biological cues.

Although persistent periodic sampling of midwater communities is rare, in even those most seemingly stable low- and mid-latitude regions, deep biological communities do respond to seasonal changes in the physical environment occurring in the surface ocean. These can be conveyed through integrative water column processes like upwelling (Messíe et al. 2023) or can reflect seasonal changes to prey communities (e.g., Hannides et al. 2020). In regions where more periodic sampling of midwater communities has occurred on multiyear or decadal timescales, abundance patterns of both epipelagic and mesopelagic animals do reveal consistent structuring of midwater communities alongside overarching regional oceanography (e.g., Ralston et al. 2015).

3.2. Mesopelagic Biogeography

The identification of large marine ecosystems or provinces according to spatial biogeographical classifications is a common global ocean framework for the surface ocean. Two schemes are the 32 distinct Longhurst biogeochemical provinces (Longhurst 2007, chapter 1) and the large marine ecosystems, which focus on coastal waters (Sherman 1991). These horizontal biogeographical classifications are useful for delineating primary oceanographic (bathymetry and hydrography) and ecological patterns in species and habitats (productivity and food-web relationships). They can also facilitate discussion of large-scale protection and management of the global ocean and regional resource management.

Three-dimensional biogeographical frameworks that incorporate vertical and spatial dimensions have been developed from biotic and abiotic datasets, while acknowledging the stark lack of sampling across global mesopelagic habitats. Sutton et al. (2017) defined 33 global mesopelagic ecoregions (20 oceanic regions and 13 distant neritic or continental shelf–associated regions) based on differences in prevailing water masses, OMZs, temperature extremes, surface-water productivity, and biotic partitioning. Analysis of global acoustic datasets (depth and echo intensities of acoustic deep scattering layers) presents 36 spatially distinct mesopelagic provinces alongside the environmental drivers of diel vertical migration (DVM) (Proud et al. 2017). The vertical and spatial delineation of the mesopelagic layer by the major environmental parameters influencing deep chemical and biotic processes results in 13 distinguishable biogeochemical provinces (Reygondeau et al. 2018). The resultant macroecological patterns in midwater species distribution are very poorly known, but biogeographical frameworks that incorporate spatial variation in vertical temperature, light, and oxygen, for example, could be used to better constrain mesopelagic biodiversity patterns, especially relative to physiological limits of key species or assemblages.

The tools of population genetics have been applied to shallow planktonic organisms (Dischereit et al. 2022, Jennings et al. 2010, Marlétaz et al. 2017, Peijnenburg et al. 2004, Urban et al. 2022) but only sparsely to deeper-living species (e.g., Christianson et al. 2022, Goetze et al. 2015, Hirai et al. 2020, Johnson et al. 2022, Miyamoto et al. 2010). There are many questions to be addressed about how truly cosmopolitan deep-sea species are and how diversification might happen across the water column and across major oceanographic features, with few apparent boundaries to separate populations.

3.3. Vertical Migration

A unique feature of midwater ecosystems is the periodic, cyclic change in the vertical positions of many of the animals over the course of each day and night, known as DVM. The upper sunlit regions of the ocean host a resident community of animals that are finely tuned to hiding in plain sight (Johnsen 2014) and are generally not closely tied to deeper waters. When light leaves the epipelagic, under the cover of darkness, a range of gelata, fishes, crustaceans, cephalopods, and other taxa move into these depths both to eat and to escape being eaten (Clarke & Backus 1956). Other species stay put and prey upon the animals that migrate past them (Robison et al. 2020). It can be illuminating to flip our viewpoint on vertical migration: Some animals would prefer to live in shallow waters, but during the day or a full moon cycle those waters become too dangerous, so they migrate downward to avoid predation.

Regular migrations between deep and more food-rich, shallower waters are powerful in how they connect energy flows between animal communities living, swimming, and feeding across often distant depth zones. The implication for sampling is that neighbors during the day may not be dinner partners at night. Subtle changes in light across the water column also largely structure predator–prey interactions and can ultimately dictate survival in the midwater.

There is a rich history of research into the overall patterns of DVM among different members of midwater communities (e.g., Angel 1989, Bandara et al. 2021, Hannides et al. 2020). The trends differ depending on where you are, the time of the year (or lunar cycle), and whether you are using nets or sound to assess the migration (discussed in Section 4.1). Early trawling work proposed that nearly half of the zooplankton and micronekton community vertically migrate (Maynard et al. 1975), and more recently, acoustics have given a picture of the bulk movements of many layers of organisms in response to both daily cycles and short-term predatory activities (Benoit-Bird & Moline 2021, Klevjer et al. 2012). DVM in pelagic environments is often generalized as a single primary layer of animals moving from a mean daytime depth up to a shallower mean nighttime depth. However, these water-column migrations may be considered a "ladder of migrations," with numerous layers and migrators passing the carbon baton in a relay between multiple depth horizons (Vinogradov 1970). These vertical ladders are key in connecting species and organic matter from surface waters through the deep midwater (see Section 5) and even down to the seafloor. Important work remains to more finely characterize the nuances and overall patterns and key players of vertical migration in different regions.

During vertical transitions into different environments, migration brings hazards along with the opportunities (Robison et al. 2020). Animals moving through the water put themselves at increased risk of overlapping the capture area of ambush and sit-and-wait predators (see **Figure 6** in Section 5.1, later in this article). Depending on the rate and timing of their movements, they may also encounter changing illumination environments that challenge their ability to camouflage. During their migration, they may also enter low-oxygen waters and need to tolerate additional metabolic demands on top of their locomotory activity. Nonetheless, the desire to access the rich resources of the shallower communities drives many animals and their larvae (Nonaka et al. 2021) to undergo these transitions each day.

In the same way that vertical distributions can follow a number of different patterns, patchy spatial distribution may be seen in midwater habitats—sometimes in relation to a shelf, seamount, or other topographic feature, and sometimes without any apparent drivers.

4. ASSESSING DIVERSITY

Despite the importance of understanding the abundance and distribution of midwater organisms, it is extremely challenging to establish even simple baselines (Cook et al. 2020, Gates et al. 2017,

Milligan et al. 2018, Robison et al. 2017). Baselines are essential for managing the habitat, detecting change over time, quantifying biomass and carbon transport, and detecting the effects of acute perturbations.

4.1. Sampling Methods

Remotely operated vehicles (ROVs) can be considered the workhorses of midwater research. They can carry a range of imaging devices, profile with environmental and biochemical sensors, conduct manipulative experiments, make behavioral observations, and collect targeted specimens in near-pristine condition. There are additional techniques for identifying and counting midwater animals, which fall into several categories. Each has its own advantages and shortcomings, and some are more suitable for autonomous deployment or analyses. Presently, no one method can give a complete snapshot of the environment, as one might achieve with a terrestrial or intertidal survey, and only by combining perspectives can we begin to appreciate the full scope of diversity (Hetherington et al. 2022a).

4.1.1. Net-based sampling. The longest-used and most common sampling method for midwater organisms is towing a net attached to a long cable behind a ship. These trawl nets consist of a mesh that funnels its contents into a container called a cod end. They may be as small as 1 m in diameter (bongo or ring nets) or as much as 100 m long (midwater fish trawls). One popular system, the MOCNESS (Multiple Opening/Closing Net and Environmental Sensing System), allows deployment of up to 10 nets on a single cable, so that samples may be obtained from many discrete depth layers during one deployment (Wiebe et al. 1985). The E in MOCNESS is significant because it refers to the co-collection of key environmental data—temperature, pressure, salinity, oxygen, and light—along with the sampled biota.

Several factors determine which fraction of the community is effectively sampled on a given trawl (Hetherington et al. 2022a, Kwong et al. 2018). Net avoidance, when organisms evade the net opening as it moves through the water, is affected by the speed of the trawl, the size of the opening, and the pressure wave in front of the trawl, which may be related to mesh size and taper from the opening to the cod end. Avoidance can be quite significant, even leading to underestimation by an order of magnitude (Kaartvedt et al. 2012).

The condition of trawled organisms upon reaching the surface is one of the biggest challenges facing net-based collections. Their physical state depends on nearly all properties of the net: towing speed, mesh size, length, taper, and the design of the cod end. Special cod ends used on midwater Tucker trawls can close at depth and protect the animals in a cold, dark environment during the recovery of the net (Childress et al. 1978). More typically, though, the cod end is open during recovery, so organisms are exposed to surface temperatures, high trawl speeds while the cable is retrieved, and sloshing between the more protective cod end and the abrasive net. For these reasons, many gelatinous animals, particularly comb jellies and siphonophores, are not effectively retained in standard midwater trawls.

4.1.2. Acoustic surveys. By transmitting high-frequency sound into the water and listening for reflections, active acoustical instruments provide a way to estimate biomass for a large swath of the water column, down to approximately 1,000 m under the source for large targets imaged at lower frequencies (Simmonds 2005). The clear advantage is that they generate an instantaneous view of the distribution of biomass throughout the ensonified cone, even allowing for continuous recording through time (Benoit-Bird et al. 2001) and for tracking of individual animals (Båmstedt et al. 2003, Kaartvedt et al. 2007). Such measurements have provided the first and by far best views of the dynamics of vertical migration and notably led to the discovery of the deep scattering

layer of acoustically reflective animals. The main challenges when using acoustics to characterize midwater ecosystems are that the strength of the return signal varies greatly by taxon and that only a rough categorization of the targets is possible. Acoustic sensors can be a powerful method for assessing water-column biomass and behavior, especially when combined with independent methods of verifying species, and with innovative platforms to deploy devices and extend sampling ranges deep below the surface.

4.1.3. Video and imaging.

Images have been used to census deep-sea animals since the first cameras were lowered on cables. Subsequently, there have been great advances in deploying higher-definition cameras on more advanced platforms, including towed, autonomous, and remotely operated systems. Recently, there has been a dramatic increase in the acquisition of deep-sea imagery with the submersibles of Schmidt Ocean Institute, the NOAA Office of Ocean Exploration, Nautilus Live, the Monterey Bay Aquarium Research Institute, OceanX, and others. Depending on the setup of the device, imagery allows for the precise localization of organisms ranging from protozoans, phytoplankton, and marine snow up to macroplankton and even fragile gelatinous organisms, although typically not with the same device. Some limitations of video imagery are avoidance by mobile visual animals, the challenges and platform requirements of getting towed or remotely operated systems into deep waters, and the requirement for labor-intensive postprocessing by experts. Postprocessing has been facilitated by the application of machine learning to classify images based on extensive training datasets (Cowen & Guigand 2008, Gorsky et al. 2000, Kenitz et al. 2023, Luo et al. 2004, Sosik & Olson 2007), and the capabilities of these systems will continue to improve rapidly. ROVs are not only useful for carrying cameras—they also support a variety of manipulative experiments and sensors and enable the capture of unique near-pristine specimens.

4.1.4. Environmental DNA.

There is strong interest in developing ways to assess abundance and diversity without reliance on taxonomic specialists and laborious processing of fixed samples. In addition to genetic sequencing of bulk organism collections (Pitz et al. 2020) and gut contents (Damian-Serrano et al. 2022, Dischereit et al. 2022, Urban et al. 2022), one approach is to do genetic assessments of the DNA present in a water sample (e.g., Allan et al. 2021, Djurhuus et al. 2020). At its best, this method allows for detection of trace genetic signatures of organisms that have inhabited or passed through a parcel of water. While this method has an appealing simplicity, there are several challenges to overcome before it can replace traditional taxonomic efforts. First is the requirement for a robust reference dataset of sequences from identified species. This is especially challenging for the deep water column, where there has been less taxon-specific sequencing of multiple genes from vouchered specimens. Sequences that do not match anything in a reference database may still help to highlight uncharacterized diversity that merits further investigation. There are also other confounding factors that preclude generating quantitative data at this time: Primers used to amplify diagnostic regions are not equally effective across species; different types of organisms and different physiological processes will shed varying amounts of DNA into the water; and the amplification process is not linear, so the distribution of the amplified genetic products does not reflect the relative abundance of organisms or their DNA. Environmental DNA (eDNA) is a useful tool to give a presence–absence assessment for a species, do initial surveys of a site, and monitor a particular species through time or across depths. Further developments will improve its application to fully characterizing deep-sea biodiversity.

4.1.5. Future trends.

While we highlighted the primary sampling tools used to study midwater ecosystems, each of these methods is rather specialized and can be costly, leading to general inaccessibility. The need for dedicated oceanographic research vessels to deploy these tools is an

additional critical impediment. To overcome these hurdles and enhance global deep-ocean observation networks, a number of so-called deep-and-cheap sampling systems are being developed and tested to add to the growing knowledgebase (e.g., Berkenpas et al. 2018).

