Fish and Fisheries

FISH and FISHERIES

ORIGINAL ARTICLE OPEN ACCESS

Mesopelagic Fish Traits: Functions and Trade-Offs

Henrike Andresen[1] | Leandro Nolé Eduardo[2,3] | M. Pilar Olivar[4] | P. Daniël van Denderen[5,6] | Jérôme Spitz[7,8] | Aurore A. Maureaud[9,10] | Anik Brind'Amour[11] | Noelle M. Bowlin[12] | Eva García-Seoane[13,14] | Tom J. Langbehn[15] | Tracey T. Sutton[16] | Heino O. Fock[1] | Anne Gro V. Salvanes[15] | Martin Lindegren[6]

[1]Thünen Institute of Sea Fisheries, Bremerhaven, Germany | [2]MARBEC, Univ. Montpellier, CNRS, Ifremer, IRD, Sète, France | [3]Departamento de Pesca e Aquicultura, Universidade Federal Rural de Pernambuco (UFRPE), Recife, Pernambuco, Brazil | [4]Institut de Ciències del Mar (CSIC), Barcelona, Spain | [5]Graduate School of Oceanography, University of Rhode Island, Narragansett, Rhode Island, USA | [6]National Institute of Aquatic Resources, Technical University of Denmark, Lyngby, Denmark | [7]CEBC (UMR 7372), CNRS/La Rochelle Univeristé, La Rochelle, France | [8]Pelagis (UAR 3462), CNRS/La Rochelle Univeristé, La Rochelle, France | [9]Department of Ecology, Evolution, and Natural Resources, Rutgers University, New Brunswick, New Jersey, USA | [10]Department of Ecology and Evolutionary Biology, Yale University, New Haven, Connecticut, USA | [11]UMR DECOD, Ifremer, Institut Agro, INRAE, Nantes, France | [12]National Oceanic and Atmospheric Administration, Southwest Fisheries Science Center, La Jolla, California, USA | [13]Institute of Marine Research (IMR), Bergen, Norway | [14]Møreforsking AS., Ålesund, Norway | [15]Department of Biological Sciences, University of Bergen, Bergen, Norway | [16]Department of Marine and Environmental Sciences, Nova Southeastern University, Dania Beach, Florida, USA

Correspondence: Henrike Andresen (henrike.andresen@thuenen.de)

Received: 8 November 2023 | **Revised:** 4 October 2024 | **Accepted:** 11 October 2024

Funding: This work was supported by European Union's Horizon 2020 research and innovation programme (817578, 817806, 817669), Agencia Estatal de Investigación (CEX2019-000928-S), Horizon 2020 Marie Sklodowska-Curie grant (101024886), Research Council of Norway (294819, 280546, RCN 301077), National Oceanic and Atmospheric Administration's RESTORE Science Program (NA19NOS4510193).

Keywords: fitness | functional traits | mesopelagic zone | trait-based approaches | vertical migration

ABSTRACT

Fishes inhabiting the mesopelagic zone of the world's oceans are estimated to account for the majority of the world's fish biomass. They have recently attracted new attention because they are part of the biological carbon pump and have been reconsidered as a contribution to food security. Hence, there is an urgent need to understand how environmental conditions and species interactions shape their assemblages, and how they contribute to the functioning of marine ecosystems. Trait-based approaches are valuable for addressing these types of questions. However, the biology and ecology of mesopelagic fishes are understudied compared to fishes in shallow and epipelagic waters. Here, we synthesise existing knowledge of traits of mesopelagic fishes and relate them to their role in survival, feeding and growth and reproduction, the key functions that contribute to fitness. Vertical migrations, specialised vision and the use of bioluminescence are among the most striking adaptations to the conditions in the mesopelagic realm. Many traits are interrelated as a result of trade-offs, which may help to understand selection pressures. While morphological traits are straightforward to observe, major knowledge gaps exist for traits that require frequent sampling, assessment under experimental conditions or age determination. The unique adaptations of mesopelagic fishes need to be included in management strategies as well as fundamental research of the habitat.

https://doi.org/10.1111/faf.12867

1 | Introduction

Mesopelagic fishes are estimated to make up the majority of the total biomass of fishes in the world (Irigoien et al. 2014). This group of fishes is defined by their shared daytime habitat in the marine 'twilight zone' or mesopelagic zone, which is conventionally set within a depth range of 200–1000 m (Reygondeau et al. 2018). However, an extent based on light intensity has been suggested to be more ecologically relevant (Kaartvedt, Langbehn, and Aksnes 2019). The sunlight penetrating to mesopelagic depths is not sufficient for photosynthesis, but the difference between night and day can still be perceived (Costello and Breyer 2017). Apart from the scarcity of light and accordingly low photoautotrophic production, the environmental conditions in the mesopelagic zone are characterised by moderate temporal fluctuations in the environment in much of its global range (Sutton et al. 2017), with some regions prone to large and persistent oxygen minimum zones (Karstensen, Stramma, and Visbeck 2008; Long et al. 2021). To survive, feed, grow and reproduce under these conditions, mesopelagic fishes have to be adapted in unique ways. The most striking difference compared to other fishes is the pronounced diel vertical migration, performed by many mesopelagic organisms (Klevjer et al. 2016). Adaptations to low and variable light conditions in the form of specialised vision and bioluminescent light organs further set the fishes of the mesopelagic zone apart from epipelagic, shallow coastal and freshwater fishes.

Early research campaigns in the 1960s–1980s carried out some foundational work on mesopelagic fish species inventories and distribution patterns (e.g., Badcock and Merrett 1976; Gjøsaeter and Kawaguchi 1980; Goodyear et al. 1972; Hulley 1981; Krefft 1974). Still, due to the effort required to reach the open ocean and the specialised gear needed to sample the mesopelagic zone, mid-water habitats remain under-represented in global databases of marine biological records, as is the deep-pelagic ocean as a whole (Eduardo et al. 2024; Webb, Vanden Berghe, and O'Dor 2010). In addition, attempts at keeping mesopelagic fishes in experimental facilities for a longer time have not been successful so far. Thus, their ecology and biology are underexplored compared to shallow water fishes, despite their almost global distribution and high overall abundance. However, mesopelagic fishes have recently gained renewed scientific and commercial attention. They occupy a central position in the oceanic food web by feeding on plankton and acting as an important prey for commercial fishes and larger top predators (Iglesias et al. 2023; van Denderen et al. 2021; Giménez et al. 2018), and they could (indirectly) even be an additional source of food for human well-being (Alvheim et al. 2020; Gjerde, Wright, and Durussel 2021; Grimaldo et al. 2020). Further, with vertical migrations, they facilitate an active export and sequestration of carbon in the deep and therefore contribute to the ocean's biological carbon pump (Robinson et al. 2010; Aksnes et al. 2017; Davison et al. 2013; Koslow et al. 2014; Pinti et al. 2023; Saba et al. 2021). They are expected to be influenced by the effects of climate change (Ariza et al. 2022) and other anthropogenic pressures such as fisheries, pollution and deep-sea mining (Drazen et al. 2020; Williams et al. 2022).

Because of the ecological importance of mesopelagic fishes and their role in global biogeochemical cycles, there is an urgent need to investigate their relationships with environmental conditions and other organisms, and to characterise their roles in their ecosystems. Trait-based approaches have proven powerful for addressing such questions (Zakharova, Meyer, and Seifan 2019; Martini et al. 2021), and are increasingly applied to describe fish diversity, fish community structure and ecological processes and functions linked to fish (reviewed by Luiz et al. 2019; Villéger et al. 2017). Our work builds on the widely used definition of traits established by Violle et al. (2007): 'Any morphological, physiological or phenological feature measurable at the individual level, from the cell to the whole-organism level, without reference to the environment or any other level of organization'. However, the definition has been expanded as necessary to include behavioural (e.g., Nock, Vogt, and Beisner 2016) and life-history characteristics (e.g., Litchman, Ohman, and Kiørboe 2013), as well as measurements at other relevant organisational levels (Dawson et al. 2021). We take an eco-evolutionary perspective (Gutiérrez-Cánovas et al. 2024) and focus on functional traits that contribute to the core life functions survival, feeding, and growth and reproduction (Figure 1), which are the components of fitness (Violle et al. 2007; Litchman and Klausmeier 2008; Litchman, Ohman, and Kiørboe 2013). Community compositions depend on traits (Kiørboe, Visser, and Andersen 2018), and trait compositions have an effect in the ecosystem (Maureaud et al. 2019; Pecuchet et al. 2017). Studies with an ecosystem perspective often focus on effect traits, which express a species' influence on ecosystem processes regardless of adaptive advantages, and response traits, which express a species' ability to adapt to environmental changes (Suding et al. 2008; Díaz et al. 2013). The two perspectives are complementary, as functions that influence organism performance also have an effect in ecosystem processes (Villéger et al. 2017), for example, growth rates influence secondary production (Gutiérrez-Cánovas et al. 2024). In this study, we concentrate on traits that concern aspects of individual fitness, to elucidate the key adaptations to the mesopelagic habitat. While the core life functions apply across all life forms, traits materialise in different ways between taxa (Kiørboe, Visser, and Andersen 2018). Trait sets that have been established for epipelagic and coastal fish species (e.g., Beukhof, Dencker, et al. 2019) cannot simply be transferred to mesopelagic species because of their specific adaptations.

In this review, we aim to provide an overview of the current knowledge of mesopelagic fish traits, in order to provide a conceptual framework for future trait-based studies and data collection efforts. We do not include epipelagic taxa (e.g., tuna or sharks, for the latter, see Schaber et al. 2022) or fishes affiliated with benthic habitats (seamounts: Fock et al. 2002; Mid Atlantic Ridge: Fock, Pusch, and Ehrich 2004; Koslow 1996) that use the mesopelagic zone for foraging or interact with the mesopelagic fauna at the transition from open ocean to continental shelf (Trueman et al. 2014). This review follows previous trait-based ontologies developed for other organism groups (Litchman and Klausmeier 2008; Litchman, Ohman, and Kiørboe 2013), by classifying traits according to their contributions to fitness, namely survival, feeding, and growth and reproduction (Figure 1). We address the vertical migration behaviour first, because it is a key trait in the mesopelagic that transcends all functions and influences many other traits. Subsequently, our work centres around a review of traits structured by the three main functions.

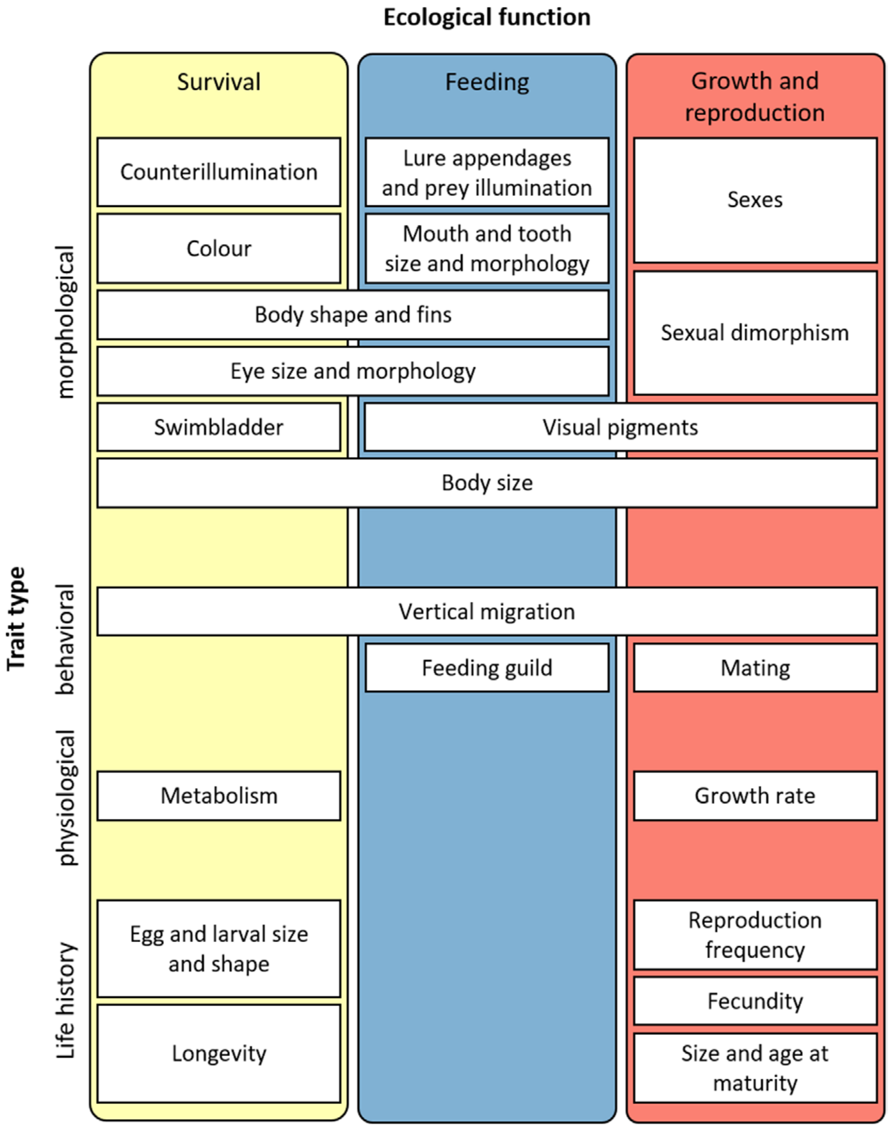

FIGURE 1 | Mesopelagic fish traits discussed in the text, arranged by trait type and ecological function. Adapted from Litchman, Ohman, and Kiørboe (2013).