4.2. Patterns of Diversity

While each of these approaches can give unique perspectives on midwater diversity, they are all dependent on a robust taxonomic framework, whether morphological (for images), genetic (for eDNA), or using both together (net samples). A detailed and accurate picture also requires combining these tools to sample across a broad range of taxa. Failure to do so can result in vastly different pictures of marine communities, inaccurate assessments of total biomass (Kaartvedt et al. 2012), or inaccurate assessments of the relative biomass of microbes and different categories of animals in the deep (Hetherington et al. 2022a).
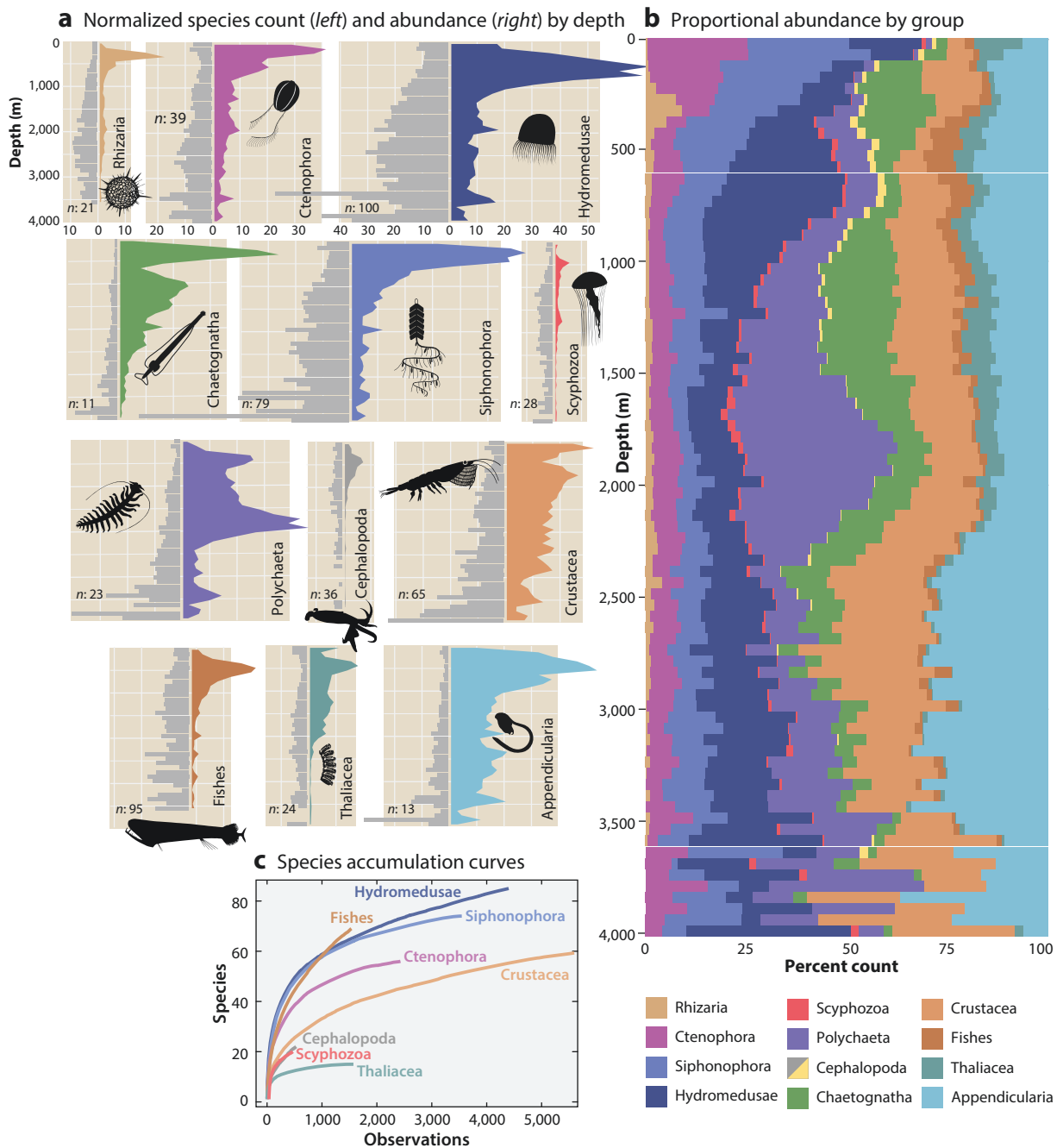
Given these caveats, what can we say about the most prominent members of midwater communities? Viruses, bacteria, archaea, and protists are all important and abundant in the deep water column, but these organisms have been addressed elsewhere (e.g., Herndl et al. 2023, Robinson et al. 2010, Santoro et al. 2019), so we constrain our discussion here to animals and some macroscopic protists. Similarly, deep-diving mammals are important predators dependent on the deep midwater, but they have been the topic of their own review (Braun et al. 2022).

In some groups, species richness decreases with depth (Priede & Froese 2013, Roe 1988), yet there are still surprisingly high levels of diversity in the deep (McClain & Schlacter 2015), and many uniquely deep-sea species have not yet been formally described. Although overall there is a general pattern of decrease in diversity from the surface to great depths (**Figure 2**), the actual trends for pelagic taxa are more involved (Robison et al. 2010). Given dense enough observations (380,000 organisms were annotated from ROV footage to obtain the data shown in **Figure 2a,b**), one can distinguish more nuanced trends. Off the California coast to approximately 150 km offshore, among the major water-column-associated animals, there is not a monotonic or exponential decline in diversity; the species discovery rate and the Simpson's diversity (not shown) are relatively constant through the water column (**Figure 2a**). Several datasets have shown a subsurface maximum in species richness at approximately 500 m. Similar patterns of declining abundance and diversity have been seen in previous studies (Angel 1993), and subsurface diversity maxima are seen in many of the fish taxa covered by Priede & Froese (2013), such as the anglerfishes, dragonfishes (stomiids), lanternfishes (myctophids), and slickheads.

In our results, while the abundance decreased and species composition changed with depth, the major clades occurred at approximately the same relative ratios down to 4,000 m. An often quoted paradigm is that total biomass and diversity decline exponentially with depth in the water column, but these results are based on trawls at a few depths, and the broad patterns have not been thoroughly assessed. Nonetheless, there are caveats to interpreting assessments of deep-sea diversity. Not only are deeper samples rare, but taxonomic effort and sampling opportunities fall off with depth. A much larger proportion of shallow species are likely to be distinguished, while the deepest species harbor more cryptic or undescribed species that are identified only at the group level. Species accumulation curves (**Figure 2c**) indicate that there are many species left to be discovered for the temperate eastern Pacific, and indeed, the depth distributions for major midwater lineages extend beyond 8,000 m (Jamieson & Linley 2021, Jamieson et al. 2023). Combined with genetic sampling, taxonomic efforts on deep-sea fauna will greatly expand our view of true deep diversity.

One way to gain insight is to consider what groups are relatively more abundant in the deep water column than in shallow waters or in the benthos (**Figure 3**). Deep-sea benthic samples

show high abundances of polychaete worms; amphipods and isopods (Peracarida); echinoderms; bivalves; agglutinated foraminifera; nematodes; and, on hard substrates, octocorals (Cnidaria), tunicates, and sponges. There is some overlap in major clades with deep-water-column taxa, but the pelagic species are typically from different families than those on the bottom or in the

a Normalized species count (*left*) and abundance (*right*) by depth

b Proportional abundance by group

c Species accumulation curves

(Caption appears on following page)

Figure 2 (*Figure appears on preceding page*)

Diversity and abundance based on remotely operated vehicle (ROV) footage. (*a*) Normalized species counts (species per day; *gray bars*, *left side of each subpanel*) and abundance (individuals per hour; *colored areas*, *right side of each subpanel*) for major water-column groups at different depths. The depth and count axis labels shown in the top row also apply to the other subpanels; note that the subpanel for crustaceans excludes copepods, which are not well visualized by the ROV. General trends include a subsurface maximum in abundance across nearly all lineages. Chaetognaths show indications of a bimodal distribution, potentially indicating avoidance of the low-oxygen zone. Species richness normalized by observation time (*left bars*) remains constant for most taxa across depth. (*b*) Relative abundance of organisms encountered during ROV observations. The overall community composition is strikingly consistent with depth down to 4,000 m. Hydromedusae, siphonophores, and polychaetes (primarily the detritivore *Poeobius meseres*) are abundant through the mesopelagic. (*c*) Species accumulation curves based on a smaller dataset. These curves show the relative diversity (including undescribed yet distinguishable species) and the expected discovery of new species when monitored by regular ROV observations. The analyses in panel *a* and *b* are based on 380,000 unique annotations of macroscopic water-column organisms gathered over 1,879 h of submersible dives spanning more than 20 years in the eastern North Pacific (Martini & Haddock 2017).

sediments. For example, water-column amphipods are often lanceolids and commensal hyperiids (**Figures 4e** and **5a–c**) rather than lysianassids, which are famously associated with hadal (very deep) trenches. The dominant polychaetes are *Poeobius*, which feeds on marine snow, and *Pelagobia*, *Tomopteris*, and *Swima* (**Figure 4b**), which are predatory rather than interstitial in sediments and burrows. Many clades are endemic to the water column: phaeodarian radiolarians, ctenophores, diverse medusae (hydrozoans and scyphozoans), siphonophores, squid, stomiids (dragonfish and viperfish), myctophids (lanternfish), appendicularians (larvaceans), and salps (**Figure 4**).

An interesting region is the benthic boundary layer—water just above (maybe up to 50 m above) the seafloor. As with many transition zones, this narrow stratum has unique diversity and offers increased opportunities for predation by pelagic animals. Many species, including medusae, polychaetes, and ctenophores, specialize in living there. Some benthic organisms—even sea stars and tube anemones—also spend important periods of their life as meroplanktonic larvae that drift in the water column before settling, often metamorphosing, and maturing on the bottom. This is a counterpoint to the primarily pelagic organisms that bud from polyps attached to benthic substrates, or indeed other platforms of opportunity.

As discussed in Section 2, the fully three-dimensional midwater environment means that there are no (nonliving) obstacles to bump into or hide behind. This also means that there are few surfaces to which polyps can be attached. Organisms have adapted to these conditions by
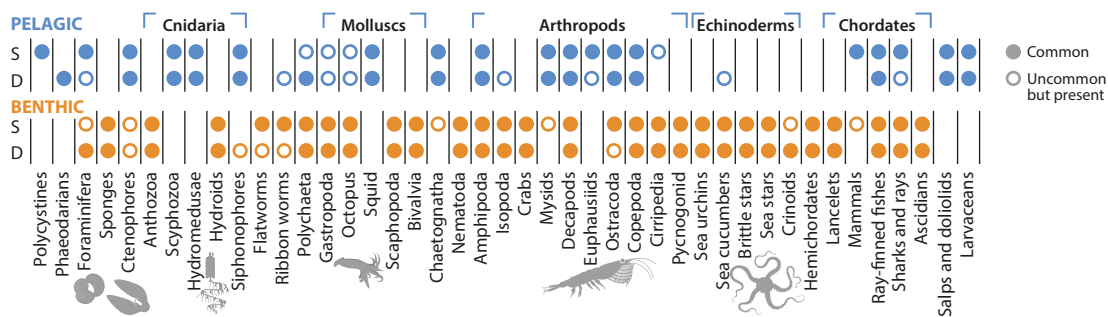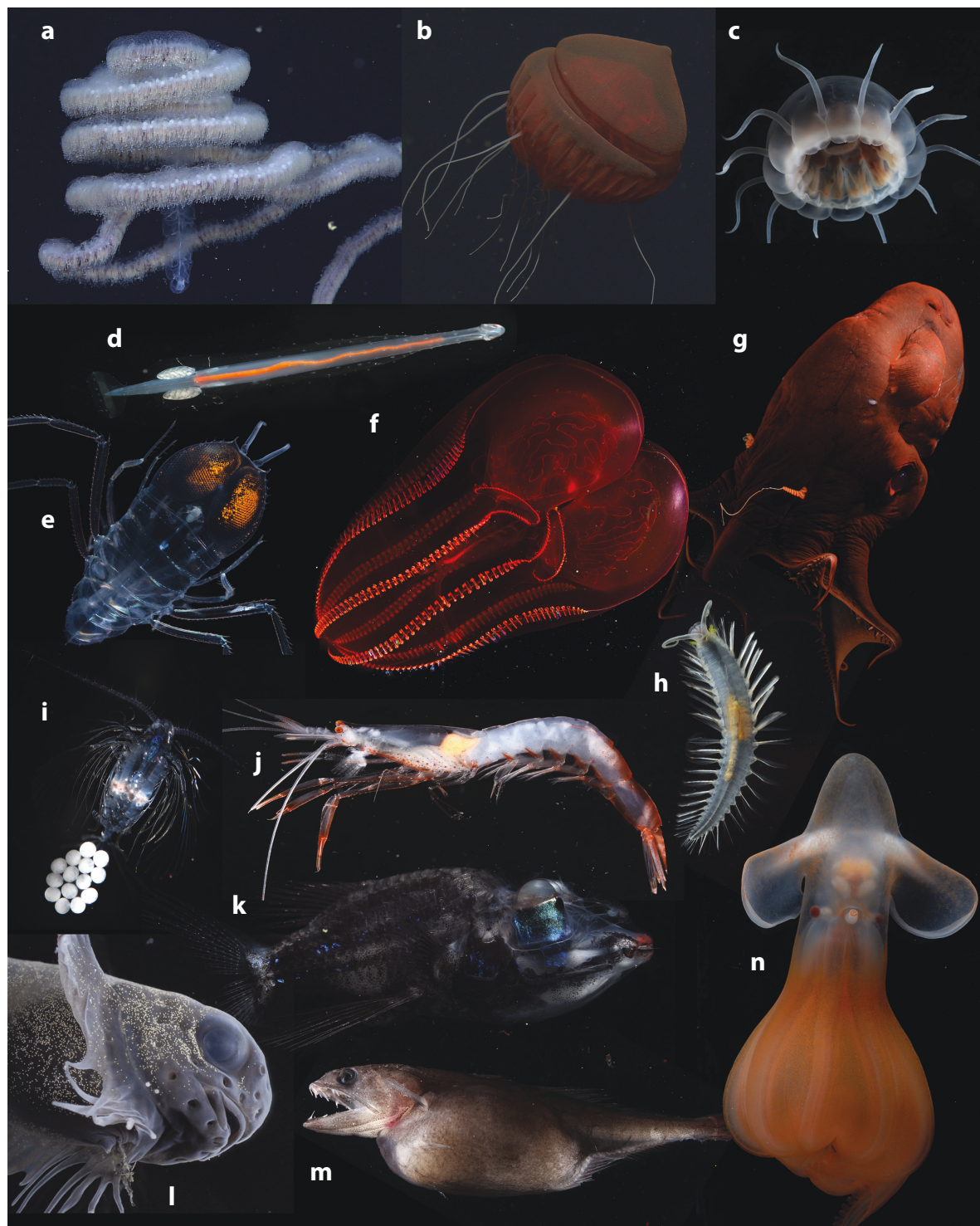

Figure 3

Matrix of animal habitat dominance. Shallow (S) and deep (D) portions of the pelagic water column and benthic habitats are utilized by different lineages, both at the family level and at higher taxonomic levels. Polycystines and phaeodarians are two clades of radiolarians (Rhizaria) containing silica structures. Some water-column specialists, including the bristlemouth fish *Cyclothone* and the hydromedusa *Aegina*, may be among the most abundant animals on Earth, given their prominence in this vast environment. Filled circles mean that the organisms are common in that habitat, open circles mean that they are uncommon but present, and no circles means that they are rare or do not occur.