We then address interrelationships and trade-offs among traits and implications for adaptations to a changing world. Finally, we identify what knowledge is needed to improve our understanding and to provide informed advice for conservation and management.

2 | Vertical Migration—A Key Trait Affecting Multiple Ecological Functions

A great range of mesopelagic organisms, including fishes, perform diel vertical migrations (DVM) (Haddock and Choy 2024; Eduardo et al. 2024; Bianchi and Mislan 2016; Clarke 1980). They spend the daylight hours at several hundred metres depth where resources are scarce, but the low light intensity reduces the risk of becoming prey to visually hunting predators. At dusk, they ascend to the plankton-rich epipelagic zone to feed during the relatively safe darkness of the night (Aksnes et al. 2017; Langbehn et al. 2019; Rosland and Giske 1994; Røstad, Kaartvedt, and Aksnes 2016a, 2016b; Sutton 2013). This diel vertical migration is probably the largest animal movement on the planet in terms of biomass (Irigoien et al. 2014; Klevjer et al. 2016; Hays 2003). It was first detected by hydroacoustic methods (Duvall and Christensen 1946), where mesopelagic fishes, together with other organisms, were found to form a clear and ubiquitous sound-reflecting layer across the world's ocean, the so-called Deep Scattering Layer (Tont 1976; Davison et al. 2013; Boersch-Supan, Rogers, and Brierley 2017).

Among mesopelagic fish species, there is a continuum from strong-to-weak-to-no migration behaviour, with additional ontogenic, temporal and spatial differences. Eggs and larvae of mesopelagic fishes hatch and develop in the epipelagic zone, and pre-metamorphosing larvae of many species undertake DVM of some 50 m in this zone (Dove, Tiedemann, and Fock 2021). A downward shift in distribution is observed for metamorphosing larvae. Thereafter, vertical migration is performed in many taxa by post-metamorphic to adult stages, but may cease in the oldest senescent period of life (Marshall 1980; Gartner 1991;

Stefanescu and Cartes 1992; Porteiro and Sutton 2007; Sassa et al. 2007; Olivar et al. 2018).

Many mesopelagic fishes migrate daily, such as most lanternfishes (Myctophidae), lightfishes (Phosichthydae) and many dragonfishes (Stomiidae; Eduardo et al. 2024; Badcock 1970; Badcock and Merrett 1976; Hulley 1981; Roe and Badcock 1984; Gartner et al. 1987; Sassa et al. 2002; Fock, Pusch, and Ehrich 2004; Ross et al. 2010; Sutton 2013; Olivar et al. 2017). The highest night-time concentrations of migrant mesopelagic fishes are generally found within the upper 100 m and some even concentrate in the neustonic layer directly at the water surface, for example, some myctophids such as *Myctophum* spp. and *Gonichthys* spp. (Olivar et al. 2016). However, some mesopelagic fish species, such as some stomiids, for example, *Chauliodus* spp., and a few myctophids, for example, *Benthosema glaciale* (Sutton, Letessier, and Bardarson 2013) or *Stenobrachius leucopsarus* (Watanabe et al. 1999), show an asynchronous migration, where part of the population remains at depth as long as they have undigested prey in the stomachs (Sutton and Hopkins 1996; Watanabe et al. 1999). Other groups, such as hatchetfishes (Sternoptychidae) or a few myctophids, only perform a limited upward displacement and do not reach the upper epipelagic layers (Watanabe et al. 1999; Eduardo, Bertrand, et al. 2020). Finally, several taxa typically do not migrate at all, such as bristlemouths (Gonostomatidae) of the genus *Cyclothone* (Sarmiento-Lezcano et al. 2023), some stomiids (e.g., *Malacosteus niger*, Kenaley 2008; Williams et al. 2001) or bathylagids (e.g., *Bathylagus pacificus*, Yancey, Lawrenceberrey, and Douglas 1989).

Migration is an evolved adaptive behaviour, and the mechanism that triggers it is the change in light intensity at dawn and dusk (Bianchi and Mislan 2016; Sutton 2013). It should be noted that the extent of the 'ocean twilight zone' is dynamic and is not limited to a fixed depth range (Kaartvedt, Langbehn, and Aksnes 2019). For instance, with increasing turbidity or during winter at higher latitudes, light intensities decrease and the daytime distribution of many species shifts upwards, indicating that light exposure, not depth per se, is decisive of their depth distributions (Aksnes et al. 2017; Langbehn et al. 2019). In addition to light, temperature, oxygen levels, nutrient availability, topography and the presence of predators or prey can modify this behaviour (Netburn and Koslow 2015; Boswell et al. 2020; Urmy and Benoit-Bird 2021). For instance, adult *B. glaciale* (age 2+ years) have been shown to invert their vertical migration behaviour corresponding with seasonal patterns in the abundance of the zooplankton they feed on (Dypvik, Klevjer, and Kaartvedt 2012). Spatial variation in environmental conditions can lead to geographical differences in migration intensity within species (e.g., Eduardo, Lucena-Frédou, et al. 2020), and in the vertical position and extent of the deep scattering layer (Netburn and Koslow 2015; Loutrage et al. 2023).

The vertical migrations require morphological and physiological adaptations. Migrating species often track a 'light comfort zone' (Aksnes et al. 2017; Langbehn et al. 2019; Røstad, Kaartvedt, and Aksnes 2016a, 2016b), a narrow range of light intensities, followed across a wide range of water depths. In contrast, non-migratory species remain at constant depth and experience a wide range of light levels over a diel cycle. In clear waters during a sunny day, mesopelagic daytime light intensities can span roughly 10 orders of magnitude (Warrant and Locket 2004; Kaartvedt, Langbehn, and Aksnes 2019). Accordingly, there are different degrees of specialisation in vision between migration strategies. Vertical migration, achieved through active vertical swimming, is usually aided by the presence of a gas-filled swimbladder. However, during growth and maturation of some species, including species of myctophids and melamphaids, the gas is gradually replaced by lipids (Neighbors and Nafpaktitis 1982) with buoyancy and reserve functions (Godø, Patel, and Pedersen 2009), and many species have no functional swimbladder throughout their entire lives. Each type can occur in migratory or non-migratory species, involving trade-offs between tissue composition and the costs of active swimming and gas exchange (Davison 2011). Observations made from submersibles report mesopelagic fishes hovering in the water column often in a slightly oblique position (Backus et al. 1968; Gartner et al. 2008). Alternation between periods of vertical swimming, followed by passive horizontal gliding, has been observed in some mesopelagic fishes, which is suggested to reduce the energy cost of swimming by up to 50% (Weihs 1974; Torgersen and Kaartvedt 2001) and may also help to control swimbladder volume to avoid breakage or collapse due to pressure changes (Kaartvedt et al. 2008). Many mesopelagic fishes have an adipose fin (non-rayed fin), which may have a sensory function and detect changes in pressure and thus water depth (Reimchen and Temple 2004; Buckland-Nicks, Gillis, and Reimchen 2012). Further, migrators regularly cross large temperature gradients of up to 20°C (Klevjer et al. 2016; Wang et al. 2019). For the transition from colder and zonally hypoxic depths to warmer and well-oxygenated surface waters, some myctophids have a species-specific integrated stress response with antioxidant and heat shock enzymes, as is also found in intertidal organisms (Lopes et al. 2013).

To conclude, migratory behaviour is not only associated with survival strategies and resource acquisition, but it also has implications for energy allocation to growth and reproduction. More traits related to these three ecological functions are addressed in the following sections.

3 | Traits by Ecological Function

3.1 | Survival

Determinants of fish survival change with development (Olla et al. 1996). Ontogeny has enormous implications on the way a fish responds to environmental and biotic factors. This is evident not only in terms of changes in size and body shape, but also in terms of habitat preferences. Eggs and larvae of mesopelagic fishes are found mostly in the epipelagic zone (Moser and Ahlstrom 1970, 1996; Röpke 1993; Sabatés 2004; Olivar, Rubiés, and Salat 1992). This allows the larvae to develop in layers with more abundant food, ultimately avoiding mortality by starvation. However, this advantage also implies higher vulnerability to advective processes and to predation, the other two main larval mortality risks (Houde 2002). Small egg sizes, limited yolk reserves and chorion fragility point to a short embryonic developmental duration, which reduces the likelihood of predation mortality on the egg stage. Such a rapid development has been confirmed by incubation of artificially fertilised eggs of *Benthosema pterotum*, where hatching occurred from 10 to 16 h after artificial fertilisation (Gjøsæter and Tilseth 1988). The focus in this section is on the broad range of adaptations that reduce the risk of mortality through predation in adult mesopelagic fishes and, where applicable, corresponding adaptations at earlier life stages. This section is structured to resemble the successive stages of the interplay between prey and predator. First, we describe the main means by which mesopelagic fishes can evade detection by their predators, and then address adaptations hampering pursuit and capture by a predator. Finally, we discuss potential adaptations by which a mesopelagic fish avoid ingestion in the event it has been detected and captured.

The primary mechanism by which mesopelagic fishes reduce encounters with potential predators is through diel vertical migration. Other means include a variety of morphological traits related to fish conspicuity. In the early stages, the main strategy is to avoid detection through transparency. In some cases, fish body tissues remain very transparent even during the juvenile and adult stages, such as in several *Cyclothone* spp., several Lophiiformes and the ‘Half-naked Hatchetfish’ (*Argyropelecus hemigymnus*, Sternoptychidae). However, throughout ontogeny, transparency declines as the eyes become pigmented, visceral organs become larger and there is a progressive completion of fins, body musculature and skeleton. To limit detection, many mesopelagic fishes conceal their body silhouettes via counterillumination (Herring and Widder 2001; Warrant and Locket 2004; Young et al. 1980). This form of camouflage is achieved with light-emitting photophores on the ventral body, which blur its shadow when viewed from below. The intensity is regulated according to the ambient light intensity recorded by the eyes (Young et al. 1980; Priede 2017), sometimes with eye-facing photophores as a reference (Davis et al. 2020). Remarkably, the use of bioluminescence for counterillumination has also evolved in three families of sharks, namely the mesopelagic Etmopteridae (‘lantern sharks’), Dalatiidae, and, as recently confirmed, the Somniosidae (Duchatelet, Marion, and Mallefet 2021). Another adaptation to appear invisible is to have silvery body flanks, such as found among many lightfishes and hatchetfishes. However, at low light intensity, these silvery scales may make fish very conspicuous to predators capable of producing bioluminescent flashes. In such cases, this can be counteracted by the presence of ventral body photophores surrounded by black chromatophores that may disperse black pigment at night (Herring 2002; Warrant and Locket 2004). Unlike mesopelagic crustaceans that often use red coloration to become unrecognisable, only a few mesopelagic fishes are reddish in colour (some Cetomiimidae, Barbourisiidae and Setarchidae).

In the event a mesopelagic prey is detected by a predator, a range of adaptations help it to escape. First, they need to sense the predator. The low light in the mesopelagic zone and the night feeding pattern have led to a number of evolutionary adaptations on the eyes of mesopelagic fishes. These adaptations generally increase the fish's ability to capture dim ambient light, or brighter point sources from bioluminescence, and thus allows them to detect prey, mates or potential predators (Locket 1977; Warrant and Locket 2004; Helfman et al. 2009; Turner et al. 2009). Already the larvae show a variety of morphological eye specialisations (round or narrow, sessile or borne on stalks) that have been related to their location in the water column, and explained as enlargement in the larval visual field (Weihs and Moser 1981; Ahlstrom, Moser, and Cohen 1984; Kawaguchi and Moser 1984; Moser, Ahlstrom, and Paxton 1984). In addition, the structure of larval eye retina, with an earlier development of rods for scotopic vision (low light conditions) has been observed in myctophids compared to larvae of epipelagic fishes. This is interpreted as an adaptive response to an impending deep mesopelagic adult lifestyle (Sabatés, Bozzano, and Vallvey 2003; Bozzano, Pankhurst, and Sabatés 2007). In adult mesopelagic fishes, sensitivity to light is increased in many species by enlarged eyes, which may be spherical or tubular. Spherical eyes placed laterally on the head allow a fish to detect predators in a large part of its surroundings. Binocular vision with tubular eyes allows the estimation of distance, but leaves the fish blind in other directions and thus vulnerable to attack (Wagner 2001; Warrant and Locket 2004; Priede 2017). However, the field of view of such fishes can be extended in other ways. For instance, several species of Argentiniformes (e.g., *Winteria telescopa* and *Rhynchohyalus natalensis*) have accessory retinas that collect light from multiple directions, not necessarily producing a well-focused image, but sufficient vision to detect movement (Warrant and Locket 2004; Priede 2017).

In addition to vision, the lateral line system provides mesopelagic fishes with the ability to detect and locate nearby animals, including predators. This detection of motion and pressure gradients is achieved with sensory organs called neuromasts that are capable of detecting changes in flow direction, velocity and acceleration (Denton and Gray 1989; van Netten and McHenry 2014; Bleckmann and Zelick 2009; Marranzino and Webb 2018). The degree of development and complexity of the lateral line system, including the number, location and size of neuromasts, varies widely among mesopelagic fishes and may correlate with life-history strategies (Marshall 1954, 1980; Bleckmann and Zelick 2009; Marranzino and Webb 2018). In general, fishes living in habitats with higher levels of hydrodynamic stimuli (e.g., turbulence and flow) have more canal neuromasts, while species inhabiting calmer and slower moving water have more superficial neuromasts (Marshall 1971). The proliferation of the latter type in many mesopelagic fishes emphasises the detection of flow velocity, increasing sensitivity to hydrodynamic disturbances from other midwater animals (e.g., predators, prey and conspecifics; Marshall 1996; Marranzino and Webb 2018).

If detected by a predator, the targeted fish may try to escape. As soon as the ossification of fins starts in late larval stages, pectoral fins add lift and inertial propulsion contributing to improve swimming skills (Weihs 1980; Webb and Weihs 1986; Fuiman 1983; Osse and van den Boogaart 1995), which are vital for prey capture and predator avoidance (Fuiman and Magurran 1994). Among adult mesopelagic fishes, predator escape has been shown to be achieved primarily by rapid vertical escape reactions by diving at speeds up to 15–20 cm/s (Christiansen et al. 2021). Another adaptation to evade predators includes the emission of trains of light flashes from patches of luminous tissues on the head that may distract a predator during pursuit (Herring 2002; Priede 2017; Chevallay et al. 2024).

Schooling is an anti-predation behaviour of many epipelagic fish species. Mesopelagic fishes have been found to form aggregations (e.g., Saunders et al. 2013; Gauthier, Oeffner, and O'Driscoll 2014) that are probably largely a response to the environment and consist of mixed species. Yet, acoustic observations, including those within the deep scattering layer, suggest that schooling in the narrower sense, with social interactions and coordinated movements, may also occur situationally as a defence tactic in some mesopelagic taxa (Benoit-Bird, Moline, and Southall 2017; Christiansen et al. 2021; Kaartvedt, Knutsen, and Holst 1998; Marchal and Lebourges 1996; Ménard and Marchal 2003).

Prey selection by marine mega-predators, such as cetaceans, can be influenced by the nutritional quality of prey species (Spitz, Ridoux, and Brind'Amour 2014). Those with poor nutritional quality should be neglected by predators. Mesopelagic fishes vary greatly between species in terms of energy densities and nutrient concentrations (Chouvelon et al. 2022). Myctophids can be particularly targeted by cetaceans and seabirds. In contrast, the alepocephalid *Xenodermichthys copei* is one of the most abundant mesopelagic fishes on the slope of the Bay of Biscay in the Northeast Atlantic, but is surprisingly absent from the diets of all predators studied in the area. A possible explanation may be that this lean species carries limited nutritional value, which reduces its risk of predation by becoming a trophic cul-de-sac (Spitz et al. 2010), at least in the presence of other, high-energy prey.

Once captured, most mesopelagic fishes have limited adaptations to avoid being ingested. They are usually small and have no physical defence traits preventing ingestion, such as body armour, spines or chemical substances. This may be due to phylogenetic constraints, or because such traits do not carry a selective advantage. Either way, we argue that mesopelagic fishes foremostly rely on avoiding detection.

3.2 | Feeding

Mesopelagic species have developed adaptations to cope with the reduced food supply at depth (Drazen and Sutton 2017; Eduardo et al. 2024; Herring 2002; Priede 2017). In turn, these adaptations may hinder successful competition in habitats with higher food supply. As such, a limited number of ‘pseudoceanic’ species show increased abundance around locations with higher productivity like seamounts (e.g., Porteiro and Sutton 2007; Cherel et al. 2020), islands (Krefft 1974) or shelf edges and canyons (Hulley and Prosch 1987; Duncan et al. 2022; Loutrage et al. 2023). There are only few reports of phytoplankton in the guts of mesopelagic fishes (Robison 1984). Nearly all mesopelagics are therefore strictly carnivorous, feeding either on zooplankton (zooplanktivores) or large invertebrates and other fishes (micronektonivores; Drazen and Sutton 2017). However, it has recently been noted that mesopelagic food webs can also be fuelled by a variety of nutritional sources, including surface dwelling phytoplankton and bacteria, sinking particles and suspended particles (Gloeckler et al. 2018; Bode, Olivar, and Henández-León 2021; Eduardo et al. 2023). The isotopic signatures of nitrogen ^{15}N in food particles and micronekton tissue allows discrimination of feeding strategies in the deep (Bode, Olivar, and Henández-León 2021; Gloeckler et al. 2018), and generally, reveal the use of different trophic sources within mesopelagic species (e.g., Chouvelon et al. 2022; Eduardo et al. 2023). The turnover of ^{15}N in so-called source amino acids in the microbial food web is higher and thus its accumulation in animal tissue indicates the degree of dependence on the microbial food web component in the diet. In particular, deep dwelling non-migrators can have a high dependency on the microbial food web (e.g., 50% of diet in *Cyclothone atrum*, see Gloeckler et al. 2018), while for mesopelagic migrators, this fraction lies in the range of 10%–20% (e.g., myctophid *Benthosema glaciale*, Bode, Olivar, and Henández-León 2021).

Earlier studies argued that a decreasing abundance of food with depth would cause the diets of deep sea fishes to become more general, but few examples corroborate the ‘eat anything you see in a food-poor environment’ hypothesis (Drazen and Sutton 2017). High specialisation and several mechanisms to avoid competitive exclusion were identified for the most abundant mesopelagic fish species (Hopkins and Gartner 1992; Hopkins and Sutton 1998; Eduardo, Bertrand, et al. 2020; Eduardo et al. 2021, 2023; Loutrage et al. 2024a). It seems that many of the unique adaptations in mesopelagic species are more likely to ensure a higher capture-per-encounter rate than a greater diversity of prey (Drazen and Sutton 2017), resulting in complex patterns of niche partitioning (Helfman et al. 2009; Sutton 2013; Eduardo, Bertrand, et al. 2020; Eduardo et al. 2021). To meet increasing energy requirements during ontogeny, some species have adopted a strategy of shifting their food resources by feeding on larger or higher trophic level prey, while others appear to maintain their food sources but most likely increase the amount of prey ingested (Loutrage et al. 2024b).

This section discusses the main mechanisms and adaptations that permeate the feeding process of mesopelagic fishes, from finding or attracting prey to capturing prey.

3.2.1 | Finding Prey

As with the visual detection of predators for survival, mesopelagic fishes have developed various visual adaptations that help them find prey in dim light. For example, some have elongated ‘tubular’ eyes with large, distal, spherical lenses that focus a sharp image onto the main retina, which lines the weakly concave base of the eye (Munk 1980). This eye morphology increases the sensitivity to light and provides well-developed binocular vision. While there are no cues in the deep sea to judge distance using monocular vision, binocular vision allows the stereoscopic estimation of prey distance, based on the slight disparity between images falling on the two retinae (Warrant and Locket 2004). A good example is *Stylephorus chordatus* (Stylephoriformes), that possesses forward-facing tubular eyes facilitating the location and pursuit of prey, while leveraging on its high-speed suction feeding mechanism (Priede 2017). Moreover, ambush predators such as the hatchetfish *Argyropelecus aculeatus* (Sternoptychidae) feature dorsally oriented tubular eyes (upward-looking), which aid the detection of prey silhouetted against the subdued downwelling light from above (Warrant and Locket 2004; Priede 2017). In fishes with laterally placed, spherical eyes, binocular overlap is limited, as is the case with most shallow-water fishes (Munk 1980). The field of view can be enhanced with an aphakic gap, an enlargement of the pupil beyond the margin of the lens (Warrant and Locket 2004; Davis et al. 2020). This gap is typically a rostral elongation of the pupil, which increases the collection of light from the front, as is relevant for foraging, but can be an enlargement in all directions, which is beneficial in darker water, at the cost of image resolution (Warrant, Collin, and Locket 2003). For example, in bristlemouths (Gonostomatidae), the eye becomes smaller, but the relative pupil diameter and the aphakic gap increase with depth (Warrant, Collin, and Locket 2003).

A remarkable feature recently discovered is the ability of mesopelagic fishes to detect multiple wavelengths (de Busserolles et al. 2017). Colour vision in vertebrates is usually achieved through the interaction of various photopigments in the cone cells found in the retina. Each of these photopigments reacts to a certain wavelength of light. In the darkness, vertebrates detect the few available light particles with their light-sensitive rod cells, which contain only a single type of the photopigment rhodopsin—explaining why nearly all vertebrates are colour-blind at night. Some mesopelagic fishes, however, have expanded their repertoire of rhodopsins. As an example, the Silver Spinyfin (*Diretmus argenteus*, Trachichthyiformes) has 38 rhodopsins and two cone opsins. This allows the vision to cover the bioluminescence wavelength spectrum produced by deep-sea organisms, which gives rise to several advantages for prey detection (Musilova et al. 2019).

Another trait that aids visual hunting is the generation of light to detect prey. Some stomiids, for example, *Malacosteus* spp. and *Aristostomias* spp., have large red-emitting photophores below the eye that illuminate organisms such as red mesopelagic crustaceans (Denton et al. 1985; Sutton 2005). This far-red bioluminescence is only visible to conspecifics and not their predators or prey (Herring and Cope 2005; Turner et al. 2009; Widder et al. 1984). Similarly, some myctophids such as the 'Headlight Lanternfish' (*Diaphus effulgens*) and other species of this genus use head photophores to produce blue light and expose largely transparent prey (Land and Osorio 2011).

Further, non-visual senses become more important with increasing darkness. In melamphaids, lateral line organs with wide canal pores are located on the large head. In combination with small eyes and no role in schooling behaviour, these highly developed cranial lateral lines are concluded to take the function of detecting prey (Marshall 1996; Deng, Wagner, and Popper 2013).

3.2.2 | Attracting Prey

Another way of creating feeding opportunities is ambush feeding using bioluminescent lures that attract prey organisms. The lures emit light that mimics the bioluminescence of their prey's food sources or conspecifics, luring unsuspecting prey towards them and making it easier to capture them (Widder 2010). The majority of female ceratioid anglerfishes have an anterior dorsal-fin spine that is modified as a luring apparatus. In contrast to intrinsic self-luminescence (e.g., Myctophidae, Stomiiformes; Haddock, Moline, and Case 2010; Priede 2017), the 'lure' (esca) at the end of the 'fishing rod' (illicium) consists of a fleshy outgrowth colonised by bioluminescent bacteria (Pietsch 2009). Stomiid dragonfishes, which are very efficient micronektonivores, use elaborate mental (chin) luminescent barbels as lures (Priede 2017). Interestingly, even in distantly related sharks, analogous adaptations have evolved.

3.2.3 | Capture and Ingestion

Most mesopelagic fishes have relatively large jaws already as larvae, a feature that has been related to their capacity to ingest a large range of prey sizes when prey are encountered. A subsequent positive allometric growth of jaw length in relation to total body length during larval development has been observed for nearly all mesopelagic fishes (Contreras et al. 2019). Adult mesopelagic fishes exhibit an exceptional diversity of feeding morphologies. However, our functional interpretation of many of these adaptations is limited by the near absence of direct observations on feeding and the few data available on their feeding ecology.

A high degree of heterodonty is observed in myctophids (e.g., villiform, hooked, recurved, spade, tricuspid and caniniform teeth). Although the exact functions of diverse combinations of teeth are unknown, their variety suggests different adaptations linked to prey size and types (Martin and Davis 2020). For instance, species actively capturing mobile prey are characterised by stronger teeth and jaws and less developed gill rakers in order to limit water resistance and gain speed during the strike (the sequence between the opening and the closing of the mouth). Dragonfishes show remarkable adaptations to gain speed and capture large prey of even more than 50% of their own size (Battaglia et al. 2018). Some species of this family have even lost the floor on their oral cavity to reduce resistive forces and compensate for their long jaws (Kenaley 2012). Their long fang-like teeth could be used more to lock their relatively large prey in their mouths rather than for biting. Some of these teeth are also transparent, which could complete their camouflage strategy by making them invisible to prey (Velasco-Hogan et al. 2019). Some species (e.g., Chiasmodontidae or Evermannellidae) have long inward depressible teeth allowing prey to enter, but not exit the mouth. Such teeth allow them to handle and eat large prey, sometimes larger than the predator itself (Parin 1971).

The Pelican Eel (*Eurypharynx pelecanoides*, Saccopharyngiformes) is an ultimate example of the surprising morphological diversity of fishes in the deep and the difficulty of linking morphological traits to feeding behaviour. In spite of its huge and disproportionate mouth and jaws, its diet is composed of small prey (Nielsen, Bertelsen, and Jespersen 1989). Recent observations of live animals and biomechanical considerations indicated that they engulfed these prey with a large amount of water like lunge feeding in baleen whales. Further understanding of feeding behaviours in the deep sea will undoubtedly challenge our current conceptions of prey capture patterns in mesopelagic fishes (Schembri 2018).