(Caption appears on following page)

Figure 4 (*Figure appears on preceding page*)

Diverse morphologies of midwater animals. (*a*) The siphonophore *Apolemia* can grow to great lengths and appears to subsist on gelatinous prey. (*b*) The coronate scyphozoan *Paraphyllina* is one of the larger deep-sea medusae. (*c*) *Sigiweddellia* is a recently described genus of narcomedusae, which are hydrozoan predators of other jellies. (*d*) *Eukrohnia fowleri* is one of the two known bioluminescent species of chaetognaths. (*e*) *Cystisoma* is a large (up to 10 cm) transparent amphipod with elaborate eyes. (*f*) *Lampocteis* is an abundant yet only recently described deep lobate ctenophore. (*g*) *Vampyroteuthis* is a cephalopod that spends most of its time in the oxygen minimum zone and is thought to eat detritus. (*h*) *Swima bombiviridis* is a bioluminescent polychaete found below 3,000 m and often just above the seafloor. (*i*) Copepods and other organisms sometimes carry large yolky eggs through the water column. (*j*) Pasiphaeid shrimp have elongate feeding appendages. (*k*) *Opisthoproctus* spookfish have tubular upward-looking eyes. Although this specimen was in good condition, fish lenses rapidly crystallize, and its eyes would normally be transparent. (*l*) Liparid snailfish have giant pores that house flow-detecting sensors. (*m*) *Chiasmodon*, the giant swallower, is an example of a predator that subsists on one meal (which can be larger than its own body) for months. (*n*) *Cirrothauma* is a cirrate octopus with reduced lensless eyes. Photos in panels *a* and *b* provided by the Monterey Bay Aquarium Research Institute; photos in panels *j* and *m* taken by C.A. Choy; all other photos by S.H.D. Haddock.

attaching their polyps to other animals. For example, the hydroid phase of the medusa *Pandea rubra* is attached to the shells of pteropods (Pagès et al. 2007) (**Figure 5b,i**), the medusa *Earleria* (formerly *Foersteria*) buds from polyps that grow on the carapaces of pasiphaeid shrimp (Widmer et al. 2010), and the hydroids of *Bythotiara* are embedded within a doliolid (Robison et al. 2005a) (**Figure 5e,f**). Pycnogonids (sea spiders) are found riding in and upon medusae, even several hundred meters above the seafloor (**Figure 5d**).

Given the broad range of lineages that are adapted to life in the water column, it is clear that evolution into and out of the deep sea and transitions between benthic and pelagic existence have occurred numerous times (Friedman et al. 2020, Priede & Froese 2013). Accurately estimating these transitions requires a phylogeny with diverse representation, so it is more tractable in some lineages than others. For ctenophores, at least six transitions may be seen, and for sea cucumbers, there have been perhaps eight such transitions between deep and shallow life (Bessho-Uehara et al. 2023). A fascinating future direction is to apply phylogenetically informed morphometric analyses like those of Friedman et al. (2020) to deep-sea invertebrates.

4.3. Vignettes of Deep-Water-Column Specialists

Here, we briefly discuss five groups—ctenophores, siphonophores, chaetognaths, larvaceans, and squid—that represent some of the exclusively marine lineages that reach their highest abundance and diversity in the open ocean. They can each be challenging to sample, whether due to fragility or agility, and their significance to the community is rarely quantified in detail. Examining their natural history, physiology, population dynamics, and genetics is important for understanding life in the ocean as a whole.

4.3.1. Ctenophores. Ctenophores (comb jellies) are gelatinous predators (**Figure 4f**) that range from shallow tropical waters down to 10,000 m (Jamieson et al. 2023). They feed using sticky feeding structures rather than stinging cells and are not closely related to cnidarians, despite superficial similarities. Because ctenophores are so fragile, much of the deep-living diversity is in families that are yet to be described. Ctenophores can be broad extreme specialist feeders or broad generalists. They span a wide range of trophic levels in the food web, including predating upon detritivores as well as on fish and other jellies.

4.3.2. Siphonophores. Because siphonophores (**Figure 4a**) grow by continuous budding of zooids and elongation of their tubelike stem, they can reach lengths of tens of meters in the still waters of the deep sea. They have essentially peeled their polyps off the seafloor and drift without need of a substrate. With an array of swimming bells at one end, they pull the train of specialized zooids along behind them like a locomotive. Each feeding zooid has an attendant

(*Caption appears on following page*)

Figure 5 (*Figure appears on preceding page*)

Associations in the midwater. (*a–c*) Parasitic amphipods can have scyphozoan (panel *a*), hydromedusan (panel *b*), or ctenophore (panel *c*) hosts. (*d*) A pycnogonid seaspider was found living associated with the hydromedusa *Aeginura*. (*e,f*) Polyps (*green arrows*) of the medusa *Bythotiara* (panel *e*) are housed within the chambers of the doliolid *Doliolula* (panel *f*). (*g*) A copepod with eggs (*green arrow*) lives inside a salp. (*b,i*) *Pandea* (panel *b*) is a medusa whose polyps are deposited on a shelled pteropod (panel *i*, *green arrow*). (*j*) A *Haliphron* octopus holds a *Phacellophora* medusa. (*k*) *Deepstaria* is a giant scyphomedusa, shown here with a pilot isopod *Anuropus* (*green arrow*). Photo in panel *i* provided by S. Bush; photos in panels *j* and *k* provided by the Monterey Bay Aquarium Research Institute; all other photos by S.H.D. Haddock.

tentacle ornamented with batteries of stinging cells, as do their closest relatives, the hydromedusae. Siphonophores display diverse feeding modes, including as generalists, fish specialists, and gelatinous specialists, as with species of *Apolemia* (Damian-Serrano et al. 2021). Despite being nonvisual sit-and-wait predators, some species even use bioluminescent lures to attract prey (Haddock et al. 2005, Pugh & Haddock 2016). Because of their abundance, large sizes, and ability to independently process the prey of their many stomachs, siphonophores can have a predatory impact out of proportion to their basic numerical abundance (Choy et al. 2017, Damian-Serrano et al. 2021).

4.3.3. Chaetognaths. Chaetognaths, known as arrow worms, are said to be second only to copepods among shallow-water plankton, and they have high abundance and diversity in the deep sea as well. While shallow species may be less than 1 cm long, in the deep, chaetognaths commonly reach lengths of 5 cm or more. They are ambush predators that often drift rigid and motionless and then, when they sense vibration, suddenly lunge and grab prey with their raptor-like paralyzing hooks. Like other deep-sea taxa, some chaetognaths brood their young in specialized pouches on either side of the body (**Figure 4***d*).

4.3.4. Appendicularians. Appendicularians (larvaceans) look like tiny tadpoles, and as members of the urochordates, they are one of the invertebrates most closely related to vertebrates. They are readily visible in underwater video by their mucus houses, which they use to filter feed (see Section 5.4). Their tail is flattened dorsally rather than laterally, and they use it to pump water through a fine mucus mesh that retains even microbial and protozoan-size particles (e.g., Hopcroft & Robison 1999). Once the inner filter becomes damaged or clogged, the larvacean abandons it, swims away, and begins secreting the precursor to the next house, like a shower cap covering its headlike trunk.

4.3.5. Squid. Squid are arguably the most active and versatile predators of the water column. They can reach high swimming speeds, have acute vision, and can apprehend prey using suckers, hooks, or even suckers lined with tooth-like serrations. They use bioluminescence for a variety of offensive and defensive purposes, sometimes showing three different functions in a single organism. The most massive invertebrate on the planet is not the giant squid *Architeuthis* but the colossal squid *Mesonychoteuthis*, which spends its adult life in the deeper recesses of the water column (Rosa et al. 2017). Squid are important prey for numerous larger fishes and deep-diving mammal species. In deep waters, they tend to have more gelatinous forms and thus may be digested quickly and be masked from diet studies if identifications from remnant hard parts like beaks are not included (Chen et al. 2022) (discussed further in Section 5).

5. FOOD WEBS AND LINKAGES

5.1. Unique Water-Column Dynamics

Midwater food webs stretch across the water column in complex and curious ways, and it is certain that many ecological nuances and feeding linkages remain undiscovered. Chemosymbioses, like
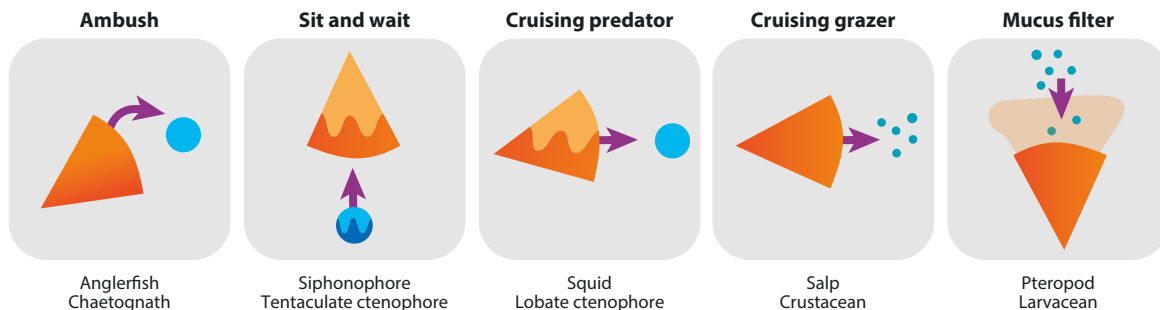
Figure 6

Feeding strategies in the deep water column. In addition to taxonomic and morphological diversity, there is significant functional diversity in modes of feeding. Many of these feeding strategies are optimized for low energy expenditure and opportunism of large, infrequent meals. They are also complexed with vertical migration behaviors and general vertical distributions, which overall influence the structure of midwater food webs and the transport and transformation of organic matter across the water column. Sinusoidal fills on predators (*orange*) and prey (*blue*) indicate groups where many members participate in diel vertical migration.

those at hydrothermal vents and seeps, have not yet been found in the deep water column, and feeding takes place mostly through predation, parasitism, or detritivory (**Figure 6**). Several aspects of midwater food webs differ substantially from those in shallower and nearshore waters. The general absence of primary producers in the midwater means that herbivory is uncommon, so to a large extent, sinking and suspended particulate organic matter (marine snow) lies at the base of the deep-sea food web. As discussed in Section 4.1, assessments of midwater species diversity are strongly dictated by sampling method, and so are analyses of the interactions or food-web linkages between and among species. An integrative combination of methods, employed across major animal groups and through the water column, will ultimately provide the most balanced, comprehensive view of midwater food webs.

Midwater feeding strategies may be divided into a few main classes that are employed convergently across many taxa (Kiørboe 2011). These strategies have different metabolic demands (sudden bursts of energy versus steady cruising) and target food of different sizes, morphologies, and behaviors (**Figure 6**). As with all living systems, intake of energy must match or exceed that required for growth, reproduction, base metabolism, and locomotion; adaptations of deep-living animals represent nearly every weighting of factors to balance this equation.

Analyzing an animal's stomach for ingested prey is the most direct and quantitative method for identifying food-web linkages. Numbers, weights, and frequencies of prey items from gut-content analyses provide insight into diets and feeding strategies. In the midwater, diet analysis is burdened by formidable logistical constraints owing to the vastness of the deep sea and the diversity of inhabitants. Retrieving midwater animals from depth with their gut contents intact has been the classic approach for diet studies of fishes, generating numerous insights and rewriting what we think about the impact and diversity of fish ecology (Choy et al. 2013, Clarke 1980, Portner et al. 2017, Sutton & Hopkins 1996). However, visual inspection of gut contents favors morphologically robust predators (which happen to swallow their prey intact) and their more robust prey items, which can resist digestion enough to be counted. Gut-content analysis is less well suited to identifying diaphanous gelatinous or soft-bodied prey, and only with the use of submersibles and imaging has the importance of the jelly web become more widely known (Robison 2004). Biochemical (stable isotopes and fatty acids) or genetic techniques (discussed in Section 4.1) may also be applied to unconventional predators and gelatinous prey. One way to resolve primary midwater feeding relationships and better describe water-column food webs is to focus on the diets

of abundant or dominant taxa as well as their dominant predators and employ a range of tools, including stomach contents, biochemical and molecular tracers, and imaging technologies.

5.2. Increasing Awareness of the Jelly Web

In the same way that the abundance and diversity of gelatinous animals has been underappreciated, their roles and positions in deep-sea food webs have not been fully explored (Choy et al. 2017, Hetherington et al. 2022b, Robison 2004). Given their phylogenetic, morphological, and functional diversity, it is not possible to generalize about jellies. Rather than occupying a single niche—as either predator or prey—or being trophic dead ends that nothing else wants to consume, jellies are food for many deep-sea species, spanning most of the animal groups reviewed in Section 4 (Choy et al. 2017, Drazen & Sutton 2017, Hoving & Haddock 2017). Given their fragile nature, when gelatinous animals are consumed, they quickly become unrecognizable in gut-content analyses, leading to common underestimates of their importance as prey.

As predators, different gelatinous groups employ many feeding strategies, including acting as detritivores (mainly among salps) and as first-order predators (feeding on detritivores or herbivores). In the numerous cases where they consume other kinds of jellies, they may even feed four or more levels removed from primary production as a diminutive sort of top predator. Medusae in the deep sea have very different dynamics than conspicuous coastal species such as sea nettles, moon jellies, and mauve stingers. They may have stable distributions both vertically and through the year, apportioning their prey by different depth specializations and prey-capture strategies and according to the dynamics of vertical migration. Given these unique and varied attributes, future research—particularly studies that integrate multiple sampling and analysis strategies—is sure to connect the diversity of gelatinous species, line by line, into the deep midwater food web.

5.3. Midwater Buffet for Mobile and Deep-Diving Pelagic Predators

Midwater communities are an important food resource for many large marine top predators, including pinnipeds, sharks, whales and dolphins, fishes, and seabirds (Braun et al. 2022, Young et al. 2015). Some species, such as tunas (Duffy et al. 2017, Graham et al. 2007, Holland & Grubbs 2008), toothed whales (Spitz et al. 2011), and elephant seals (Yoshino et al. 2020), directly feed upon organisms that form deep scattering layers, matching the timing and depth of their diving to the position of the layer. Of these deep divers, sperm, beaked, and pilot whales feed disproportionately on large, deep-dwelling cephalopods and octopods and to a lesser extent on mesopelagic fishes and crustaceans (Spitz et al. 2011). Bigeye tuna from around Hawaiian waters exhibit deep-diving behavior to feed on vertically migrating myctophids and midwater shrimps during the day and night (Holland & Grubbs 2008). These feeding interactions may be enhanced in areas of abrupt topography where higher densities of micronekton may be found, such as seamounts, fish-aggregating devices, or oil-drilling platforms. The rapid digestion rates of some epipelagic predators (e.g., tunas and dolphinfish), which feed on shallow components of the deep scattering layer at night and digest their food items during the day, may mask the importance of micronekton as prey if diet studies are unable to account for the diel periodicity of feeding.