3.3 | Growth and Reproduction

Spawning strategy and energy investment in growth, maturation and fecundity are closely interrelated among fishes (Winemiller and Rose 1992; Pecuchet et al. 2017). This also applies to the mesopelagic zone with its scarcity of resources. Growth and reproduction of mesopelagic fishes have been recently reviewed by Caiger, Lefebve, and Llopiz (2021). They point out that life-history strategies are related to migratory behaviour and the position in the water column.

Childress et al. (1980) highlighted the main life-history strategies of mesopelagic migrators in contrast to epipelagic and bathypelagic non-migratory species regarding growth and energy allocation. Mesopelagic migrants, such as many myctophids, are often characterised by early maturation and repeated reproduction. They grow asymptotically to a small final size, so that their growth is comparatively low in absolute terms. These migratory fishes store energy with high levels of lipids (Childress and Nygaard 1973), and prioritise these apparently crucial reserves over growth in size. Early maturity is often found in both mesopelagic and epipelagic species that are subject to substantial interannual variation in recruitment (Kristoffersen and Salvanes 1998; Pecuchet et al. 2017; Beukhof, Frelat, et al. 2019). Non-migratory mesopelagic and bathypelagic fishes have more species with non-asymptotic growth (Caiger, Lefebve, and Llopiz 2021). These grow rapidly to a generally larger size, and their reproduction tends to be delayed to a single event in the last year of life (semelparous reproduction; Childress et al. 1980). They keep the energy allocated to growth at a comparably high level, but greatly reduce the caloric density and reach much greater body sizes for a given caloric input (Childress et al. 1980). As typical ambush predators, they have reduced locomotor abilities and lower metabolism (Childress 1975; Childress and Somero 1979; Somero and Childress 1980). Remarkably, the highly abundant mesopelagic genus *Cyclothone* is also non-migratory with low caloric density and metabolism, but with small body sizes and very divergent life history strategies (Caiger, Lefebve, and Llopiz 2021; Miya and Nemoto 1991).

A semelparous reproduction benefits from a large body size, which maximises fecundity. Among mesopelagic vertical migrators, reproducing more than once over the course of their lives (iteroparity) and spawning repeatedly over a season (batch spawning) is a way to increase reproductive output even with the constraints of a small body size (Lowerre-Barbieri et al. 2011). Some can achieve lifetime fecundities comparable to epipelagic fishes (Caiger, Lefebve, and Llopiz 2021). Further, iteroparity and batch spawning are generally strategies to increase the chances of offspring survival in unpredictable or aseasonal environments (e.g., the low-latitude mesopelagic), and are proposed to keep intraspecific competition for food low through low offspring densities (Nakayama, Rose, and Fuiman 2011).

Reproductive output can be modified by the allocation of resources to male and female reproduction. Size dimorphism with larger females is common in fishes. The larger body size in females of some myctophids and several stomiids may benefit egg production. The smaller size of male individuals may prevent intraspecific competition for scarce resources, regarding the amount of food as well as the size or type of prey (Clarke 1983). Protandrous hermaphroditism has a similar effect in some species of Gonostomatidae, where small males develop into large females (Watson 1996). Intraspecific competition is also reduced with a spatial separation of males and females (Clarke 1983), as occurs, for example, in species of myctophids (Hulley and Prosch 1987). Furthermore, a higher egg-producing biomass can be achieved with a female-biased sex ratio. For example, females are more abundant than males in some stomiids (Clarke 1983). However, spatial separation and unequal sex ratios have to be balanced with the probability of encounter between males and females for fertilisation. Some mesopelagic migrants form aggregations in surface waters for synchronised spawning (e.g., Flynn and Paxton 2012). Another challenge is the encounter between mating partners in almost complete darkness. For finding, identifying and selecting mating partners, fishes have morphological and sensory adaptations. Bioluminescent structures can differ between sexes in size, position, number or be present only in either males or females, which suggests a role in mating. Caudal organ flashes of myctophids ('lanternfishes') are most likely a sexual signal. Yet, in other cases, sexual differences in bioluminescent structures may just be a consequence of size dimorphism (Herring 2007). Further, mesopelagic population densities are often low and potential mating partners too far away to be seen. Hence, additional olfactory cues, that is, pheromones, are used, which have a larger perception distance than visual stimuli (Herring 2000). Dimorphism in olfactory organs occurs in species of mesopelagic Sternoptychidae and Gonostomatidae (*Cyclothone*, Badcock and Merrett 1976) and one genus of myctophids (*Loweina*; Martin and Smith 2024), but in other mesopelagic fishes, both sexes have well-developed olfactory organs. Sexual dimorphism in the olfactory system is more common in bathypelagic fishes (Marshall 1967, cited at Baird, Jumper, and Gallaher 1990), for example, males in ceratioid anglerfishes have a large olfactory apparatus (Bertelsen 1951, cited at Clarke 1983). Low population density in connection with low mobility should favour the evolution of monogamous pair bonds (Whiteman and Côté 2004). This is carried to the extreme in ceratioid anglerfishes, where the small body of the male and the large body of the female in several families become permanently fused.

4 | Discussion

4.1 | Trade-Offs

The preceding sections suggest that many traits are interrelated. Such dependencies among traits occur when the simultaneous evolution of two or more traits is constrained (Stearns 1992). Trait expressions are therefore the result of trade-offs between and within the key missions of life—to feed, survive, grow and reproduce (Litchman and Klausmeier 2008; Litchman, Ohman, and Kiørboe 2013; Charnov, Gislason, and Pope 2013). Trade-offs between life-history traits are well studied across the animal kingdom, such as number versus quality of offspring (Pianka 1970), or current versus future reproduction (Patrick et al. 2022). Yet, trade-offs do not only concern energy allocation. For example, the energy allocated to reproduction can be at the cost of time invested in foraging activities, and both must be balanced against predation risk

(Kiørboe 2008). Under such pressures, similar ecological strategies may evolve in different taxonomic groups (Litchman, Ohman, and Kiørboe 2013). Here, we describe the major dichotomies that we observed through this review of individual traits in mesopelagic fishes.

The most noticeable trade-offs occur in connection with migration behaviour. Reduced competition may have been one advantage driving the initial colonisation of the mesopelagic zone and deep sea (Priede and Froese 2013). A downside of a mesopelagic existence seems to be a precarious energy balance in a food-limited environment. Each migratory behaviour strategy has its own effect on energy allocation, which leads to trait correlations. The study by Childress et al. (1980) has had a major influence on our conception of the physiological priorities of energy usage between migrators and non-migrators. The authors point out that the differences in growth do not necessarily imply an energetic trade-off with the energy expended on migration. Rather, they propose that the reduced risk of visual predation at greater depths relieves pressures on locomotion ability. This reduces the need to store energy and allows non-migrators to grow to a large body size with lower tissue density. While the larger body size in non-migratory species might serve as an additional refuge from predation, this is unlikely to be the main selective force. This is supported by the fact that species migrating to evade predators to depths inhabited by non-migratory species are typically small. Likewise, the abundant non-migratory species of the genus *Cyclothone* have reduced metabolic rates but remain small (Childress and Seibel 1998). Instead, a large body size coupled with low adult mortality allows for high fecundity in a semelparous strategy (Caiger, Lefebve, and Llopiz 2021). Still, the energetic trade-offs associated with migratory behaviour are complex and surrounded by uncertainty, especially since our current knowledge is based on only a small number of studied species (Caiger, Lefebve, and Llopiz 2021). The scarcity of information limits our understanding of the energetic costs associated with migration and the overall energy requirements of mesopelagic fishes (McMonagle et al. 2023). There is also a lack of knowledge on the importance of alternative food sources for non-migrators, such as detrital aggregates (Bode, Olivar, and Henández-León 2021).

The allocation of energy between somatic growth versus maturation and reproduction is a universal trade-off. Acknowledging that trade-offs are not strictly binary and differ between environments, Winemiller and Rose (1992) developed the equilibrium–periodic–opportunistic (EPO) model for fishes. Three major life-history strategies, characterised by trade-offs between juvenile survival, fecundity and generation time, are linked to differences in the stability and predictability of the environment. A continuum from small, early maturing, short-lived species to larger, later maturing, long-lived species also exists in mesopelagic fishes. Mesopelagic migrants typically have short generation times compared to species from demersal and shallow coastal habitats (Caiger, Lefebve, and Llopiz 2021). They would largely be placed towards the opportunistic strategy (e.g., García-Seoane et al. 2015), which according to the continuum of Winemiller's triangular life-history model (Winemiller 2005) is typical for unpredictable environments. Yet, also the predictable aseasonal but oligotrophic conditions of most mesopelagic habitats in the open ocean appear to promote opportunistic spawning. However, the high proportion of studies from higher latitudes and on myctophids (Caiger, Lefebve, and Llopiz 2021) may bias this perspective.

Another evolutionary trade-off in mesopelagic fishes is the degree of reliance on different sensory abilities, especially on vision. Selective pressures against elaborate eyes are less apparent than trade-offs in energy allocation, also because this trait affects the detection of predators, prey and conspecific signals, and thus serves multiple functions. In addition to somatic investment, constructional constraints balance eye size against jaw (-muscle) size (Hulsey and Hollingsworth Jr. 2011). Further, enhanced vision requires the brain capacity to process visual information.

Concerning bioluminescence, Ruxton and Bailey (2005) conclude from a simulation study using a sternoptychid as a model organism that the energetic cost of mate attraction flashes is trivial and that signalling must be traded off against alerting predators. In lanternfishes, caudal light organs for reproductive communication appear to constrain the evolution of caudal morphology for optimal swimming styles (Martin, Davis, and Smith 2022).

Even for fishes in general, trade-offs and interrelations between traits are only known for a small number of species (Villéger et al. 2017). The biology, ecology and physiology of mesopelagic fishes are not well studied yet for a systematic quantitative analysis to provide more insight into ecological constraints.

4.2 | Key Knowledge Gaps and Needs for Further Research

There are still major gaps in our knowledge of mesopelagic fishes and their traits, particularly with regard to their physiology and life history. The most important knowledge gaps are due to methodological constraints limiting both field and laboratory work. Sampling the mesopelagic zone of the open ocean requires long cruises and is very laborious with deep trawls at different depths, day and night, which limits the number of studies carried out. Moreover, disparities in scientific research capacities and funding of deep-sea research persist among nations, limiting mesopelagic research to certain geographic regions and groups. Research on mesopelagic fishes in polar regions is scarce, with the presence of single myctophids in the deep scattering layer of the Central Arctic Ocean having only recently been confirmed (Snoeijs-Leijonmalm et al. 2022). Studies in the Southern Ocean appear to have set necessary priorities on their critical role in food webs (e.g., Saunders et al. 2014; Cherel et al. 2010; Van de Putte et al. 2006). Most reproduction studies originate from temperate and subtropical regions of the Northern Hemisphere (Caiger, Lefebve, and Llopiz 2021), but a notable study revealed that many myctophids in the Southern Ocean do not reach maturity but are sustained by immigration (Saunders et al. 2017). Omitting regional faunas can bias our perception of mesopelagic fishes in general (Caiger, Lefebve, and

Llopiz 2021), and neglecting intraspecific regional variation can lead to inaccurate trait values being used in studies (de Juan et al. 2022), with consequences for global biogeochemical models (Belcher et al. 2020).

It has proven difficult to impossible to keep mesopelagic fishes alive in aquarium facilities long enough to obtain realistic physiological measurements, for example, of metabolic demands, and feeding, digestion and respiration rates, which would be important for carbon budgets (McMonagle et al. 2023). Respiration rates have been estimated indirectly by measuring the enzyme activities of the electron transport system in shock-frozen samples (Belcher et al. 2020). Respiration rates were particularly higher than expected in the sub-Antarctic region compared to the subtropical region, which was attributed to lipid-rich diets. Such results can help to refine existing empirical allometric relationships to include a wider range of latitudes and habitat depths (Belcher et al. 2020). Water temperature plays an important role in determining where fish species can survive, grow and reproduce. Cold adaptation is present in Antarctic mesopelagic fishes; their metabolic rate is about twice that of ecologically equivalent California species at similar temperatures, but similar at their respective native temperatures (Torres and Somero 1988). This kind of information of temperature tolerances is a valuable addition to the indirect knowledge of realised thermal niches based on species' habitat ranges.

A drawback already pointed out by the early pioneers on ichthyoplankton studies (Moser and Ahlstrom 1970; Robertson 1977) is that the eggs of myctophids (the most abundant mesopelagic fish family) are largely unknown. A sampling bias in favour of epipelagic layers is a contributing factor (Webb, Vanden Berghe, and O'Dor 2010), but further studies covering the entire mesopelagic zone using many different types of plankton nets have not solved this issue (Moser and Ahlstrom 1996). The fragility of these eggs seems the more likely explanation for the absence in plankton samples (Moser, Ahlstrom, and Paxton 1984). Larvae of mesopelagic fishes do not differ greatly from those of other fishes and share the epipelagic habitat (Salvanes and Kristoffersen 2001). Therefore, it is expected they have similar high mortalities as those of other teleosts. However, this is potentially conflicting with the low fecundity combined with a short lifespan, which would imply a low juvenile mortality.

At present, there is not enough information available about most mesopelagic species' life histories. The weak annual temperature variability in the deep sea of the tropics is a challenge to age and growth determination via growth increments in otoliths. There are other annual periodicities that result in seasonal growth fluctuations, although sometimes less pronounced (Morales-Nin and Panfili 2005). As for fishes in general, the frequency of growth ring deposition needs to be validated. Two growth cycles per year have been demonstrated in more equatorial areas (Yosef and Casselman 1995, cited at Morales-Nin and Panfili 2005), but few studies on mesopelagic fishes have verified annual increments (see, e.g., Gjøsæter 1981). Most studies on age and growth of myctophids are based on reading of daily growth micro-increments (Gjøsæter 1987; Young et al. 1988; Gartner 1991; Linkowsky, Radtke, and Lenz 1993), and radiometric dating is another option. A validation of the periodicity of ring deposition through repeated sampling over the seasons is usually hampered by the low frequency of expeditions to oceanic mesopelagic habitats. Knowledge of other traits that require repeated sampling, like spawning seasons, also suffers from this problem. Such studies can focus on the more accessible marginal seas and regions along continental shelves, and semi-enclosed Norwegian fjords are successfully used as natural infrastructure to generate new knowledge on life histories of mesopelagic fish under fluctuating environments (e.g., Folkvord et al. 2016; Goodson, Giske, and Rosland 1995 for *Maurolicus muelleri*). Life-history traits are important for population dynamics and recovery from disturbance, and Luiz et al. (2019) recommend that they should also be more widely included in future studies of community assembly and functional diversity, because of their coupling with energy allocation.

One accessible way of obtaining trait data that is very valuable in the study of mesopelagic fishes is morphological characterisation. Whether expressed in categories or as continuous ratios measured on pictures or preserved specimens, under the premise that 'form follows function', morphological traits can serve as proxies especially for movement and possible prey types (Villéger et al. 2017). Such data can be compared between communities in relation to the environment and used to calculate functional diversity and redundancy indices (e.g., Aparecido et al. 2023), which inform about the continuation of ecosystem functions in the event of species losses.

Trait-based approaches are the foundation of functional diversity, which provides a link between biodiversity and the contributions of species to ecosystem functioning and processes (Cardinale et al. 2012; Duffy et al. 2016; Maureaud et al. 2019). There is no consensus which traits to use (Villéger et al. 2017). Villéger et al. (2017) offer guidelines on how to choose, measure and code (e.g., quantitative, categorical) traits of fishes. Examples can also be found in published trait databases such as Beukhof, Dencker et al. (2019) for demersal and pelagic fishes from shelf seas, and Quimbayo et al. (2021) for reef fishes. Such publications of readily usable trait data foster standardisation among studies, but there is no single universal approach that should be applied in all cases. De Juan et al. (2022) recommend high-quality trait databases with the raw data in their original form, so researchers can decide how to code the traits. Other types of repositories maximise the number of traits measured and the extent of taxa covered, a prominent example being FishBase, which has been in existence since the 1990s (Froese and Pauly 2000). With an adequate data foundation, missing trait information can be inferred from trait associations and phylogenetic relatedness (Thorson et al. 2023). The choice of traits and their coding depends on the research question, planned data analysis, data quality and variability within the study system. When examining mesopelagic habitats, it becomes essential to encompass the distinctive traits exhibited by mesopelagic fishes. Among these traits, vertical migrations stand out as having particularly important effects. Figure 2 illustrates migration behaviours as four ordered categories that can be derived from observations of day and night depth distributions. Other important adaptations to the mesopelagic environment include specialised vision and the utilisation of bioluminescence (Figure 2). The various functions of bioluminescence are associated with different traits. For example,

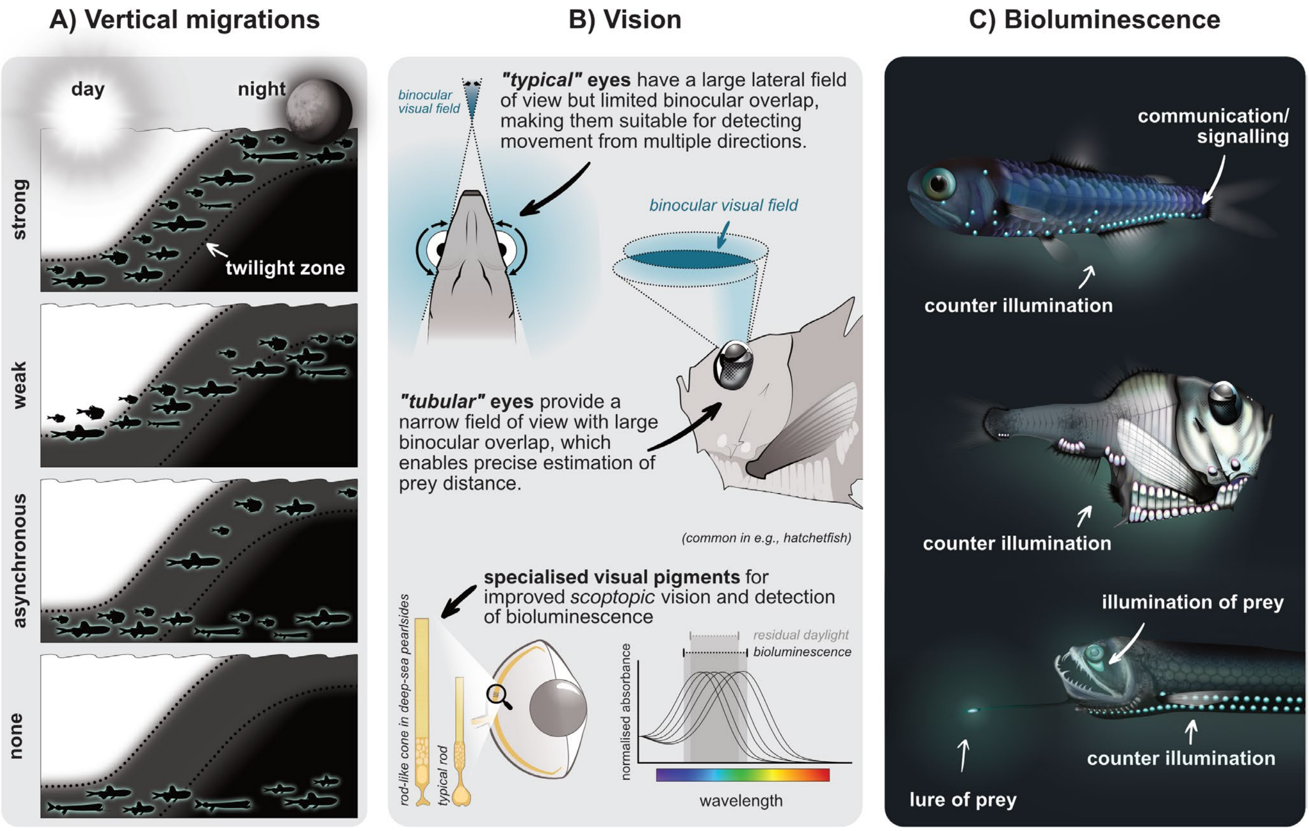

FIGURE 2 | Key traits that should complement commonly used fish traits when studying mesopelagic fish. Graphical elements in panel B adopted from Warrant and Locket (2004), de Busserolles et al. (2017) and Musilova et al. (2019).

counterillumination is a category of camouflage or detectability trait, while prey lures indicate ambush predation as a feeding strategy. All these traits likely play a role in shaping the community assembly.

4.3 | Future Perspectives With Considerations for Management and Conservation

Migratory mesopelagic fishes actively transfer carbon from the surface to the mesopelagic zone and deeper and therefore actively contribute to carbon sequestration and climate regulation (Anderson et al. 2019). The estimated carbon fluxes differ between regions, but are estimated at the order of 20%–50% of the sinking flux, or 15%–30% of the total carbon export (e.g., Hidaka et al. 2001; Davison et al. 2013; Ariza et al. 2015; Belcher, Saunders, and Tarling 2019; Hernández-León et al. 2019). Mesopelagic fishes also connect shallow and deep-sea food webs and constitute prey for commercially harvested species and for vulnerable oceanic predators, including sharks, marine mammals and tunas (Baird, Hopkins, and Wilson 1975; Watanabe et al. 1999; Angel and Pugh 2000; Robinson et al. 2010; Potier et al. 2007). Given their ecological importance, the question arises as to how vulnerable they are to current and future anthropogenic pressures, including climate change and commercial fishing. Traits are increasingly being used to guide the management and conservation needs of individual species and groups (Butt et al. 2022). Studying traits and trade-offs may help to understand selection pressures and potential resilience. The need for knowledge on migration traits becomes also evident when considering depth-dependent threats, such as microplastic pollution or deep-sea mining (Baalkhuyur et al. 2018; Ferreira et al. 2023; Drazen et al. 2020).

The mesopelagic domain is an old, stable and large habitat, and its inhabitants may have evolved adaptations so specialised that they leave little leeway to react to climate change and fishing (St John et al. 2016). In general, vertically migrating species have the capacity to endure strong temperature, oxygen and salinity changes. However, this concerns daily, short-term changes, while through climate change, they are additionally confronted with long-term effects. Species sensitive to temperature have limited options to shift their range to colder regions at higher latitudes as the climate warms, due to differing light regimes that affect safe nightly feeding times (Langbehn et al. 2022). They may neither be able to shift to deeper, cooler waters, as they have evolved to track a light comfort zone (Langbehn et al. 2019). Many mesopelagic fishes may be capable of physiologically surviving elevated temperatures, but it may be suboptimal for growth and reproduction. More importantly, like for all animals, climate change alters the trophic environment, such as the quality and quantity of prey. For example, expected changes in thermal stratification alter vertical particle and nutrient fluxes that support part of the mesopelagic communities (e.g., Li et al. 2020). Additionally, increased stratification and oxygen consumption are expected to lead to an expansion of the depth range of oxygen minimum zones, exacerbated by longer basin water residence times in marginal seas and fjords (Aksnes et al. 2019; Pitcher et al. 2021). This would influence migration behaviour, physiology and species compositions (Bianchi et al. 2013; Duncan, Hagen, and Fock 2024; Koslow et al. 2011, 2014; Seibel 2011), with consequences for the biological carbon pump. Changes in the vertical or horizontal distribution and abundance of mesopelagic fishes will also affect higher trophic levels (e.g., Péron, Weimerskirch, and Bost 2012).

Recent studies investigating the economic viability of a mesopelagic fishery have reached mixed conclusions in a variety of settings, with results ranging from concerns about feasibility (Paoletti et al. 2021; Vastenhoud et al. 2023) to suggestions of economic profitability from a private perspective (Quang, Kourantidou, and Jin 2024; Groeneveld, Richter, and Sen 2024), while some stress the high level of uncertainty (Kourantidou and Jin 2022; Prellezo et al. 2024). However, there is broad agreement that the impact on marine ecosystems, and ultimately the societal cost, is potentially high, and that there are still significant gaps in the knowledge needed to assess sustainability. Life-history characteristics are driving population dynamics and need to be assessed in view of the ecological impact of any fishery, whether on target species or on by-catch (King and McFarlane 2003; Wiedmann et al. 2014). Early maturity and short generation time may allow rapid recovery from adverse events (Winemiller and Rose 1992). For this reason, myctophids could generally be expected to be resilient to some levels of fisheries exploitation (García-Seoane et al. 2015). However, some species may only experience one reproductive season in a short life (Knorrn et al. 2024), and with low fecundity compared to commercially exploited epipelagic species, renewal rates of mesopelagic stock biomass may be low (Catul, Gauns, and Karuppasamy 2011). Further research is needed to determine the productivity and resilience across mesopelagic fish taxa in order to ensure long-term sustainable fishing and management of this largely unexploited marine resource, while considering ecosystem dependencies and functioning (van der Meer et al. 2023). We believe that a trait-based approach describing the general ecology of mesopelagic fishes, including the key traits and trade-offs involved in survival, feeding and growth and reproduction, can be instrumental in providing a first step towards improved knowledge and insight to management and conservation.

Acknowledgements

HA and LNE were financed within the TRIATLAS project, which has received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement No. 817578. MPO, JS, AB and ML acknowledge funding from the European Union's Horizon 2020 Project SUMMER (grant agreement 817806). MPO also acknowledges the institutional support of the AEI 'Severo Ochoa Centre of Excellence' accreditation (CEX2019-000928-S). PDvD was funded by the European Union's Horizon 2020 research and innovation programme under the Marie Sklodowska-Curie grant agreement No 101024886. TJL received funding from the Research Council of Norway under grant no. 294819. EG-S thanks the projects HARMES (Research Council of Norway project number 280546) and MEESO (EU H2020 research and innovation programme, Grant Agreement No 817669) for financial support. TTS was funded by the National Oceanic and Atmospheric Administration's RESTORE Science Program under award NA19NOS4510193 to Nova Southeastern University. AGVS received funding for project HypOnFjordFish from the Norwegian research council (RCN 301077).

Data Availability Statement

The authors have nothing to report.

References

Ahlstrom, E. H., H. G. Moser, and D. M. Cohen. 1984. "Argentinoidei: Development and Relationships." In *Ontogeny and Systematics of Fishes*, Special Publication Number 1, edited by H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall Jr., and S. L. Richardson, 155–169. Gainesville, FL: American Society of Ichthyologists and Herpetologists.