Large, predatory mesopelagic fishes (over 1 m in size) and cephalopods are understudied but key consumers of midwater prey, foraging across the expanse of the water column. For example, snake mackerels, lancetfishes, moonfishes, and cutlassfishes feed exclusively on midwater crustacean, fish, cephalopod, and gelatinous prey (Chen et al. 2022, Jackson et al. 2000). The majority of these species have poorly resolved diets because they are not commercially viable, despite being harvested as bycatch alongside numerous valued species and sharing the same water-column habitats. A few focused studies found that dietary niche partitioning allows the coexistence of these

mesopelagic predators and their harvested counterparts (tunas, billfishes, and sharks) (Choy et al. 2013, Potier et al. 2007, Young et al. 2010). Other studies have employed mesopelagic fishes as biological samplers of otherwise difficult-to-sample midwater communities, tracking large spatial and temporal shifts in midwater prey across environmental gradients (Hopkins & Baird 1973; Portner et al. 2017, 2020).

5.4. Midwater Food-Web Fluxes and Biogeochemical Cycling

Midwater food webs play central roles in the movement and transformation of carbon (and other key elements and compounds, discussed in Section 8) between the atmosphere, the surface ocean, and the deep seafloor. Given the enormity of the habitat and the unparalleled midwater biomass and diversity (Childress & Thuesen 1992), it is natural for oceanographers to want to summarize the midwater in terms of carbon units and to place a value on its potential for carbon burial—known as blue carbon. Numerous excellent reviews have synthesized the roles of protistan and metazoan plankton as well as fishes in structuring food-web processes that mediate carbon cycling and vertical export (or sequestration) within the framework of the biological pump (Drazen & Sutton 2017, Herndl et al. 2023, Saba et al. 2021, Steinberg & Landry 2017). Our discussion focuses on midwater ecosystems as a long and wide highway across which numerous and varied biogeochemical alterations of organic matter occur by diverse, underappreciated members of midwater communities. Thoughtful incorporation of these midwater groups in regional and global ecosystem and biogeochemical models will undoubtedly influence the predictive power and findings under distinct climate change scenarios (Choy et al. 2016, Woodstock & Zhang 2022).

Most pelagic carbon cycle studies focus on the conspicuous imbalance of carbon supply and demand in deep waters and aim to constrain and quantify the flux of carbon out of the euphotic zone through (*a*) the passive sinking of particulate organic matter or particles (see Lam et al. 2011, McDonnell et al. 2015) and (*b*) active transport through vertical migration and feeding (Robinson et al. 2010) (see Section 3.3). The amount of carbon leaving the surface ocean is controlled by environmental conditions (temperature, light, and nutrients) that dictate primary production, and the resultant rain of particle material can be highly diverse in composition, spanning multiple origins, associated microbial communities, compositions, and fates (Herndl et al. 2023, Kharbush et al. 2020). Any eventual burial of carbon at depth is influenced by the uptake and repackaging of organic matter during the long passage—taking between six weeks and three months—through the midwater (Alldredge & Silver 1988, Shanks & Trent 1980). Recent studies have highlighted the outsized roles that gelatinous species can play in exporting organic matter— especially species that can rapidly increase their populations in response to ideal food conditions. Salps, doliolids, and pyrosomes are pelagic tunicates, and when abundant, they can ingest substantial portions of phytoplankton populations and particle fields across a range of particle sizes, producing large, quickly sinking fecal pellets and carcasses that more easily escape repackaging (Durkin et al. 2021, Huffard et al. 2020, Steinberg et al. 2023). Transport of material into deeper waters can be especially accentuated by long vertical migrations within the pelagic tunicates, for example, by pyrosomes (Henschke et al. 2019).

Beyond the pelagic tunicates, numerous other organisms impact organic matter through remineralization and repackaging in deeper waters and thus influence overall biogeochemical cycling across the midwater. The highly abundant midwater polychaete *Poeobius meseres* is coprophagic, deploying a mucus web to collect fecal pellets, sinking phytoplankton cells, and eggs from across mesopelagic and upper bathypelagic depths (Uttal & Buck 1996). Larvaceans are active filter feeders that interact with small particles through the construction of mucus houses, and the houses themselves host small ecosystems of bacteria and zooplankton (Steinberg et al. 1997). Larvacean fecal pellets can dominate sediment trap samples (Wilson et al. 2013), and

the discarded mucus houses of giant larvaceans are carbon rich and sink rapidly to the seafloor (Robison et al. 2005b). These are a few examples of underappreciated midwater organisms that interact with and transform the constant rain of detritus connecting surface- and deep-ocean ecosystems.

An exciting area of ongoing research is the active reenvisioning of midwater food webs to achieve a more refined understanding of marine biogeochemical cycling relative to underway climate change. New approaches, particularly those that weave together multiple tools, are actively overcoming some of the primary challenges with working on deep-sea food webs (e.g., sampling at great depths, adequately capturing both soft- and hard-bodied taxa, and attaining full coverage through time and space). Biochemical tracers such as lipids, isotopes, and heavy metals have been particularly powerful for uncovering and quantifying food-web processes across the water column and seafloor and have done so in ways that can allow for inclusion in global and regional marine ecosystem models [see reviews by Parzanini et al. (2019) and Pethybridge et al. (2018)]. For example, surface-derived fish and squid carrion from fishing vessels were found to be important food resources for abyssopelagic grenadiers, a finding made possible through the combined use of stomach contents and stable isotope signatures (Drazen et al. 2008). A suite of recent studies have employed amino acid compound-specific isotope analysis to link small suspended organic particles to mesozooplankton and micronekton food webs that span the water column (Choy et al. 2015; Gloeckler et al. 2018; Hannides et al. 2013, 2020). These smaller particles are generally overlooked as a food source or key carbon export component in favor of larger aggregates or sinking particles, and it is likely that other key food-web linkages will continue to be revealed in the midwater as sampling, methods, and integrative techniques evolve.

6. SENSORY MODES

6.1. Potential Sensory Modalities

Given the scale and properties of the water column, there are trade-offs for using four major types of senses: scent, sound, flow, and light. Chemical cues may be produced intentionally or inadvertently by organisms. They diffuse slowly and over short distances, but they are relatively persistent, so they afford opportunities for finding food and mates. They may also be advected by currents to eventually leave a trail leading far downstream. Shallow copepods demonstrate extremely effective trail-following behavior (both chemical and hydrodynamic) when finding mates (Tsuda & Miller 1998, Yen & Lasley 2011). Using their long antennae, typically spread to the sides in a T-shape, they can sense chemical gradients and differences between the left and right scents they encounter. On a larger scale, scavengers quickly arrive at up-current carcasses, and even sinking marine snow leaves a trail in its wake. Chemical signals must play important roles throughout the deep water column, but they are incredibly challenging to quantify at depth, and natural behaviors are difficult or impossible to reproduce using deep-sea animals in the lab. Much of what is known was demonstrated in shallow or even freshwater species and then extrapolated to other environments based on morphology. Because rare deep-sea taxa are extremely dilute—on average far from a potential mate—it is reasonable to assume we will someday find many chemical mechanisms that help bring together mates, predators, and parasites. The dwarf male anglerfish, its much larger female, and some of the specific host–commensal associations (**Figure 5**) might be promising subjects.

To our knowledge, no pelagic invertebrates use sound for communication, but for marine mammals, sound serves critical roles for long-distance dialog and for locating prey. Vibrations through the water, whether perceptible as sound or as nearby flow, are important for many midwater interactions. Mechanosensory structures on chaetognaths, fishes, crustaceans, and even ctenophores and hydromedusae can alert them to nearby water motion, eliciting a predatory lunge or a quick

escape. Animals not only detect the flow generated by others but also take great care in masking their own wake (Yen & Strickler 1996). Fishes use lateral lines and exposed neuromasts to detect flow around their bodies (Mogdans 2019). Using their sensitivity to flow, many midwater organisms will sit motionless in the water column for hours or likely days on end. Only when a threat is sensed, or a potential meal, do organisms need to expend the energy to move, and even with hydromedusae, these movements can be rapid and effective (Meech et al. 2021).
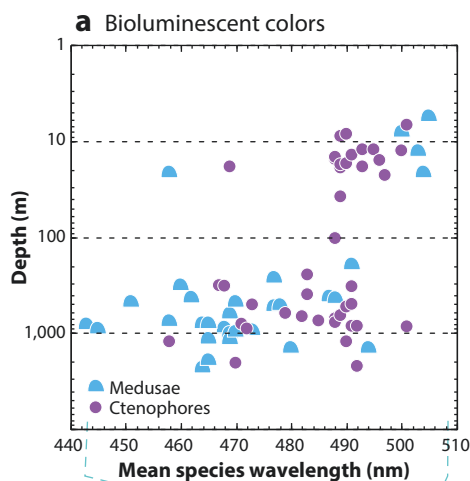
6.2. Bio-Optical Interactions

Regardless of the definition of the vertical boundaries of the mesopelagic zone, the ambient light field ranges from dim blue light to darkness. Rather than reduce their dependence on vision in this dim environment, many organisms have enhanced their visual capabilities with high-performing and specialized eyes (Baldwin Fergus et al. 2015, Wagner 2002). The effectiveness of visual communication is enhanced by the uniformity of the visual field (Johnsen 2014), the clarity of most deep water (**Figure 7**), and sensitive photoreceptors. These conditions make an ideal backdrop for bioluminescent communication, in which organisms make their own light to serve a variety of functions (Haddock et al. 2010). Bioluminescence is so useful that approximately three-fourths of the macroscopic animals in the midwater are able to produce bioluminescent light (Martini & Haddock 2017), compared with fewer than half in deep benthic environments (Martini et al. 2019). Organisms enhance their visual sensitivity using lenses, filters, reflectors, morphology, and neural summation of optical signals.
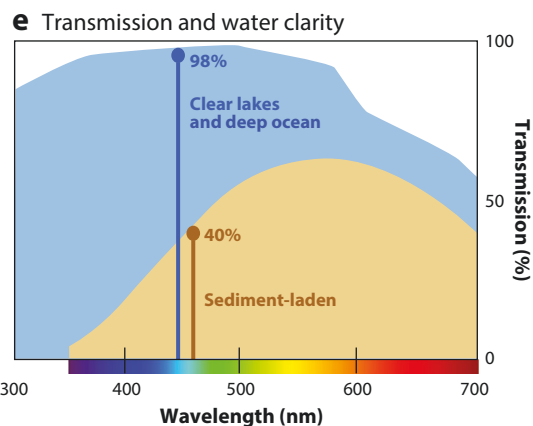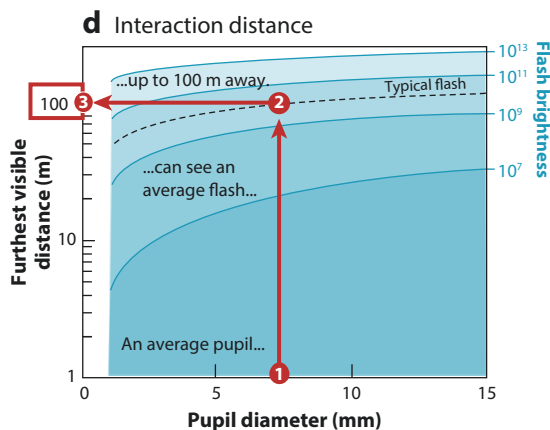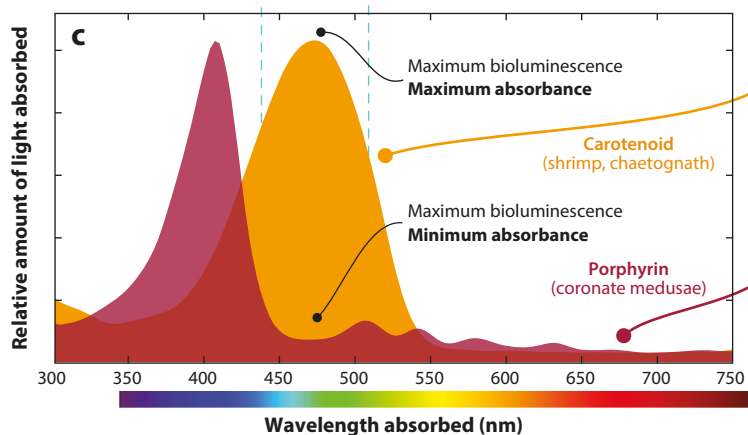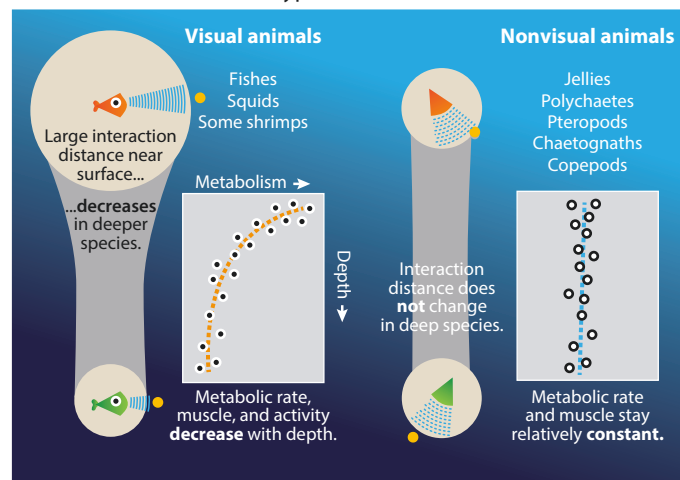
Different wavelengths of downwelling light from the surface are absorbed and scattered by pigments, particles, and the water itself until primarily blue-green light remains, with a maximum emission around 475 nm (**Figure 7e**). Both the colors of bioluminescence produced (Haddock & Case 1999) and the visual sensitivities of water-column animals (Carleton et al. 2020, Douglas & Partridge 1997) shift from green toward blue in deep-sea waters (**Figure 7a**). The most common colors of luminescence emission in the deep sea match the wavelengths that transmit the farthest and that can be detected most effectively. Given the eye sizes and sensitivity of a deep-sea fish and the brightness of a typical flash, it is estimated that bioluminescence can be seen at a distance of 100 m in deep waters (Warrant & Locket 2004) (**Figure 7d**). In the upper regions of the midwater zone, the backdrop of dim blue light provides visual predators with an effective strategy of looking for the dark silhouettes of potential prey. This is why so many fish and squid have upward-looking eyes (de Busserolles et al. 2020, Wagner et al. 2009) (**Figure 4**) or orient themselves to view the water above them (Luck & Pietsch 2008, Thomas et al. 2017, Wagner et al. 2009, Young 1975). In response to this hunting strategy, potential prey hide using counterillumination, in which bioluminescence masks their silhouettes, matching the light field from above and even from the sides (Haddock et al. 2010, Johnsen 2014).