Aksnes, D. L., J. Aure, P.-O. Johansen, G. H. Johnsen, and A. G. V. Salvanes. 2019. "Multi-Decadal Warming of Atlantic Water and Associated Decline of Dissolved Oxygen in a Deep Fjord." *Estuarine, Coastal and Shelf Science* 228: 106392. https://doi.org/10.1016/j.ecss.2019.106392.

Aksnes, D. L., A. Røstad, S. Kaartvedt, U. Martinez, C. M. Duarte, and X. Irigoien. 2017. "Light Penetration Structures the Deep Acoustic Scattering Layers in the Global Ocean." *Science Advances* 3, no. 5: e1602468. https://doi.org/10.1126/sciadv.1602468.

Alvheim, A. R., M. Kjellevold, E. Strand, M. Sanden, and M. Wiech. 2020. "Mesopelagic Species and Their Potential Contribution to Food and Feed Security—A Case Study From Norway." *Food* 9, no. 3: 344. https://doi.org/10.3390/foods9030344.

Anderson, T. R., A. P. Martin, R. S. Lampitt, C. N. Trueman, S. A. Henson, and D. J. Mayor. 2019. "Quantifying Carbon Fluxes From Primary Production to Mesopelagic Fish Using a Simple Food Web Model." *ICES Journal of Marine Science* 76: 690–701. https://doi.org/10.1093/icesjms/fsx234.

Angel, M. V., and P. R. Pugh. 2000. "Quantification of Diel Vertical Migration by Micronektonic Taxa in the Northeast Atlantic." In *Island, Ocean and Deep-Sea Biology. Developments in Hydrobiology*, edited by M. B. Jones, J. M. N. Azevedo, A. I. Neto, A. C. Costa, and A. M. F. Martins, vol. 152, 161–179. Dordrecht: Springer Netherlands. https://doi.org/10.1007/978-94-017-1982-7_16.

Aparecido, K. C., T. Frédou, L. N. Eduardo, et al. 2023. "Living in Darkness: Functional Diversity of Mesopelagic Fishes in the Western Tropical Atlantic." *Frontiers in Marine Science* 10: 1117806. https://doi.org/10.3389/fmars.2023.1117806.

Ariza, A., J. C. Garijo, J. M. Landeira, F. Bordes, and S. Hernández-León. 2015. "Migrant Biomass and Respiratory Carbon Flux by Zooplankton and Micronekton in the Subtropical Northeast Atlantic Ocean (Canary Islands)." *Progress in Oceanography* 134: 330–342. https://doi.org/10.1016/j.pocean.2015.03.003.

Ariza, A., M. Lengaigne, C. Menkes, et al. 2022. "Global Decline of Pelagic Fauna in a Warmer Ocean." *Nature Climate Change* 12, no. 10: 928–934. https://doi.org/10.1038/s41558-022-01479-2.

Baalkhuyur, F. M., E.-J. A. Bin Dohaish, M. E. A. Elhalwagy, et al. 2018. "Microplastic in the Gastrointestinal Tract of Fishes Along the Saudi Arabian Red Sea Coast." *Marine Pollution Bulletin* 131: 407–415. https://doi.org/10.1016/j.marpolbul.2018.04.040.

Backus, R. H., J. E. Craddock, R. L. Haedrich, et al. 1968. "*Ceratoscopelus maderensis*: Peculiar Sound-Scattering Layer Identified With This Myctophid Fish." *Science* 160, no. 3831: 991–993. https://doi.org/10.1126/science.160.3831.991.

Badcock, J. 1970. "The Vertical Distribution of Mesopelagic Fishes Collected on the SOND Cruise." *Journal of the Marine Biological Association of the United Kingdom* 50: 1001–1044. https://doi.org/10.1017/S0025315400005920.

Badcock, J., and N. R. Merrett. 1976. "Midwater Fishes in the Eastern North Atlantic. I. Vertical Distribution and Associated Biology in 30°N, 23°W, With Developmental Notes on Certain Myctophids." *Progress in Oceanography* 7, no. 1: 3–58. https://doi.org/10.1016/0079-6611(76)90003-3.

Baird, R. C., T. L. Hopkins, and D. F. Wilson. 1975. "Diet and Feeding Chronology of *Diaphus taaningi* (Myctophidae) in the Cariaco Trench." *Copeia* 1975, no. 2: 356–365. https://doi.org/10.2307/1442891.

Baird, R. C., G. Y. Jumper, and E. E. Gallaher. 1990. “Sexual Dimorphism and Demography in 2 Species of Oceanic Midwater Fishes (Stomiiformes, Sternoptychidae) From the Eastern Gulf of Mexico.” *Bulletin of Marine Science* 47, no. 2: 561–566.

Battaglia, P., G. Ammendolia, V. Esposito, T. Romeo, and F. Andaloro. 2018. “Few but Relatively Large Prey: Trophic Ecology of *Chauliodus sloani* (Pisces: Stomiidae) in Deep Waters of the Central Mediterranean Sea.” *Journal of Ichthyology* 58, no. 1: 8–16. https://doi.org/10.1134/S0032945218010034.

Belcher, A., K. Cook, D. Bondyale-Juez, et al. 2020. “Respiration of Mesopelagic Fish: A Comparison of Respiratory Electron Transport System (Ets) Measurements and Allometrically Calculated Rates in the Southern Ocean and Benguela Current.” *ICES Journal of Marine Science* 77, no. 5: 1672–1684. https://doi.org/10.1093/icesjms/fsaa031.

Belcher, A., R. A. Saunders, and G. A. Tarling. 2019. “Respiration Rates and Active Carbon Flux of Mesopelagic Fishes (Family Myctophidae) in the Scotia Sea, Southern Ocean.” *Marine Ecology Progress Series* 610: 149–162. https://doi.org/10.3354/meps12861.

Benoit-Bird, K. J., M. A. Moline, and B. L. Southall. 2017. “Prey in Oceanic Sound Scattering Layers Organize to Get a Little Help From Their Friends.” *Limnology and Oceanography* 62: 2788–2798. https://doi.org/10.1002/lno.10606.

Bertelsen, E. 1951. “The Ceratioid Fishes. Ontogeny, Taxonomy, Distribution, and Biology.” *Dana Report* 39: 1–276.

Beukhof, E., T. S. Dencker, M. L. D. Palomares, and A. Maureaud. 2019. “A Trait Collection of Marine Fish Species From North Atlantic and Northeast Pacific Continental Shelf Seas.” PANGAEA. https://doi.org/10.1594/PANGAEA.900866.

Beukhof, E., R. Frelat, L. Pecuchet, et al. 2019. “Marine Fish Traits Follow Fast-Slow Continuum Across Oceans.” *Scientific Reports* 9: 17878. https://doi.org/10.1038/s41598-019-53998-2.

Bianchi, D., E. D. Galbraith, D. A. Carozza, K. A. S. Mislan, and C. A. Stock. 2013. “Intensification of Open-Ocean Oxygen Depletion by Vertically Migrating Animals.” *Nature Geoscience* 6, no. 7: 545–548. https://doi.org/10.1038/ngeo1837.

Bianchi, D., and K. A. S. Mislan. 2016. “Global Patterns of Diel Vertical Migration Times and Velocities From Acoustic Data.” *Limnology and Oceanography* 61, no. 1: 353–364. https://doi.org/10.1002/lno.10219.

Bleckmann, H., and R. Zelick. 2009. “Lateral Line System of Fish.” *Integrative Zoology* 4: 13–25. https://doi.org/10.1111/j.1749-4877.2008.00131.x.

Bode, A., M. P. Olivar, and S. Henández-León. 2021. “Trophic Indices for Micronektonic Fish Reveal Their Dependence on the Microbial System in the North Atlantic.” *Scientific Reports* 11: 8488. https://doi.org/10.1038/s41598-021-87767-x.

Boersch-Supan, P. H., A. D. Rogers, and A. S. Brierley. 2017. “The Distribution of Pelagic Sound Scattering Layers Across the Southwest Indian Ocean.” *Deep Sea Research Part II: Topical Studies in Oceanography* 136: 108–121. https://doi.org/10.1016/j.dsr2.2015.06.023.

Boswell, K. M., M. D'Elia, M. W. Johnston, et al. 2020. “Oceanographic Structure and Light Levels Drive Patterns of Sound Scattering Layers in a Low-Latitude Oceanic System.” *Frontiers in Marine Science* 7: 51. https://doi.org/10.3389/fmars.2020.00051.

Bozzano, A., M. P. Pankhurst, and A. Sabatés. 2007. “Early Development of Eye and Retina in Lanternfish Larvae.” *Visual Neuroscience* 24: 423–436. https://doi.org/10.1017/s0952523807070484.

Buckland-Nicks, J. A., M. Gillis, and T. E. Reimchen. 2012. “Neural Network Detected in a Presumed Vestigial Trait: Ultrastructure of the Salmonid Adipose Fin.” *Proceedings of the Royal Society B: Biological Sciences* 279: 553–563. https://doi.org/10.1098/rspb.2011.1009.

Butt, N., B. S. Halpern, C. C. O'Hara, et al. 2022. “A Trait-Based Framework for Assessing the Vulnerability of Marine Species to Human Impacts.” *Ecosphere* 13, no. 2: e3919. https://doi.org/10.1002/ecs2.3919.

Caiger, P. E., L. S. Lefebve, and J. K. Llopiz. 2021. “Growth and Reproduction in Mesopelagic Fishes: A Literature Synthesis.” *ICES Journal of Marine Science* 78, no. 3: 765–781. https://doi.org/10.1093/icesjms/fsaa247.

Cardinale, B. J., J. E. Duffy, A. Gonzalez, et al. 2012. “Biodiversity Loss and Its Impact on Humanity.” *Nature* 486, no. 7401: 59–67. https://doi.org/10.1038/nature11148.

Catul, V., M. Gauns, and P. K. Karuppasamy. 2011. “A Review on Mesopelagic Fishes Belonging Tofamily Myctophidae.” *Reviews in Fish Biology and Fisheries* 21: 339–354. https://doi.org/10.1007/s11160-010-9176-4.

Charnov, E. L., H. Gislason, and J. G. Pope. 2013. “Evolutionary Assembly Rules for Fish Life Histories.” *Fish and Fisheries* 14: 213–224. https://doi.org/10.1111/j.1467-2979.2012.00467.x.

Cherel, Y., C. Fontaine, P. Richard, and J. P. Labat. 2010. “Isotopic Niches and Trophic Levels of Myctophid Fishes and Their Predators in the Southern Ocean.” *Limnology and Oceanography* 55, no. 1: 324–332. https://doi.org/10.4319/lo.2010.55.1.0324.

Cherel, Y., E. V. Romanov, P. Annasawmy, D. Thibault, and F. Ménard. 2020. “Micronektonic Fish Species Over Three Seamounts in the Southwestern Indian Ocean.” *Deep-Sea Research Part II: Topical Studies in Oceanography* 176: 104777. https://doi.org/10.1016/j.dsr2.2020.104777.

Chevallay, M., C. Guinet, P. Goulet, and T. J. du Dot. 2024. “Hunting Tactics of Southern Elephant Seals *Mirounga leonina* and Anti-Predatory Behaviours of Their Prey.” *Marine Ecology Progress Series* 736: 167–179. https://doi.org/10.3354/meps14582.

Childress, J. J. 1975. “The Respiratory Rates of Midwater Crustaceans as a Function of Depth Occurrence and Relation to the Oxygen Minimum Layer Off Southern California.” *Comparative Biochemistry and Physiology Part A: Physiology* 50, no. 4: 787–799. https://doi.org/10.1016/0300-9629(75)90146-2.

Childress, J. J., and M. H. Nygaard. 1973. “Chemical Composition of Midwater Fishes as a Function of Depth of Occurrence Off Southern California.” *Deep-Sea Research* 20, no. 12: 1093–1109. https://doi.org/10.1016/0011-7471(73)90023-5.

Childress, J. J., and B. A. Seibel. 1998. “Life at Stable Low Oxygen Levels: Adaptations of Animals to Oceanic Oxygen Minimum Layers.” *Journal of Experimental Biology* 201: 1223–1232. https://doi.org/10.1242/jeb.201.8.1223.

Childress, J. J., and G. N. Somero. 1979. “Depth-Related Enzymic Activities in Muscle, Brain and Heart of Deep-Living Pelagic Marine Teleosts.” *Marine Biology* 52, no. 3: 273–283. https://doi.org/10.1007/bf00398141.

Childress, J. J., S. M. Taylor, G. M. Cailliet, and M. H. Price. 1980. “Patterns of Growth, Energy Utilization and Reproduction in Some Meso- and Bathypelagic Fishes Off Southern California.” *Marine Biology* 61, no. 1: 27–40. https://doi.org/10.1007/BF00410339.

Chouvelon, T., C. Munschy, S. Bruzac, et al. 2022. “High Inter-Species Variability in Elemental Composition of the Twilight Zone Fauna Varies Implications for Predators and Exploitation by Humans.” *Environmental Research* 204: 112379. https://doi.org/10.1016/j.envres.2021.112379.

Christiansen, S., T. A. Klevjer, A. Røstad, D. L. Aksnes, and S. Kaartvedt. 2021. “Flexible Behaviour in a Mesopelagic Fish (*Maurolicus muelleri*).” *ICES Journal of Marine Science* 78, no. 5: 1623–1635. https://doi.org/10.1093/icesjms/fsab075.