Because many organisms in the water column are able to make their own light, predators are faced with a challenge. Many predators are transparent, or nearly so, in order to hide and avoid their own predators (Cronin 2016). However, this means that anything they ingest can potentially glow within their stomachs. The paradigm for bioluminescent displays is that nearby flashes repel, while distant flashes or steady glows attract. To avoid drawing attention to their glowing meal, many animals have orange or red pigmentation in their gut that specifically absorbs blue light (Johnsen 2005) (**Figures 4** and **5**). In the case of shrimp and chaetognaths, they use carotenoid pigments that absorb at nearly the exact wavelengths of bioluminescent emission (**Figure 7c**).

The use of bioluminescence to attract prey is well known from the example of the anglerfish's glowing lure, but recently this has been shown to be more widespread, with siphonophores (Haddock & Dunn 2015, Haddock et al. 2005) employing both bioluminescent and fluorescent (excited by ambient light) lures to attract their prey.

a Bioluminescent colors

b The visual interactions hypothesis

Visual animals

Fishes
Squids
Some shrimps

Large interaction distance near surface...

Metabolism →

...**decreases** in deeper species.

Metabolic rate, muscle, and activity **decrease** with depth.

Nonvisual animals

Jellies
Polychaetes
Pteropods
Chaetognaths
Copepods

Interaction distance does **not** change in deep species.

Metabolic rate and muscle stay relatively **constant.**

c

Bioluminescent emission

Maximum bioluminescence **Maximum absorbance**

Carotenoid
(shrimp, chaetognath)

Maximum bioluminescence **Minimum absorbance**

Porphyrin
(coronate medusae)

d Interaction distance

...up to 100 m away. Typical flash

...can see an average flash...

An average pupil...

e Transmission and water clarity

98%

Clear lakes and deep ocean

40%

Sediment-laden

(Caption appears on following page)

Figure 7 (*Figure appears on preceding page*)

Bio-optical interactions. (*a*) Mean wavelengths of bioluminescence for ctenophores and medusae. The bioluminescence of shallow organisms is predominantly greener (longer wavelengths) than that of deeper species. Panel adapted with permission from Haddock & Case (1999). (*b*) The visual interactions hypothesis (see Section 7), which attempts to explain why some animals have declining metabolic rates with depth but others do not. Vertical trends are evolutionary trends leading to differences in species rather than changes that manifest during vertical migration. (*c*) Relative amounts of light absorbed by different animals at different wavelengths. The perceived colors of animal pigments show what wavelengths they do not absorb. Orange carotenoids are well optimized for absorbing bioluminescence, but porphyrins—despite appearing brick red when illuminated—have an absorbance minimum at bioluminescent wavelengths and may be serving another function. (*d*) Distance at which a typical bioluminescent flash may be seen in the deep ocean. Panel adapted with permission from Warrant & Locket (2004); copyright 2004 Cambridge Philosophical Society. (*e*) Effects of sediment on water clarity and transmission of blue-green light. This striking difference is important when considering human impacts on midwater ecosystems.

7. PHYSIOLOGY

A standard assumption about deep-sea organisms is that they have low metabolic rates and can tolerate low oxygen levels, so they have little to contribute to global respiration or consumption, since they live in a food-poor environment (Childress 1995). In truth, deep communities play important roles in biogeochemical cycling; on a global scale, what the deep ocean may lack in per-volume biomass, it more than makes up for in its overwhelming scale. There are many types of adaptations related to living in the deep sea, spanning from molecules to behavior. These can be divided into two broad categories. The first relates to gathering energy and includes effective oxygen capture, surviving periods of hypoxia, metabolic efficiency, maintaining activity sufficient to capture prey and avoid predators, and many behavioral specializations. The second relates to driving vital cellular processes under deep-sea conditions with as little energy as possible and includes maintaining enzyme function, oxygen binding, functional lipid membranes, and protein structure.

In the deep water column, aerobic metabolism—production of ATP by respiration of oxygen—can alternate with periods of anaerobic metabolism, which enable forays into hypoxic environments. These activities, however, incur a debt that must be paid back later, in the same way that a sprinter's muscles ache from the anaerobic buildup of lactic acid. In some special cases, animals may draw upon a passive reserve of oxygen to survive periods of hypoxia (Thuesen et al. 2005). To assess relative capacity for aerobic metabolism, one must standardize respiratory rates for body mass and environmental temperature. Controlling for these variables leads to the surprising observation that for organisms like chaetognaths and medusae, the mass-specific metabolic rate does not decline with depth (Thuesen & Childress 1993, 1994). In contrast, metabolic rates do decrease for predators such as fishes (Torres et al. 1979) and cephalopods (Seibel et al. 1997). These observations have led to the visual interactions hypothesis (Childress 1995), which asserts that visual predators need to have higher potential metabolic rates. They retain locomotory prowess because their sphere of interaction is larger than that of nonvisual organisms (**Figure 7b,d**). For deep pelagic animals, these interactions are tied to the bioluminescent and ambient light fields, and they may be doubly affected by conditions that disrupt the clarity and stability of the surrounding habitat (see Section 8). There are many energy-related behaviors that are employed by deep-living animals: infrequent, large, opportunistic meals; low-energy feeding strategies (see Section 5.1); and efficient prey capture and handling (via behavior and morphology). Gelatinous consistency is a hallmark of many deep-sea organisms; the deep-pelagic crustacean *Gnathophausia ingens* goes from ~50% water to ~80% water within a few molts and eventually reaches ~90% water at maturity (Childress & Price 1983).

Even at the molecular, cellular, and tissue levels, at some point organisms must adapt to the high pressure and low temperature for basic cellular processes to continue. One well-studied

system is the protective osmolyte known as trimethylamine *N*-oxide (TMAO) (Samerotte et al. 2007, Yancey 2005). TMAO protects against pressure-related disruption of protein folding and binding. TMAO concentrations in fish muscles have an almost suspiciously linear increase with depth (Yancey et al. 2001), yet at some point, adding more TMAO would make it impossible for cells to stay osmotically balanced with seawater. The iso-osmotic boundary is extrapolated to be reached at a depth of 8,200 m (Yancey et al. 2014), and incredibly, no fishes have been collected from a depth below that threshold. Other animals do not use TMAO, and the adaptations that allow them to function down to full ocean depth beyond 10,000 m remain unknown.

In addition to protein function, the lipid membranes of cells and mitochondria must exist in a Goldilocks zone—not too rigid and not too flexible (Somero 2022). If they are too brittle, they will crack and rupture, and if they are too permeable, they will leak what they are supposed to regulate. Even more challenging is that membranes cannot rest in a stable state indefinitely. Membranes must break and re-form for cell division and vesicle formation to occur, and these processes are challenged by the strong stabilizing effect of pressure (Stühmer 2015). In deep-sea comb jellies (ctenophores), lipid bilayers achieve the Goldilocks zone by altering both the length and unsaturation state (number of double bonds) of their long hydrocarbon tails (Winnikoff et al. 2021). Other mechanisms of lipid adaptation are under investigation through high-pressure biochemical characterization, molecular dynamics modeling, and comparative phylogenetics.

One interesting aspect of pressure adaptation is that it seems to be governed by thresholds and exponential changes, not simple linear gradients—the example of TMAO and pressure notwithstanding. Although the deep water column is relatively stable and homogeneous compared with shallow or coastal waters, vertically migrating organisms will still experience significant changes, particularly in temperature, light, and oxygen. They may also occupy a completely different set of conditions during the day and night. Density gradients in shallow waters lead to differential sinking rates and the formation of thin layers of marine snow. Similar abrupt changes are seen at the thermocline (the region of rapid temperature change beneath the shallow mixed surface zone) and above the OMZ. Some species have narrow distributions in relation to these invisible boundaries (Greene et al. 1992, Widder et al. 1999), while others traverse them freely and have broad or bimodal distributions. Though pressure itself is linear, adaptation in response to pressure is not. For example, organisms from 1,500 m may be brought to the surface without suffering from pressure drops, but ones from below 2,200 m may rapidly decline. These nonlinear processes hold promise for future detailed studies.

To supplement the inspiring and challenging fieldwork by deep-sea pioneers, present-day researchers have access to genomics capabilities and biochemical tools. The power of genome and transcriptome sequencing, proteomics, and lipidomics is that a single organism, collected from 6,000-m depth and never seen before or since, can still share the secrets of its deep-sea adaptations. Indeed, applications of novel methods to deep-sea organisms have already provided answers to fundamental biological questions (Bracken-Grissom et al. 2020, Okada et al. 2019, Schultz et al. 2023), and this progress will continue at an even greater pace as more midwater organisms are studied.

8. THREATS AND TIES TO SOCIETY

Owing to the vastness of the midwater and its little-known inhabitants, deep midwater habitats have often been equated to storehouses of inexhaustible resources or dumping grounds with a limitless capacity to absorb our pollution and waste. A rapidly growing body of scientific work has demonstrated clear and measurable threats to deep midwater ecosystems and documented impacts from natural changes and human activities on land or at sea (Robison 2009). The search

for viable deep midwater resources has centered primarily on fisheries, pharmaceuticals, and minerals. Evidence of fundamental changes in the deep midwater environment is most prevalent from persistent, large-scale climate change—for example, ocean deoxygenation (Breitburg et al. 2018, Levin 2018), rising temperatures and acidification, reorganization of food webs and species distributions, pollution (chemical contamination and physical waste), and resource extraction (Ramirez-Llodra et al. 2011). Because many deep-sea animals live near their physiological limits (Seibel 2011, Seibel & Childress 2013), they can be very sensitive to even small changes in their habitat (van der Sluijs et al. 2011, Wishner et al. 2018).

Deepwater fisheries are globally widespread, harvesting primarily intermediate to top predator pelagic or benthopelagic species such as orange roughy, Patagonian toothfish, armorhead, and scabbardfish. While the majority of these fisheries operate in waters shallower than ~1,500 m, fisheries are extending into deeper waters, as are their unique ecosystem impacts (Morato et al. 2006, Norse et al. 2012). Fisheries specific to true midwater taxa focus on highly valuable species that primarily occupy upper-ocean habitats (the epipelagic and upper mesopelagic), such as tunas, mackerel, anchoveta, herring, and billfishes. Mesopelagic fisheries for mid-trophic-level fishes such as biomass-dominant myctophids have been actively debated since the mid-twentieth century, but only experimental or small-scale commercial fisheries in a few regions of the ocean have occurred since. Global population growth has brought considerable attention to the high abundance and biomass of mesopelagic fishes as a possible food or feed source, but there are issues with palatability and high lipid contents. The sheer scale of the midwater suggests an enormous biomass and potentially underutilized food or feed resource.

Proposed climate mitigation strategies such as CO_2 sequestration (Seibel & Walsh 2001, 2003) or carbon storage by sinking seaweed (Boyd et al. 2022, Ricart et al. 2022) will have large and unanticipated consequences for deep-sea communities. Vertical connectivity spanning surface, midwater, and deep-seafloor ecosystems will also serve to increase the potential scale and scope of climate mitigation activities that are actively being explored (Levin et al. 2023). While a kelp forest may grow back seasonally, hydrothermal vent fields, manganese nodule fields, and deep-sea coral gardens are established over thousands of years. A precautionary approach is critical when essentially irreversible changes are a possibility.

Human activities (maritime and terrestrial) and their numerous fingerprints are increasingly evident in the deep midwater. In addition to the more conspicuous oil platforms and offshore wind farms and the container ships that crisscross the globe daily, there are many unseen threats to midwater ecosystems. The pervasive assortment of organic and heavy-metal pollutants in pelagic habitats and food webs are derived from oil spills and leaks, burning of fossil fuels, intentional dumping, and industrial processes. Chemicals of concern include well-known hazards like mercury, DDT, and PCBs, as well as less familiar compounds like PAHs (polycyclic aromatic hydrocarbons). These contaminants have been studied for decades because many of them bioaccumulate through midwater food webs and can be eventually harvested into food supplies through high-seas fisheries. The acute effects of oil release are amplified by transport with marine snow particles through the water column and to the seafloor (Passow & Ziervogel 2016, Passow et al. 2012). Other contaminants also attach to particles and sink into deeper waters (Dachs et al. 2002), where they are ingested and enter midwater food webs, often bioaccumulating to levels higher than those on land or in surface waters (Looser et al. 2000, Romero-Romero et al. 2017).

Direct dumping of waste or incidental pollution from fisheries and other maritime industries is evident across the midwater. Plastic waste, particularly smaller microplastics, is well documented as gyre-sized, rotating swaths at the ocean surface (Law 2017). Microplastics also cycle throughout midwater depths (Choy et al. 2019, Zhao et al. 2022), within the bodies of midwater organisms (Hamilton et al. 2021), and in their predators (Choy & Drazen 2013, Jackson et al. 2000, Santos

et al. 2021), even down to abyssal and hadal depths (Kane et al. 2020, Woodall et al. 2014). Increasingly, species are found to ingest plastic in deep waters, but the impacts on ecosystems and populations are largely unknown. Contaminants can be carried on the surfaces of plastics, and plastics themselves can induce acute physical impacts from gut blockage or be transferred through the food web by consumption of prey containing plastic waste.

There is growing interest and activity aimed at commercial harvesting of metallic nodules sitting atop the deep seafloor. These nodules are rich in prized rare-earth metals, accumulating extremely slowly over millions of years, and are purported to help meet the growing need for materials used in battery manufacture. The impacts of mining on the deep seafloor are relatively well studied compared with the effects on the surrounding waters, but there are still critical knowledge gaps in both domains (Amon et al. 2022, Levin et al. 2020). Although mining activities would be carried out primarily by large vehicles deployed to the benthos, the impacts will stretch across the midwater as a result of large upper-water-column discharges, with deleterious impacts that include noise, heavy-metal pollutants, and changes in light, among others (Drazen et al. 2020, Haddock & Choy 2020).

Many of these threats span the water column and proliferate through midwater ecosystems by way of vertical migration, feeding, and the rain of organic matter. They highlight the acute sensitivity and interconnectedness of what is an otherwise faraway, out-of-sight, and out-of-mind place. Deep-sea waters buffer global climate change through the absorption of large amounts of CO_2 and heat while consequently suffering ecosystem impacts from deoxygenation, acidification, and ocean warming. Protecting this habitat not only protects its storybook menagerie of inhabitants but also reinforces a critical reservoir of planetary diversity and helps stabilize our own environment as well.

9. FUTURE RESEARCH QUESTIONS

A tremendous range of studies and approaches have produced a rich and nuanced ecological understanding of deep pelagic communities, yet numerous important and exciting research questions remain. Answering these questions is becoming more tractable given technological advances and cross-disciplinary science.

Some basic questions are related to establishing baselines and detecting the dynamics of the community:

- What is the true species diversity and abundance of the entire midwater community, minimizing sampling bias?
- What are the primary regional differences in community composition, and what are the main environmental and ecological drivers across depth layers?

Behavioral questions are particularly challenging, given the difficulty of collecting animals alive, much less observing them in a natural setting:

- How do animals find mates?
- What are the main sensory modes, and how are the signals parsed and integrated?

Genetic methods offer some of the most powerful ways of determining relationships and revealing new diversity, and can answer questions such as the following:

- How is presence in the deep sea related to emergence in polar regions, where the temperature can be the same but the pressure is vastly different?
- What species (if any) are truly cosmopolitan, and where are there cryptic species that have been thought to be globally distributed?

■ What are the invisible boundaries that drive speciation and diversification in the deep water column?

What we have seen of life histories indicates a fascinating blend of longevity and opportunism, and these results are also critical for management and approaching sustainability. Questions in this area include the following:

■ In evolutionary time, how old are lineages?
■ When and how often did species transition to and from the deep sea?
■ In modern times, what are the life spans of different species, and how do we determine their ages?

Basic questions like who eats whom lead to more sophisticated analyses of the intricacies of deep food webs. Applying a diversity of tools should help answer questions related to food-web structure, especially in deeper waters:

■ What are the rate estimates of feeding, metabolism, and growth for abundant midwater species?
■ Can we incorporate these rates into more comprehensive ecosystem and biogeochemical models in order to evaluate carbon flux and overall predator impacts on key prey populations across the water column?
■ How rigid or flexible are feeding strategies across generalists, specialists, and opportunists, given low food concentrations and great distances of potential prey?

Baseline datasets of species diversity, distribution, and connectivity are essential during the time of stark environmental change that is currently underway and expected to continue. As our ecological knowledge grows for individual species and functional groups, the field will continue to reckon with the grand challenge of weaving each of the pieces together into a comprehensive understanding of entire midwater food webs and ecosystems. Given the many stressors on deep pelagic ecosystems, pursuit of this knowledge is urgent. Midwater ecologists are encouraged to partner with modelers to incorporate their life's work into a framework that might prepare policymakers and the scientific community for ongoing changes to the deep ocean.

DISCLOSURE STATEMENT

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LITERATURE CITED

Allan EA, DiBenedetto MH, Lavery AC, Govindarajan AF, Zhang WG. 2021. Modeling characterization of the vertical and temporal variability of environmental DNA in the mesopelagic ocean. *Sci. Rep.* 11:21273

Alldredge AL, Silver MW. 1988. Characteristics, dynamics and significance of marine snow. *Prog. Oceanogr.* 20:41–82

Amon DJ, Gollner S, Morato T, Smith CR, Chen C, et al. 2022. Assessment of scientific gaps related to the effective environmental management of deep-seabed mining. *Mar. Policy* 138:105006

Angel MV. 1989. Vertical profiles of pelagic communities in the vicinity of the Azores Front and their implications to deep ocean ecology. *Prog. Oceanogr.* 22:1–46

Angel MV. 1993. Biodiversity of the pelagic ocean. *Conserv. Biol.* 7:760–72

Baldwin Fergus JL, Johnsen S, Osborn KJ. 2015. A unique apposition compound eye in the mesopelagic hyperiid amphipod *Paraphronima gracilis*. *Curr. Biol.* 25:473–78

Båmstedt U, Kaartvedt S, Youngbluth M. 2003. An evaluation of acoustic and video methods to estimate the abundance and vertical distribution of jellyfish. *J. Plankton Res.* 25:1307–18

Bandara K, Varpe Ø, Wijewardene L, Tverberg V, Eiane K. 2021. Two hundred years of zooplankton vertical migration research. *Biol. Rev.* 96:1547–89

Benoit-Bird KJ, Au WWL, Brainard RE, Lammers MO. 2001. Diel horizontal migration of the Hawaiian mesopelagic boundary community observed acoustically. *Mar. Ecol. Prog. Ser.* 217:1–14

Benoit-Bird KJ, Moline MA. 2021. Vertical migration timing illuminates the importance of visual and nonvisual predation pressure in the mesopelagic zone. *Limnol. Oceanogr.* 66:3010–19

Berkenpas EJ, Henning BS, Shepard CM, Turchik AJ, Robinson CJ, et al. 2018. A buoyancy-controlled lagrangian camera platform for in situ imaging of marine organisms in midwater scattering layers. *IEEE J. Ocean. Eng.* 43:595–607

Bessho-Uehara M, Mallefet J, Haddock SHD. 2023. Glowing sea cucumbers: bioluminescence in Holothuroidea. In *The World of Sea Cucumbers: Challenges, Advances, and Innovations*, ed. A Mercier, J-F Hamel, A Suhrbier, C Pearce. San Diego, CA: Academic. In press

Boyd PW, Bach LT, Hurd CL, Paine E, Raven JA, Tamsitt V. 2022. Potential negative effects of ocean afforestation on offshore ecosystems. *Nat. Ecol. Evol.* 6:675–83

Bracken-Grissom HD, DeLeo DM, Porter ML, Iwanicki T, Sickles J, Frank TM. 2020. Light organ photosensitivity in deep-sea shrimp may suggest a novel role in counterillumination. *Sci. Rep.* 10:4485

Braun CD, Arostegui MC, Thorrold SR, Papastamatiou YP, Gaube P, et al. 2022. The functional and ecological significance of deep diving by large marine predators. *Annu. Rev. Mar. Sci.* 14:129–59

Breitburg D, Levin LA, Oschlies A, Grégoire M, Chavez FP, et al. 2018. Declining oxygen in the global ocean and coastal waters. *Science* 359:eaam7240

Carleton KL, Escobar-Camacho D, Stieb SM, Cortesi F, Marshall NJ. 2020. Seeing the rainbow: mechanisms underlying spectral sensitivity in teleost fishes. *J. Exp. Biol.* 223:jeb193334

Charette MA, Smith WHF. 2010. The volume of Earth's ocean. *Oceanography* 23(2):112–14

Chen RS, Portner EJ, Choy CA. 2022. Gelatinous cephalopods as important prey for a deep-sea fish predator. *Mar. Biol.* 169:155

Childress JJ. 1995. Are there physiological and biochemical adaptations of metabolism in deep-sea animals? *Trees* 10:30–36

Childress JJ, Barnes AT, Quetin LB, Robison BH. 1978. Thermally protecting cod ends for the recovery of living deep-sea animals. *Deep-Sea Res. I* 25:419–22

Childress JJ, Price MH. 1983. Growth rate of the bathypelagic crustacean *Gnathophausia ingens* (Mysidacea: Lophogastridae). *Mar. Biol.* 76:165–77

Childress JJ, Seibel BA. 1998. Life at stable low oxygen levels: adaptations of animals to oceanic oxygen minimum layers. *J. Exp. Biol.* 201:1223–32

Childress JJ, Thuesen EV. 1992. Metabolic potential of deep-sea animals: regional and global scales. In *Deep-Sea Food Chains and the Global Carbon Cycle*, ed. GT Rowe, V Pariente, pp. 217–36. Dordrecht, Neth.: Kluwer Acad.

Choy CA, Drazen JC. 2013. Plastic for dinner? Observations of frequent debris ingestion by pelagic predatory fishes from the central North Pacific. *Mar. Ecol. Prog. Ser.* 485:155–63

Choy CA, Haddock SHD, Robison BH. 2017. Deep pelagic food web structure as revealed by in situ feeding observations. *Proc. R. Soc. B* 284:20172116

Choy CA, Popp BN, Hannides CCS, Drazen JC. 2015. Trophic structure and food resources of epipelagic and mesopelagic fishes in the North Pacific Subtropical Gyre ecosystem inferred from nitrogen isotopic compositions. *Limnol. Oceanogr.* 60:1156–71

Choy CA, Portner E, Iwane M, Drazen JC. 2013. Diets of five important predatory mesopelagic fishes of the central North Pacific. *Mar. Ecol. Prog. Ser.* 492:169–84

Choy CA, Robison BH, Gagne TO, Erwin B, Firl E, et al. 2019. The vertical distribution and biological transport of marine microplastics across the epipelagic and mesopelagic water column. *Sci. Rep.* 9:7843

Choy CA, Wabnitz CCC, Weijerman M, Woodworth-Jefcoats PA, Polovina JJ. 2016. Finding the way to the top: how the composition of oceanic mid-trophic micronekton groups determines apex predator biomass in the central North Pacific. *Mar. Ecol. Prog. Ser.* 549:9–25

Christianson LM, Johnson SB, Schultz DT, Haddock SHD. 2022. Hidden diversity of Ctenophora revealed by new mitochondrial COI primers and sequences. *Mol. Ecol. Resour.* 22:283–94

Clarke GL, Backus RH. 1956. Measurements of light penetration in relation to vertical migration and records of luminescence of deep-sea animals. *Deep-Sea Res. I* 4:1–14

Clarke TA. 1980. Diets of fourteen species of vertically migrating mesopelagic fishes in Hawaiian waters. *Fish. Bull.* 78:619–40

Cook AB, Bernard AM, Boswell KM, Bracken-Grissom H, D'Elia M, et al. 2020. A multidisciplinary approach to investigate deep-pelagic ecosystem dynamics in the Gulf of Mexico following *Deepwater Horizon*. *Front. Mar. Sci.* 7:548880

Cowen RK, Guigand CM. 2008. In situ Ichthyoplankton Imaging System (ISIIS): system design and preliminary results. *Limnol. Oceanogr. Methods* 6:126–32

Cronin TW. 2016. Camouflage: being invisible in the open ocean. *Curr. Biol.* 26:R1179–81

Dachs J, Lohmann R, Ockenden WA, Méjanelle L, Eisenreich SJ, Jones KC. 2002. Oceanic biogeochemical controls on global dynamics of persistent organic pollutants. *Environ. Sci. Technol.* 36:4229–37

Damian-Serrano A, Haddock SHD, Dunn CW. 2021. The evolution of siphonophore tentilla for specialized prey capture in the open ocean. *PNAS* 118:e2005063118

Damian-Serrano A, Hetherington ED, Choy CA, Haddock SHD, Lapides A, Dunn CW. 2022. Characterizing the secret diets of siphonophores (Cnidaria: Hydrozoa) using DNA metabarcoding. *PLOS ONE* 17:e0267761

de Busserolles F, Fogg L, Cortesi F, Marshall J. 2020. The exceptional diversity of visual adaptations in deep-sea teleost fishes. *Semin. Cell Dev. Biol.* 106:20–30

Dischereit A, Wangensteen OS, Præbel K, Auel H, Havermans C. 2022. Using DNA metabarcoding to characterize the prey spectrum of two co-occurring *Themisto* amphipods in the rapidly changing Atlantic-Arctic gateway Fram Strait. *Genes* 13:2035

Djurhuus A, Closek CJ, Kelly RP, Pitz KJ, Michisaki RP, et al. 2020. Environmental DNA reveals seasonal shifts and potential interactions in a marine community. *Nat. Commun.* 11:254

Douglas RH, Partridge JC. 1997. On the visual pigments of deep-sea fish. *J. Fish Biol.* 50:68–85

Drazen JC, Popp BN, Choy CA, Clemente T, Forest LD, Smith KL Jr. 2008. Bypassing the abyssal benthic food web: macrourid diet in the eastern North Pacific inferred from stomach content and stable isotopes analyses. *Limnol. Oceanogr.* 53:2644–54

Drazen JC, Smith CR, Gjerde KM, Haddock SHD, Carter GS, et al. 2020. Midwater ecosystems must be considered when evaluating environmental risks of deep-sea mining. *PNAS* 117:17455–60

Drazen JC, Sutton TT. 2017. Dining in the deep: the feeding ecology of deep-sea fishes. *Annu. Rev. Mar. Sci.* 9:337–66

Duffy LM, Kuhnert PM, Pethybridge HR, Young JW, Olson RJ, et al. 2017. Global trophic ecology of yellowfin, bigeye, and albacore tunas: understanding predation on micronekton communities at ocean-basin scales. *Deep-Sea Res. II* 140:55–73

Durkin CA, Buesseler KO, Cetinić I, Estapa ML, Kelly RP, Omand M. 2021. A visual tour of carbon export by sinking particles. *Glob. Biogeochem. Cycles* 35:e2021GB006985

Friedman ST, Price SA, Corn KA, Larouche O, Martinez CM, Wainwright PC. 2020. Body shape diversification along the benthic-pelagic axis in marine fishes. *Proc. R. Soc. B* 287:20201053

Gates AR, Benfield MC, Booth DJ, Fowler AM, Skropeta D, Jones DOB. 2017. Deep-sea observations at hydrocarbon drilling locations: contributions from the SERPENT Project after 120 field visits. *Deep-Sea Res. II* 137:463–79

Gloeckler K, Choy CA, Hannides CCS, Close HG, Goetze E, et al. 2018. Stable isotope analysis of micronekton around Hawaii reveals suspended particles are an important nutritional source in the lower mesopelagic and upper bathypelagic zones. *Limnol. Oceanogr.* 63:1168–80

Goetze E, Andrews KR, Peijnenburg KTCA, Portner E, Norton EL. 2015. Temporal stability of genetic structure in a mesopelagic copepod. *PLOS ONE* 10:e0136087

Gorsky G, Picheral M, Stemmann L. 2000. Use of the Underwater Video Profiler for the study of aggregate dynamics in the North Mediterranean. *Estuar. Coast. Shelf Sci.* 50:121–28

Graham BS, Grubbs D, Holland K, Popp BN. 2007. A rapid ontogenetic shift in the diet of juvenile yellowfin tuna from Hawaii. *Mar. Biol.* 150:647–58

Greene CH, Widder EA, Youngbluth MJ, Tamse A, Johnson GE. 1992. The migration behavior, fine structure, and bioluminescent activity of krill sound-scattering layers. *Limnol. Oceanogr.* 37:650–58

Haddock SHD, Case JF. 1999. Bioluminescence spectra of shallow and deep-sea gelatinous zooplankton: ctenophores, medusae and siphonophores. *Mar. Biol.* 133:571–82