Clarke, T. A. 1980. “Diets of Fourteen Species of Vertically Migrating Mesopelagic Fishes in Hawaiian Waters.” *Fishery Bulletin* 78: 619–640.

Clarke, T. A. 1983. “Sex Ratios and Sexual Differences in Size Among Mesopelagic Fishes From the Central Pacific Ocean.” *Marine Biology* 73: 203–209. https://doi.org/10.1007/BF00406889.

Contreras, T., M. P. Olivar, P. A. Hulley, and M. L. Fernández de Puelles. 2019. “Feeding Ecology of Early Life Stages of Mesopelagic Fishes in the Equatorial and Tropical Atlantic.” *ICES Journal of Marine Science* 76, no. 3: 673–689. https://doi.org/10.1093/icesjms/fsy070.

Costello, M. J., and S. Breyer. 2017. “Ocean Depths: The Mesopelagic and Implications for Global Warming.” *Current Biology* 27, no. 1: R36–R38. https://doi.org/10.1016/j.cub.2016.11.042.

Davis, A. L., T. T. Sutton, W. M. Kier, and S. Johnsen. 2020. “Evidence That Eye-Facing Photophores Serve as a Reference for Counterillumination in an Order of Deep-Sea Fishes.” *Proceedings of the Royal Society B: Biological Sciences* 287, no. 1928: 20192918. https://doi.org/10.1098/rspb.2019.2918.

Davison, P. 2011. “The Specific Gravity of Mesopelagic Fish From the Northeastern Pacific Ocean and Its Implications for Acoustic Backscatter.” *ICES Journal of Marine Science* 68, no. 10: 2064–2074. https://doi.org/10.1093/icesjms/fsr140.

Davison, P. C., D. M. Checkley Jr., J. A. Koslow, and J. Barlow. 2013. “Carbon Export Mediated by Mesopelagic Fishes in the Northeast Pacific Ocean.” *Progress in Oceanography* 116: 14–30. https://doi.org/10.1016/j.pocean.2013.05.013.

Dawson, S. K., C. P. Carmona, M. González-Suárez, et al. 2021. “The Traits of “trait ecologists”: An Analysis of the Use of Trait and Functional Trait Terminology.” *Ecology and Evolution* 11: 16434–16445. https://doi.org/10.1002/ece3.8321.

de Busserolles, F., F. Cortesi, J. V. Helvik, et al. 2017. “Pushing the Limits of Photoreception in Twilight Conditions: The Rod-Like Cone Retina of the Deep-Sea Pearlsides. *Science*.” *Advances* 3, no. 11: eaao4709. https://doi.org/10.1126/sciadv.aao4709.

de Juan, S. D., J. Bremner, J. Hewitt, et al. 2022. “Biological Traits Approaches in Benthic Marine Ecology: Dead Ends and New Paths.” *Ecology and Evolution* 12: e9001. https://doi.org/10.1002/ece3.9001.

Deng, X., H.-J. Wagner, and A. N. Popper. 2013. “Interspecific Variations of Inner Ear Structure in the Deep-Sea Fish Family Melamphaidae.” *Anatomical Record* 296: 1064–1082. https://doi.org/10.1002/ar.22703.

Denton, E. J., and J. A. B. Gray. 1989. “Some Observations on the Forces Acting on the Neuromasts in Fish Lateral Line Canals.” In *The Mechanosensory Lateral Line: Neurobiology and Evolution*, edited by S. Coombs, P. Görner, and H. Münz, 229–246. New York: Springer.

Denton, E. J., P. J. Herring, E. A. Widder, M. F. Latz, and J. F. Case. 1985. “The Roles of Filters in the Photophores of Oceanic Animals and Their Relation to Vision in the Oceanic Environment.” *Proceedings of the Royal Society of London. Series B. Biological Sciences* 225, no. 1238: 63–97. https://doi.org/10.1098/rspb.1985.0051.

Díaz, S., A. Purvis, J. H. C. Cornelissen, et al. 2013. “Functional Traits, the Phylogeny of Function, and Ecosystem Service Vulnerability.” *Ecology and Evolution* 3, no. 9: 2958–2975. https://doi.org/10.1002/ece3.601.

Dove, S., M. Tiedemann, and H. O. Fock. 2021. “Latitudinal Transition of Mesopelagic Larval Fish Assemblages in the Eastern Central Atlantic.” *Deep Sea Research Part I: Oceanographic Research Papers* 168: 103446. https://doi.org/10.1016/j.dsr.2020.103446.

Drazen, J. C., C. R. Smith, K. M. Gjerde, et al. 2020. “Midwater Ecosystems Must Be Considered When Evaluating Environmental Risks of Deep-Sea Mining.” *Proceedings of the National Academy of Sciences* 117, no. 30: 17455–17460. https://doi.org/10.1073/pnas.2011914117.

Drazen, J. C., and T. T. Sutton. 2017. “Dining in the Deep: The Feeding Ecology of Deep-Sea Fishes.” *Annual Review of Marine Science* 9: 337–366. https://doi.org/10.1146/annurev-marine-010816-060543.

Duchatelet, L., R. Marion, and J. Mallefet. 2021. “A Third Luminous Shark Family: Confirmation of Luminescence Ability for *Zameus squamulosus* (Squaliformes; Somniosidae).” *Photochemistry and Photobiology* 97, no. 4: 739–744. https://doi.org/10.1111/php.13393.

Duffy, J. E., J. S. Lefcheck, R. D. Stuart-Smith, S. A. Navarrete, and G. J. Edgar. 2016. “Biodiversity Enhances Reef Fish Biomass and Resistance to Climate Change.” *Proceedings of the National Academy of Sciences of the United States of America* 113, no. 22: 6230–6235. https://doi.org/10.1073/pnas.1524465113.

Duncan, S. E., W. Hagen, and H. O. Fock. 2024. “Mesopelagic Fish Assemblages in the Mauritanian Upwelling System Off Northwest Africa With Oxygen as a Major Driving Force.” *Marine Ecology Progress Series* 733: 95–110. https://doi.org/10.3354/meps14524.

Duncan, S. E., A. F. Sell, W. Hagen, and H. O. Fock. 2022. “Environmental Drivers of Upper Mesopelagic Fish Assemblages in the Benguela Upwelling Systems During Austral Summer.” *Marine Ecology Progress Series* 688: 133–152. https://doi.org/10.3354/meps14017.

Duvall, G. E., and R. J. Christensen. 1946. “Stratification of Sound Scatterers in the Ocean.” *Journal of the Acoustical Society of America* 18: 254. https://doi.org/10.1121/1.1902470.

Dypvik, E., T. A. Klevjer, and S. Kaartvedt. 2012. “Inverse Vertical Migration and Feeding in Glacier Lanternfish (*Benthosema glaciale*).” *Marine Biology* 159: 443–453. https://doi.org/10.1007/s00227-011-1822-4.

Eduardo, L. N., A. Bertrand, M. Mincarone, et al. 2021. “Distribution, Vertical Migration, and Trophic Ecology of Lanternfishes (Myctophidae) in the Southwestern Tropical Atlantic.” *Progress in Oceanography* 199: 102695. https://doi.org/10.1016/j.pocean.2021.102695.

Eduardo, L. N., A. Bertrand, M. M. Mincarone, et al. 2020. “Hatchetfishes (Stomiiformes: Sternoptychidae) Biodiversity, Trophic Ecology, Vertical Niche Partitioning and Functional Roles in the Western Tropical Atlantic.” *Progress in Oceanography* 187: 102389. https://doi.org/10.1016/j.pocean.2020.102389.

Eduardo, L. N., F. Lucena-Frédou, S. L. Bertrand, et al. 2023. “From the Light Blue Sky to the Dark Deep Sea: Trophic and Resource Partitioning Between Epipelagic and Mesopelagic Layers in a Tropical Oceanic Ecosystem.” *Science of the Total Environment* 878: 163098. https://doi.org/10.1016/J.SCITOTENV.2023.163098.

Eduardo, L. N., F. Lucena-Frédou, M. M. Mincarone, et al. 2020. “Trophic Ecology, Habitat, and Migratory Behaviour of the Viperfish *Chauliodus sloani* Reveal a Key Mesopelagic Player.” *Scientific Reports* 10, no. 1: 20996. https://doi.org/10.1038/s41598-020-77222-8.

Eduardo, L. N., M. Mincarone, T. Sutton, and A. Bertrand. 2024. “Deep-Pelagic Fishes Are Anything but Similar: A Global Synthesis.” *Ecology Letters* 27, no. 9: e14510. https://doi.org/10.1111/ele.14510.

Ferreira, G. V. B., A. K. S. Justino, L. N. Eduardo, et al. 2023. “Influencing Factors for Microplastic Intake in Abundant Deep-Sea Lanternfishes (Myctophidae).” *Science of the Total Environment* 867: 161478. https://doi.org/10.1016/j.scitotenv.2023.161478.

Flynn, A. J., and J. R. Paxton. 2012. “Spawning Aggregation of the Lanternfish *Diaphus danae* (Family Myctophidae) in the North-Western Coral Sea and Associations With Tuna Aggregations.” *Marine and Freshwater Research* 63: 1255–1271. https://doi.org/10.1071/MF12185.

Fock, H. O., B. Matthiessen, H. Zidowitz, and H. V. Westernhagen. 2002. “Diel and Habitat-Dependent Resource Utilisation by Deep-Sea Fishes at the Great Meteor Seamount: Niche Overlap and Support for the Sound Scattering Layer Interception Hypothesis.” *Marine Ecology Progress Series* 244: 219–233. https://www.jstor.org/stable/24866377.

Fock, H. O., C. Pusch, and S. Ehrich. 2004. “Structure of Deep-Sea Pelagic Fish Assemblages in Relation to the Mid-Atlantic Ridge (45°N to 50°N).” *Deep-Sea Research Part I: Oceanographic Research Papers* 51: 953–978. https://doi.org/10.1016/j.dsr.2004.03.004.

Folkvord, A., G. Gundersen, J. Albretsen, L. Asplin, S. Kaartvedt, and J. Giske. 2016. "Impact of Hatch Date on Early Life Growth and Survival of Mueller's Pearlside (*Maurolicus muelleri*) Larvae and Life-History Consequences." *Canadian Journal of Fisheries and Aquatic Sciences* 73, no. 2: 163–176. https://doi.org/10.1139/cjfas-2015-0040.

Froese, R., and D. Pauly, eds. 2000. *FishBase 2000: Concepts, Design and Data Sources*, 344. Los Baños, Laguna, Philippines: ICLARM.

Fuiman, L. A. 1983. "Growth Gradients in Fish Larvae." *Journal of Fish Biology* 23: 117–123. https://doi.org/10.1111/j.1095-8649.1983.tb02886.x.

Fuiman, L. A., and A. E. Magurran. 1994. "Development of Predator Defences in Fishes." *Reviews in Fish Biology and Fisheries* 4: 145–183. https://doi.org/10.1007/BF00044127.

García-Seoane, E., M. Fabeiro, A. Silva, and I. Meneses. 2015. "Age-Based Demography of the Glacier Lanternfish (*Benthosema glaciale*) in the Flemish Cap." *Marine and Freshwater Research* 66: 78–85. https://doi.org/10.1071/MF13229.

Gartner, J. V. 1991. "Life Histories of Three Species of Lanternfishes (Pisces: Myctophidae) From the Eastern Gulf of Mexico. II. Age and Growth Patterns." *Marine Biology* 111: 21–27. https://doi.org/10.1007/BF01986339.

Gartner, J. V., T. L. Hopkins, R. C. Baird, and D. M. Milliken. 1987. "The Lanternfishes (Pisces: Myctophidae) of the Eastern Gulf of Mexico." *Fishery Bulletin* 85: 81–98.

Gartner, J. V., K. J. Sulak, S. Ross, and A. M. Necaise. 2008. "Persistent Near-Bottom Aggregations of Mesopelagic Animals Along the North Carolina and Virginia Continental Slopes." *Marine Biology* 153: 825–841. https://doi.org/10.1007/s00227-007-0855-1.

Gauthier, S., J. Oeffner, and R. L. O'Driscoll. 2014. "Species Composition and Acoustic Signatures of Mesopelagic Organisms in a Subtropical Convergence Zone, the New Zealand Chatham Rise." *Marine Ecology Progress Series* 503: 23–40. https://doi.org/10.3354/meps10731.

Giménez, J., A. Marçalo, M. García-Polo, et al. 2018. "Feeding Ecology of Mediterranean Common Dolphins: The Importance of Mesopelagic Fish in the Diet of an Endangered Subpopulation." *Marine Mammal Science* 34, no. 1: 136–154. https://doi.org/10.1111/mms.12442.

Gjerde, K. M., G. Wright, and C. Durussel. 2021. "Strengthening High Seas Governance Through Enhanced Environmental Assessment Processes: A Case Study of Mesopelagic Fisheries and Options for a Future BBNJ Treaty." STRONG High Seas Project, 1–56.

Gjøsæter, H. 1987. "Primary Growth Increments in Otoliths of Six Tropical Myctophid Species." *Biological Oceanography* 4: 359–382.

Gjøsæter, J. 1981. "Growth, Production and Reproduction of the Myctophid Fish *Benthosema glaciale* From Western Norway and Adjacent Seas." *Fiskeridirektoratets Skrifter, Serie Havundersøkelser* 17: 78–108.