Haddock SHD, Choy CA. 2020. Treasure and turmoil in the deep sea. *New York Times*, Aug. 14. **https://www.nytimes.com/2020/08/14/opinion/deep-ocean-mining-pollution.html**

Haddock SHD, Dunn CW. 2015. Fluorescent proteins function as a prey attractant: experimental evidence from the hydromedusa *Olindias formosus* and other marine organisms. *Biol. Open* 4:1094–104

Haddock SHD, Dunn CW, Pugh PR, Schnitzler CE. 2005. Bioluminescent and red-fluorescent lures in a deep-sea siphonophore. *Science* 309:263

Haddock SHD, Moline MA, Case JF. 2010. Bioluminescence in the sea. *Annu. Rev. Mar. Sci.* 2:443–93

Hamilton BM, Rochman CM, Hoellein TJ, Robison BH, Van Houtan KS, Choy CA. 2021. Prevalence of microplastics and anthropogenic debris within a deep-sea food web. *Mar. Ecol. Prog. Ser.* 675:23–33

Hannides CCS, Popp BN, Choy CA, Drazen JC. 2013. Midwater zooplankton and suspended particle dynamics in the North Pacific Subtropical Gyre: a stable isotope perspective. *Limnol. Oceanogr.* 58:1931–46

Hannides CCS, Popp BN, Close HG, Benitez-Nelson CR, Ka'apu-Lyons CA, et al. 2020. Seasonal dynamics of midwater zooplankton and relation to particle cycling in the North Pacific Subtropical Gyre. *Prog. Oceanogr.* 182:102266

Henschke N, Pakhomov EA, Kwong LE, Everett JD, Laiolo L, et al. 2019. Large vertical migrations of *Pyrosoma atlanticum* play an important role in active carbon transport. *J. Geophys. Res. Biogeosci.* 124:1056–70

Herndl GJ, Bayer B, Baltar F, Reinthaler T. 2023. Prokaryotic life in the deep ocean's water column. *Annu. Rev. Mar. Sci.* 15:461–83

Herring P. 2001. *The Biology of the Deep Ocean*. Oxford, UK: Oxford Univ. Press

Hetherington ED, Choy CA, Thuesen EV, Haddock SHD. 2022a. Three distinct views of deep pelagic community composition based on complementary sampling approaches. *Front. Mar. Sci.* 9:864004

Hetherington ED, Damian-Serrano A, Haddock SHD, Dunn CW, Choy CA. 2022b. Integrating siphonophores into marine food-web ecology. *Limnol. Oceanogr. Lett.* 7:81–95

Hirai J, Tachibana A, Tsuda A. 2020. Large-scale metabarcoding analysis of epipelagic and mesopelagic copepods in the Pacific. *PLOS ONE* 15:e0233189

Holland KN, Grubbs RD. 2008. Fish visitors to seamounts: tunas and bill fish at seamounts. In *Seamounts: Ecology, Fisheries and Conservation*, pp. 189–201. Oxford, UK: Blackwell

Hopcroft RR, Robison BH. 1999. A new mesopelagic larvacean, *Mesochordaeus erythrocephalus*, sp. nov., from Monterey Bay, with a description of its filtering house. *J. Plankton Res.* 10:1923–37

Hopkins TL, Baird RC. 1973. Diet of the hatchetfish *Sternoptyx diaphana*. *Mar. Biol.* 21:34–46

Hoving HJT, Haddock SHD. 2017. The giant deep-sea octopus *Haliphron atlanticus* forages on gelatinous fauna. *Sci. Rep.* 7:44952

Huffard CL, Durkin CA, Wilson SE, McGill PR, Henthorn R, Smith KL. 2020. Temporally-resolved mechanisms of deep-ocean particle flux and impact on the seafloor carbon cycle in the northeast Pacific. *Deep-Sea Res. II* 173:104763

Jackson GD, Buxton NG, George MJA. 2000. Diet of the southern opah *Lampris immaculatus* on the Patagonian Shelf; the significance of the squid *Moroteuthis ingens* and anthropogenic plastic. *Mar. Ecol. Prog. Ser.* 206:261–71

Jamieson AJ, Lindsay DJ, Kitazato H. 2023. Maximum depth extensions for Hydrozoa, Tunicata and Ctenophora. *Mar. Biol.* 170:33

Jamieson AJ, Linley TD. 2021. Hydrozoans, scyphozoans, larvaceans and ctenophores observed in situ at hadal depths. *J. Plankton Res.* 43:20–32

Jennings RM, Bucklin A, Pierrot-Bults A. 2010. Barcoding of arrow worms (Phylum Chaetognatha) from three oceans: genetic diversity and evolution within an enigmatic phylum. *PLOS ONE* 5:e9949

Johnsen S. 2005. The red and the black: bioluminescence and the color of animals in the deep sea. *Integr. Comp. Biol.* 45:234–46

Johnsen S. 2014. Hide and seek in the open sea: pelagic camouflage and visual countermeasures. *Annu. Rev. Mar. Sci.* 6:369–92

Johnson SB, Winnikoff JR, Schultz DT, Christianson LM, Patry WL, et al. 2022. Speciation of pelagic zooplankton: invisible boundaries can drive isolation of oceanic ctenophores. *Front. Genet.* 13:970314

Kaartvedt S, Klevjer TA, Torgersen T, Sørnes TA. 2007. Diel vertical migration of individual jellyfish (*Periphylla periphylla*). *Limnol. Oceanogr.* 52:975–83

Kaartvedt S, Staby A, Aksnes DL. 2012. Efficient trawl avoidance by mesopelagic fishes causes large underestimation of their biomass. *Mar. Ecol. Prog. Ser.* 456:1–6

Kane IA, Clare MA, Miramontes E, Wogelius R, Rothwell JJ, et al. 2020. Seafloor microplastic hotspots controlled by deep-sea circulation. *Science* 368:1140–45

Kenitz KM, Anderson CR, Carter ML, Eggleston E, Seech K, et al. 2023. Environmental and ecological drivers of harmful algal blooms revealed by automated underwater microscopy. *Limnol. Oceanogr.* 68:598–615

Kharbush JJ, Close HG, Van Mooy BAS, Arnosti C, Smittenberg RH, et al. 2020. Particulate organic carbon deconstructed: molecular and chemical composition of particulate organic carbon in the ocean. *Front. Mar. Sci.* 7:518

Kiørboe T. 2011. How zooplankton feed: mechanisms, traits and trade-offs. *Biol. Rev.* 86:311–39

Klevjer TA, Torres DJ, Kaartvedt S. 2012. Distribution and diel vertical movements of mesopelagic scattering layers in the Red Sea. *Mar. Biol.* 159:1833–41

Kwong LE, Pakhomov EA, Suntsov AV, Seki MP, Brodeur RD, et al. 2018. An intercomparison of the taxonomic and size composition of tropical macrozooplankton and micronekton collected using three sampling gears. *Deep-Sea Res. I* 135:34–45

Lam PJ, Doney SC, Bishop JKB. 2011. The dynamic ocean biological pump: insights from a global compilation of particulate organic carbon, CaCO$_3$, and opal concentration profiles from the mesopelagic. *Glob. Biogeochem. Cycles.* 25:GB3009

Law KL. 2017. Plastics in the marine environment. *Annu. Rev. Mar. Sci.* 9:205–29

Levin LA. 2018. Manifestation, drivers, and emergence of open ocean deoxygenation. *Annu. Rev. Mar. Sci.* 10:229–60

Levin LA, Alfaro-Lucas JM, Colaço A, Cordes EE, Craik N, et al. 2023. Deep-sea impacts of climate interventions. *Science* 379:978–81

Levin LA, Amon DJ, Lily H. 2020. Challenges to the sustainability of deep-seabed mining. *Nat. Sustain.* 3:784–94

Longhurst AR. 2007. *Ecological Geography of the Sea*. San Diego, CA: Academic. 2nd ed.

Looser R, Froescheis O, Cailliet GM, Jarman WM, Ballschmiter K. 2000. The deep-sea as a final global sink of semivolatile persistent organic pollutants? Part II: organochlorine pesticides in surface and deep-sea dwelling fish of the North and South Atlantic and the Monterey Bay Canyon (California). *Chemosphere* 40:661–70

Luck DG, Pietsch TW. 2008. In-situ observations of a deep-sea ceratioid anglerfish of the genus *Oneirodes* (lophiiformes: Oneirodidae). *Copeia* 2008:446

Luo T, Kramer K, Goldgof DB, Hall LO, Samson S, et al. 2004. Recognizing plankton images from the shadow image particle profiling evaluation recorder. *IEEE Trans. Syst. Man Cybern. B* 34:1753–62

Marlétaz F, Le Parco Y, Liu S, Peijnenburg KTCA. 2017. Extreme mitogenomic variation in natural populations of chaetognaths. *Genome Biol. Evol.* 9:1374–84

Martini S, Haddock SHD. 2017. Quantification of bioluminescence from the surface to the deep sea demonstrates its predominance as an ecological trait. *Sci. Rep.* 7:45750

Martini S, Kuhnz L, Mallefet J, Haddock SHD. 2019. Distribution and quantification of bioluminescence as an ecological trait in the deep sea benthos. *Sci. Rep.* 9:14654

Maynard SD, Riggs FV, Walters JF. 1975. Mesopelagic micronekton in Hawaiian waters: faunal composition, standing stock, and diel vertical migration. *Fish. Bull.* 73:726–36

McClain CR, Schlacter TA. 2015. On some hypotheses of diversity of animal life at great depths on the sea floor. *Mar. Ecol.* 36:849–72

McDonnell AMP, Lam PJ, Lamborg CH, Buesseler KO, Sanders R, et al. 2015. The oceanographic toolbox for the collection of sinking and suspended marine particles. *Prog. Oceanogr.* 133:17–31

Meech ME, Mills CE, Haddock SHD, Meech RW. 2021. Two swimming modes in Trachymedusae; bell kinematics and the role of giant axons. *J. Exp. Biol.* 224:jeb239830

Messíe M, Sherlock RE, Huffard CL, Pennington JT, Choy CA, et al. 2023. Coastal upwelling drives ecosystem temporal variability from the surface to the abyssal seafloor. *PNAS* 120:e2214567120

Milligan RJ, Bernard AM, Boswell KM, Bracken-Grissom HD, D'Elia MA, et al. 2018. The application of novel research technologies by the Deep Pelagic Nekton Dynamics of the Gulf of Mexico (DEEPEND) consortium. *Mar. Technol. Soc. J.* 52:81–86

Miyamoto H, Machida RJ, Nishida S. 2010. Genetic diversity and cryptic speciation of the deep sea chaetognath *Caecosagitta macrocephala* (Fowler, 1904). *Deep-Sea Res. II* 57:2211–19

Mogdans J. 2019. Sensory ecology of the fish lateral-line system: morphological and physiological adaptations for the perception of hydrodynamic stimuli. *J. Fish Biol.* 95:53–72

Morato T, Watson R, Pitcher TJ, Pauly D. 2006. Fishing down the deep. *Fish Fish.* 7:24–34

Nielsen J, Hedeholm RB, Heinemeier J, Bushnell PG, Christiansen JS, et al. 2016. Eye lens radiocarbon reveals centuries of longevity in the Greenland shark (*Somniosus microcephalus*). *Science* 353:702–4

Nonaka A, Milisen JW, Mundy BC, Johnson GD. 2021. Blackwater diving: an exciting window into the planktonic arena and its potential to enhance the quality of larval fish collections. *Ichthyol. Herpetol.* 109:138–56

Norse EA, Brooke S, Cheung WWL, Clark MR, Ekeland I, et al. 2012. Sustainability of deep-sea fisheries. *Mar. Policy* 36:307–20

Okada S, Chen C, Watsuji T-O, Nishizawa M, Suzuki Y, et al. 2019. The making of natural iron sulfide nanoparticles in a hot vent snail. *PNAS* 116:20376–81

Pagès F, Corbera J, Lindsay D. 2007. Piggybacking pycnogonids and parasitic narcomedusae on *Pandea rubra* (Anthomedusae, Pandeidae). *Plankton Benthos Res.* 2:83–90

Parzanini C, Parrish CC, Hamel J-F, Mercier A. 2019. Reviews and syntheses: insights into deep-sea food webs and global environmental gradients revealed by stable isotope (δ^{15}N, δ^{13}C) and fatty acid trophic biomarkers. *Biogeosciences* 16:2837–56

Passow U, Ziervogel K. 2016. Marine snow sedimented oil released during the Deepwater Horizon spill. *Oceanography* 29(3):118–25

Passow U, Ziervogel K, Asper V, Diercks A. 2012. Marine snow formation in the aftermath of the Deepwater Horizon oil spill in the Gulf of Mexico. *Environ. Res. Lett.* 7:035301

Peijnenburg KTCA, Breeuwer JAJ, Pierrot-Bults AC, Menken SBJ. 2004. Phylogeography of the planktonic chaetognath *Sagitta setosa* reveals isolation in European seas. *Evolution* 58:1472–87

Pethybridge HR, Choy CA, Polovina JJ, Fulton EA. 2018. Improving marine ecosystem models with biochemical tracers. *Annu. Rev. Mar. Sci.* 10:199–228

Pitz KJ, Guo J, Johnson SB, Campbell TL, Zhang H, et al. 2020. Zooplankton biogeographic boundaries in the California Current System as determined from metabarcoding. *PLOS ONE* 15:e0235159

Portner EJ, Markaida U, Robinson CJ, Gilly WF. 2020. Trophic ecology of Humboldt squid, *Dosidicus gigas*, in conjunction with body size and climatic variability in the Gulf of California, Mexico. *Limnol. Oceanogr.* 65:732–48

Portner EJ, Polovina JJ, Choy CA. 2017. Patterns in micronekton diversity across the North Pacific Subtropical Gyre observed from the diet of longnose lancetfish (*Alepisaurus ferox*). *Deep-Sea Res. I* 125:40–51

Potier M, Marsac F, Cherel Y, Lucas V, Sabatié R, et al. 2007. Forage fauna in the diet of three large pelagic fishes (lancetfish, swordfish and yellowfin tuna) in the western equatorial Indian Ocean. *Fish. Res.* 83:60–72

Priede IG. 2017. *Deep-Sea Fishes: Biology, Diversity, Ecology and Fisheries*. Cambridge, UK: Cambridge Univ. Press

Priede IG, Froese R. 2013. Colonization of the deep sea by fishes. *J. Fish Biol.* 83:1528–50

Proud R, Cox MJ, Brierley AS. 2017. Biogeography of the global ocean's mesopelagic zone. *Curr. Biol.* 27:113–19

Pugh PR, Haddock SHD. 2016. A description of two new species of the genus *Erenna* (Siphonophora: Physonectae: Erennidae), with notes on recently collected specimens of other *Erenna* species. *Zootaxa* 4189:401–46

Ralston S, Field JC, Sakuma KM. 2015. Long-term variation in a central California pelagic forage assemblage. *J. Mar. Syst.* 146:26–37

Ramirez-Llodra E, Tyler PA, Baker MC, Bergstad OA, Clark MR, et al. 2011. Man and the last great wilderness: human impact on the deep sea. *PLOS ONE* 6:e22588

Reygondeau G, Guidi L, Beaugrand G, Henson SA, Koubbi P, et al. 2018. Global biogeochemical provinces of the mesopelagic zone. *J. Biogeogr.* 45:500–14

Ricart AM, Krause-Jensen D, Hancke K, Price NN, Masqué P, Duarte CM. 2022. Sinking seaweed in the deep ocean for carbon neutrality is ahead of science and beyond the ethics. *Environ. Res. Lett.* 17:081003

Roark EB, Guilderson TP, Dunbar RB, Fallon SJ, Mucciarone DA. 2009. Extreme longevity in proteinaceous deep-sea corals. *PNAS* 106:5204–8

Robinson C, Steinberg DK, Anderson TR, Arístegui J, Carlson CA, et al. 2010. Mesopelagic zone ecology and biogeochemistry—a synthesis. *Deep-Sea Res. II* 57:1504–18

Robison BH. 2004. Deep pelagic biology. *J. Exp. Mar. Biol. Ecol.* 300:253–72

Robison BH. 2009. Conservation of deep pelagic biodiversity. *Conserv. Biol.* 23:847–58

Robison BH, Raskoff K, Sherlock R. 2005a. Ecological substrate in midwater: *Doliolula equus*, a new mesopelagic tunicate. *J. Mar. Biol. Assoc. UK* 85:655–63

Robison BH, Reisenbichler KR, Sherlock RE. 2005b. Giant larvacean houses: rapid carbon transport to the deep sea floor. *Science* 308:1609–11

Robison BH, Reisenbichler KR, Sherlock RE. 2017. The coevolution of midwater research and ROV technology at MBARI. *Oceanography* 30(4):26–37

Robison BH, Sherlock RE, Reisenbichler KR. 2010. The bathypelagic community of Monterey canyon. *Deep-Sea Res. II* 57:1551–56

Robison BH, Sherlock RE, Reisenbichler KR, McGill PR. 2020. Running the gauntlet: assessing the threats to vertical migrators. *Front. Mar. Sci.* 7:64

Roe HSJ. 1988. Midwater biomass profiles over the Madeira Abyssal Plain and the contribution of copepods. In *Biology of Copepods*, ed. GA Boxshall, HK Schminke, pp. 169–81. Dordrecht, Neth.: Springer

Romero-Romero S, Herrero L, Fernández M, Gómara B, Acuña JL. 2017. Biomagnification of persistent organic pollutants in a deep-sea, temperate food web. *Sci. Total Environ.* 605–6:589–97

Rosa R, Lopes VM, Guerreiro M, Bolstad K, Xavier JC. 2017. Biology and ecology of the world's largest invertebrate, the colossal squid (*Mesonychoteuthis hamiltoni*): a short review. *Polar Biol.* 40:1871–83

Saba GK, Burd AB, Dunne JP, Hernández-León S, Martin AH, et al. 2021. Toward a better understanding of fish-based contribution to ocean carbon flux. *Limnol. Oceanogr.* 66:1639–64

Samerotte AL, Drazen JC, Brand GL, Seibel BA, Yancey PH. 2007. Correlation of trimethylamine oxide and habitat depth within and among species of teleost fish: an analysis of causation. *Physiol. Biochem. Zool.* 80:197–208

Santoro AE, Richter RA, Dupont CL. 2019. Planktonic marine archaea. *Annu. Rev. Mar. Sci.* 11:131–58

Santos RG, Machovsky-Capuska GE, Andrades R. 2021. Plastic ingestion as an evolutionary trap: toward a holistic understanding. *Science* 373:56–60

Schultz DT, Haddock SHD, Bredeson JV, Green RE, Simakov O, Rokhsar DS. 2023. Ancient gene linkages support ctenophores as sister to other animals. *Nature* 618:110–17

Seibel BA. 2011. Critical oxygen levels and metabolic suppression in oceanic oxygen minimum zones. *J. Exp. Biol.* 214:326–36

Seibel BA, Childress JJ. 2013. The real limits to marine life: a further critique of the Respiration Index. *Biogeosciences* 10:2815–19

Seibel BA, Thuesen EV, Childress JJ, Gorodezky LA. 1997. Decline in pelagic cephalopod metabolism with habitat depth reflects differences in locomotory efficiency. *Biol. Bull.* 192:262–78

Seibel BA, Walsh PJ. 2001. Potential impacts of CO_2 injection on deep-sea biota. *Science* 294:319–20

Seibel BA, Walsh PJ. 2003. Biological impacts of deep-sea carbon dioxide injection inferred from indices of physiological performance. *J. Exp. Biol.* 206:641–50

Shanks AL, Trent JD. 1980. Marine snow: sinking rates and potential role in vertical flux. *Deep-Sea Res. A* 27:137–43

Sherman K. 1991. The large marine ecosystem concept: research and management strategy for living marine resources. *Ecol. Appl.* 1:349–60

Simmonds JE. 2005. *Fisheries Acoustics: Theory and Practice*. Oxford. UK: Blackwell

Somero GN. 2022. The Goldilocks principle: a unifying perspective on biochemical adaptation to abiotic stressors in the sea. *Annu. Rev. Mar. Sci.* 14:1–23

Sosik HM, Olson RJ. 2007. Automated taxonomic classification of phytoplankton sampled with imaging-in-flow cytometry. *Limnol. Oceanogr. Methods* 5:204–16

Spitz J, Cherel Y, Bertin S, Kiszka J, Dewez A, Ridoux V. 2011. Prey preferences among the community of deep-diving odontocetes from the Bay of Biscay, Northeast Atlantic. *Deep-Sea Res. I* 58:273–82

Steinberg DK, Landry MR. 2017. Zooplankton and the ocean carbon cycle. *Annu. Rev. Mar. Sci.* 9:413–44

Steinberg DK, Silver MW, Pilskaln CH. 1997. Role of mesopelagic zooplankton in the community metabolism of giant larvacean house detritus in Monterey Bay, California, USA. *Mar. Ecol. Prog. Ser.* 147:167–79

Steinberg DK, Stamieszkin K, Maas AE, Durkin CA, Passow U, et al. 2023. The outsized role of salps in carbon export in the subarctic northeast Pacific Ocean. *Glob. Biogeochem. Cycles* 37:e2022GB007523

Stühmer W. 2015. Exocytosis from chromaffin cells: hydrostatic pressure slows vesicle fusion. *Philos. Trans. R. Soc. Lond. B* 370:20140192

Sutton TT. 2013. Vertical ecology of the pelagic ocean: classical patterns and new perspectives. *J. Fish Biol.* 83:1508–27

Sutton TT, Clark MR, Dunn DC, Halpin PN, Rogers AD, et al. 2017. A global biogeographic classification of the mesopelagic zone. *Deep-Sea Res. I* 126:85–102

Sutton TT, Hopkins TL. 1996. Trophic ecology of the stomiid (Pisces: Stomiidae) fish assemblage of the eastern Gulf of Mexico: strategies, selectivity and impact of a top mesopelagic predator group. *Mar. Biol.* 127:179–92

Thomas KN, Robison BH, Johnsen S. 2017. Two eyes for two purposes: in situ evidence for asymmetric vision in the cockeyed squids *Histioteuthis heteropsis* and *Stigmatoteuthis dofleini*. *Philos. Trans. R. Soc. Lond. B* 372:20160069

Thuesen EV, Childress JJ. 1993. Enzymatic activities and metabolic rates of pelagic chaetognaths: lack of depth-related declines. *Limnol. Oceanogr.* 38:935–48

Thuesen EV, Childress JJ. 1994. Oxygen consumption rates and metabolic enzyme activities of oceanic California medusae in relation to body size and habitat depth. *Biol. Bull.* 187:84–98

Thuesen EV, Rutherford LD, Brommer PL. 2005. The role of aerobic metabolism and intragel oxygen in hypoxia tolerance of three ctenophores: *Pleurobrachia bachei*, *Bolinopsis infundibulum* and *Mnemiopsis leidyi*. *J. Mar. Biol. Assoc. UK* 85:627–33

Toggweiler JR, Key RM. 2003. Ocean circulation: thermohaline circulation. In *Encyclopedia of Atmospheric Sciences*, ed. JR Holton, J Pyle, JA Curry, pp. 1549–55. San Diego, CA: Academic

Torres JJ, Bailey TG. 2022. *Life in the Open Ocean: The Biology of Pelagic Species*. Hoboken, NJ: Wiley & Sons

Torres JJ, Belman WW, Childress JJ. 1979. Oxygen consumption rates of midwater fishes as a function of depth of occurrence. *Deep-Sea Res. A* 26:185–97

Tsuda A, Miller CB. 1998. Mate-finding behaviour in *Calanus marshallae* Frost. *Philos. Trans. R. Soc. Lond. B* 353:713–20

Urban P, Praebel K, Bhat S, Dierking J, Wangensteen OS. 2022. DNA metabarcoding reveals the importance of gelatinous zooplankton in the diet of *Pandalus borealis*, a keystone species in the Arctic. *Mol. Ecol.* 31:1562–76

Uttal L, Buck KR. 1996. Dietary study of the midwater polychaete *Poeobius meseres* in Monterey Bay, California. *Mar. Biol.* 125:333–43

van der Sluijs I, Gray SM, Amorim MCP, Barber I, Candolin U, et al. 2011. Communication in troubled waters: responses of fish communication systems to changing environments. *Evol. Ecol.* 25:623–40

Vinogradov ME. 1970. *Vertical Distribution of the Oceanic Zooplankton*, Vol. 1. Jerusalem: Isr. Program Sci. Transl.

Wagner H-J. 2002. Sensory brain areas in three families of deep-sea fish (slickheads, eels and grenadiers): comparison of mesopelagic and demersal species. *Mar. Biol.* 141:807–17

Wagner H-J, Douglas RH, Frank TM, Roberts NW, Partridge JC. 2009. A novel vertebrate eye using both refractive and reflective optics. *Curr. Biol.* 19:108–14

Warrant EJ, Locket NA. 2004. Vision in the deep sea. *Biol. Rev.* 79:671–712

Widder E, Johnsen S, Bernstein S, Case J, Neilson D. 1999. Thin layers of bioluminescent copepods found at density discontinuities in the water column. *Mar. Biol.* 134:429–37

Widmer CL, Cailliet G, Geller J. 2010. The life cycle of *Earleria corachloeae* n. sp. (Cnidaria: Hydrozoa) with epibiotic hydroids on mid-water shrimp. *Mar. Biol.* 157:49–58

Wiebe PH, Morton AW, Bradley AM, Backus RH, Craddock JE, et al. 1985. New development in the MOCNESS, an apparatus for sampling zooplankton and micronekton. *Mar. Biol.* 87:313–23

Wilson SE, Ruhl HA, Smith KL Jr. 2013. Zooplankton fecal pellet flux in the abyssal northeast Pacific: a 15 year time-series study. *Limnol. Oceanogr.* 58:881–92

Winnikoff JR, Haddock SHD, Budin I. 2021. Depth- and temperature-specific fatty acid adaptations in ctenophores from extreme habitats. *J. Exp. Biol.* 224:jeb242800

Wishner KF, Seibel BA, Roman C, Deutsch C, Outram D, et al. 2018. Ocean deoxygenation and zooplankton: Very small oxygen differences matter. *Sci. Adv.* 4:eaau5180

Woodall LC, Sanchez-Vidal A, Canals M, Paterson GLJ, Coppock R, et al. 2014. The deep sea is a major sink for microplastic debris. *R. Soc. Open Sci.* 1:140317

Woodstock MS, Zhang Y. 2022. Towards ecosystem modeling in the deep sea: a review of past efforts and primer for the future. *Deep-Sea Res. I* 188:103851

Yancey PH. 2005. Organic osmolytes as compatible, metabolic and counteracting cytoprotectants in high osmolarity and other stresses. *J. Exp. Biol.* 208:2819–30

Yancey PH, Fyfe-Johnson AL, Kelly RH, Walker VP, Auñón MT. 2001. Trimethylamine oxide counteracts effects of hydrostatic pressure on proteins of deep-sea teleosts. *J. Exp. Zool.* 289:172–76

Yancey PH, Gerringer ME, Drazen JC, Rowden AA, Jamieson A. 2014. Marine fish may be biochemically constrained from inhabiting the deepest ocean depths. *PNAS* 111:4461–65

Yen J, Lasley R. 2011. Chemical communication between copepods: finding the mate in a fluid environment. In *Chemical Communication in Crustaceans*, ed. T Breithaupt, M Thiel, pp. 177–97. New York: Springer

Yen J, Strickler JR. 1996. Advertisement and concealment in the plankton: What makes a copepod hydrodynamically conspicuous? *Invertebr. Biol.* 115:191–205

Yoshino K, Takahashi A, Adachi T, Costa DP, Robinson PW, et al. 2020. Acceleration-triggered animal-borne videos show a dominance of fish in the diet of female northern elephant seals. *J. Exp. Biol.* 223:jeb212936

Young JW, Hunt BPV, Cook TR, Llopiz JK, Hazen EL, et al. 2015. The trophodynamics of marine top predators: current knowledge, recent advances and challenges. *Deep-Sea Res. II* 113:170–87

Young JW, Lansdell MJ, Campbell RA, Cooper SP, Juanes F, Guest MA. 2010. Feeding ecology and niche segregation in oceanic top predators off eastern Australia. *Mar. Biol.* 157:2347–68

Young RE. 1975. Function of the dimorphic eyes in the midwater squid *Histioteuthis dofleini*. *Pac. Sci.* 29:211–18

Zhao S, Zettler ER, Bos RP, Lin P, Amaral-Zettler LA, Mincer TJ. 2022. Large quantities of small microplastics permeate the surface ocean to abyssal depths in the South Atlantic Gyre. *Glob. Change Biol.* 28:2991–3006