Gjøsaeter, J., and K. Kawaguchi. 1980. "A Review of the World Resources of Mesopelagic Fish." FAO Fisheries Technical Paper. No. 193. FIRM/TI93. 151.

Gjøsæter, J., and S. Tilseth. 1988. "Spawning Behaviour, Egg and Larval Development of the Myctophid Fish *Benthosema pterotum*." *Biology* 98: 1–6. https://doi.org/10.1007/BF00392652.

Gloeckler, K., C. A. Choy, C. C. S. Hannides, 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." *Limnology and Oceanography* 63, no. 3: 1168–1180. https://doi.org/10.1002/lno.10762.

Godø, O. R., R. Patel, and G. Pedersen. 2009. "Diel Migration and Swimbladder Resonance of Small Fish: Some Implications for Analyses of Multifrequency Echo Data." *ICES Journal of Marine Science* 66, no. 6: 1143–1148. https://doi.org/10.1093/icesjms/fsp098.

Goodson, M. S., J. Giske, and R. Rosland. 1995. "Growth and Ovarian Development of *Maurolicus muelleri* During Spring." *Marine Biology* 124, no. 2: 185–195. https://doi.org/10.1007/BF00347122.

Goodyear, R. H., B. J. Zahuranec, W. L. Pugh, and R. H. Gibbs. 1972. "Ecology and Vertical Distribution of Mediterranean Midwater Fishes." *Mediterranean Biological Studies. Final Report* 1, no. 3: 91–229.

Grimaldo, E., L. Grimsmo, P. Alvarez, et al. 2020. "Investigating the Potential for a Commercial Fishery in the Northeast Atlantic Utilizing Mesopelagic Species." *ICES Journal of Marine Science* 77, no. 7–8: 2541–2556. https://doi.org/10.1093/icesjms/fsaa114.

Groeneveld, R. A., A. Richter, and S. Sen. 2024. "Climate Damage From Fishing the Mesopelagic Zone Exceeds Its Economic Benefits." *ICES Journal of Marine Science* 81: 1620–1631. https://doi.org/10.1093/icesjms/fsae108.

Gutiérrez-Cánovas, C., R. Stubbington, D. von Schiller, et al. 2024. "Use of Trait Concepts and Terminology in Freshwater Ecology: Historic, Current, and Future Perspectives." *Freshwater Biology* 69: 477–495. https://doi.org/10.1111/fwb.14230.

Haddock, S. H. D., and A. Choy. 2024. "Life in the Midwater: The Ecology of Deep Pelagic Animals." *Annual Review of Marine Science* 16: 383–416. https://doi.org/10.1146/annurev-marine-031623-095435.

Haddock, S. H. D., M. A. Moline, and J. F. Case. 2010. "Bioluminescence in the Sea." *Annual Review of Marine Science* 2, no. 1: 443–493. https://doi.org/10.1146/annurev-marine-120308-081028.

Hays, G. C. 2003. "A Review of the Adaptive Significance and Ecosystem Consequences of Zooplankton Diel Vertical Migrations." *Hydrobiologia* 503: 163–170. https://doi.org/10.1023/B:HYDR.0000008476.23617.b0.

Helfman, G. S., B. B. Collette, D. E. Facey, and B. W. Bowen. 2009. *The Diversity of Fishes, Biology Evolution and Ecology*. 2nd ed. Oxford: Wiley-Blackwell.

Hernández-León, S., M. P. Olivar, M. L. Fernández de Puelles, et al. 2019. "Zooplankton and Micronekton Active Flux Across the Tropical and Subtropical Atlantic Ocean." *Frontiers in Marine Science* 6: 535. https://doi.org/10.3389/fmars.2019.00535.

Herring, P. J. 2000. "Species Abundance, Sexual Encounter and Bioluminescent Signalling in the Deep Sea." *Philosophical Transactions of the Royal Society B: Biological Sciences* 355, no. 1401: 1273–1276. https://doi.org/10.1098/rstb.2000.0682.

Herring, P. J. 2002. *The Biology of the Deep Ocean*. Oxford: Oxford University Press.

Herring, P. J. 2007. "REVIEW. Sex With the Lights on? A Review of Bioluminescent Sexual Dimorphism in the Sea." *Journal of the Marine Biological Association of the United Kingdom* 87: 829–842. https://doi.org/10.1017/S0025315407056433.

Herring, P. J., and C. Cope. 2005. "Red Bioluminescence in Fishes: On the Suborbital Photophores of *Malacosteus, Pachystomias* and *Aristostomias*." *Marine Biology* 148: 383–394. https://doi.org/10.1007/s00227-005-0085-3.

Herring, P. J., and E. A. Widder. 2001. "Bioluminescence in Plankton and Nekton." In *Encyclopedia of Ocean Science*, edited by J. H. Steele, S. A. Thorpe, and K. K. Turekian, vol. 1, 308–317. San Diego: Academic Press.

Hidaka, K., K. Kawaguchi, M. Murakami, and M. Takahashi. 2001. "Downward Transport of Organic Carbon by Diel Migratory Micronekton in the Western Equatorial Pacific: Its Quantitative and Qualitative Importance." *Deep Sea Research Part I: Oceanographic Research Papers* 48: 1923–1939. https://doi.org/10.1016/S0967-0637(01)00003-6.

Hopkins, T. L., and J. V. Gartner. 1992. "Resource-Partitioning and Predation Impact of a Low-Latitude Myctophid Community." *Marine Biology* 114: 185–197. https://doi.org/10.1007/BF00349518.

Hopkins, T. L., and T. T. Sutton. 1998. "Midwater Fishes and Shrimps as Competitors and Resource Partitioning in Low Latitude Oligotrophic Ecosystems." *Marine Ecology Progress Series* 164: 37–45. https://doi.org/10.3354/meps164037.

Houde, E. D. 2002. "Mortality." In *Fishery Science. The Unique Contributions of Early Life Stages*, edited by L. A. Fuiman and R. G. Werner, 64–87. Oxford: Blackwell Publishing.

Hulley, P. A. 1981. "Results of the Research Cruise of FRV Walter Herwig to South America. Family Myctophidae (Osteichthyes, Myctophiformes)." *Archiv für Fischereiwissenschaft* 31, no. 1: 1–300.

Hulley, P. A., and R. M. Prosch. 1987. "Mesopelagic Fish Derivatives in the Southern Benguela Upwelling Region." *South African Journal of Marine Science* 5, no. 1: 597–611. https://doi.org/10.2989/025776187784522289.

Hulsey, C. D., and P. R. Hollingsworth Jr. 2011. "Do Constructional Constraints Influence Cyprinid (Cyprinidae: Leuciscinae) Craniofacial Coevolution?." *Biological Journal of the Linnean Society* 103, no. 1: 136–146. https://doi.org/10.1111/j.1095-8312.2011.01628.x.

Iglesias, I. S., J. A. Santora, J. Fiechter, and J. C. Field. 2023. "Mesopelagic Fishes Are Important Prey for a Diversity of Predators." *Frontiers of Marine Science* 10: 1220088. https://doi.org/10.3389/fmars.2023.1220088.

Irigoien, X., T. A. Klevjer, A. Røstad, et al. 2014. "Large Mesopelagic Fishes Biomass and Trophic Efficiency in the Open Ocean." *Nature Communications* 5, no. 1: 3271. https://doi.org/10.1038/ncomms4271.

Kaartvedt, S., T. Knutsen, and J. C. Holst. 1998. "Schooling of the Vertically Migrating Mesopelagic Fish *Maurolicus muelleri* in Light Summer Nights." *Marine Ecology Progress Series* 170: 287–290. https://doi.org/10.3354/meps170287.

Kaartvedt, S., T. J. Langbehn, and D. L. Aksnes. 2019. "Enlightening the ocean's Twilight Zone." *ICES Journal of Marine Science* 76, no. 4: 803–812. https://doi.org/10.1093/icesjms/fsz010.

Kaartvedt, S., T. Torgersen, T. A. Klevjer, A. Røstad, and J. A. Devine. 2008. "Behavior of Individual Mesopelagic Fish in Acoustic Scattering Layers of Norwegian Fjords." *Marine Ecological Progress Series* 360: 201–209. https://doi.org/10.3354/meps07364.

Karstensen, J., L. Stramma, and M. Visbeck. 2008. "Oxygen Minimum Zones in the Eastern Tropical Atlantic and Pacific Oceans." *Progress in Oceanography* 77: 331–350. https://doi.org/10.1016/j.pocean.2007.05.009.

Kawaguchi, K., and H. G. Moser. 1984. "Stomiatoidea: development." In *Ontogeny and systematics of fishes*, Special. Publication. 1. American Society of Ichthyologists and Herpetologists, edited by H. G. Moser et al., 169–180. Lawrence, KS: Allen Press.

Kenaley, C. P. 2008. "Diel Vertical Migration of the Loosejaw Dragonfishes (Stomiiformes: Stomiidae: Malacosteinae): A New Analysis for Rare Pelagic Taxa." *Journal of Fish Biology* 73: 888–901. https://doi.org/10.1111/j.1095-8649.2008.01983.x.

Kenaley, C. P. 2012. "Exploring Feeding Behaviour in Deep-Sea Dragonfishes (Teleostei: Stomiidae): Jaw Biomechanics and Functional Significance of a Loosejaw." *Biological Journal of the Linnean Society* 106, no. 1: 224–240. https://doi.org/10.1111/j.1095-8312.2012.01854.x.

King, J. R., and G. A. McFarlane. 2003. "Marine Fish Life History Strategies: Applications to Fishery Management." *Fisheries Management and Ecology* 10: 249–264. https://doi.org/10.1046/j.1365-2400.2003.00359.x.

Kiørboe, T. 2008. "Optimal Swimming Strategies in Mate-Searching Pelagic Copepods." *Oecologia* 155, no. 1: 179–192. https://doi.org/10.1007/s00442-007-0893-x.

Kiørboe, T., A. Visser, and K. H. Andersen. 2018. "A Trait-Based Approach to Ocean Ecology." *ICES Journal of Marine Science* 75, no. 6: 1849–1863. https://doi.org/10.1093/icesjms/fsy090.

Klevjer, T. A., X. Irigoien, A. Røstad, E. Fraile-Nuez, V. M. Benítez-Barrios, and S. Kaartvedt. 2016. "Large Scale Patterns in Vertical Distribution and Behaviour of Mesopelagic Scattering Layers." *Scientific Reports* 6, no. 1: 19873. https://doi.org/10.1038/srep19873.

Knorrn, A. H., K. L. Wieben, H. O. Fock, and H. Andresen. 2024. "Reproductive Biology of the Electric Lanternfish *Electrona risso* (Myctophidae) and the Bigscale Fishes *Melamphaes polylepis* and *Scopelogadus mizolepis* (Melamphaidae)." *Journal of Fish Biology* 104, no. 1: 252–264. https://doi.org/10.1111/jfb.15575.

Koslow, J. A. 1996. "Energetic and Life-History Patterns of Deep-Sea Benthic, Benthopelagic and Seamount-Associated Fish." *Journal of Fish Biology* 49, no. sA: 54–74. https://doi.org/10.1111/j.1095-8649.1996.tb06067.x.

Koslow, J. A., P. Davison, A. Lara-López, and M. D. Ohman. 2014. "Epipelagic and Mesopelagic Fishes in the Southern California Current System: Ecological Interactions and Oceanographic Influences on Their Abundance." *Journal of Marine Systems* 138: 20–28. https://doi.org/10.1016/j.jmarsys.2013.09.007.

Koslow, J. A., R. Goericke, A. Lara-López, and W. Watson. 2011. "Impact of Declining Intermediate Water-Oxygen on Deepwater Fishes in the California Current." *Marine Ecological Progress Series* 436: 207–218. https://doi.org/10.3354/meps09270.

Kourantidou, M., and D. Jin. 2022. "Mesopelagic–Epipelagic Fish Nexus in Viability and Feasibility of Commercial-Scale Mesopelagic Fisheries." *Natural Resource Modeling* 35: e12350. https://doi.org/10.1111/nrm.12350.

Krefft, G. 1974. "Investigations on Midwater Fish in Atlantic Ocean." *Berichte Der Deutschen Wissenschaftlichen Kommission Für Meeresforschung* 23, no. 3: 226–254.

Kristoffersen, J. B., and A. G. V. Salvanes. 1998. "Life History of *Maurolicus muelleri* in Fjordic and Oceanic Environments." *Journal of Fish Biology* 53: 1324–1341. https://doi.org/10.1111/j.1095-8649.1998.tb00252.x.

Land, M. F., and D. C. Osorio. 2011. "Marine Optics: Dark Disguise." *Current Biology* 21, no. 22: R918–R920. https://doi.org/10.1016/j.cub.2011.10.009.

Langbehn, T. J., D. L. Aksnes, S. Kaartvedt, Ø. Fiksen, and C. Jørgensen. 2019. "Light Comfort Zone in a Mesopelagic Fish Emerges From Adaptive Behaviour Along a Latitudinal Gradient." *Marine Ecology Progress Series* 623: 161–174. https://doi.org/10.3354/meps13024.

Langbehn, T. J., D. L. Aksnes, S. Kaartvedt, Ø. Fiksen, G. Ljungström, and C. Jørgensen. 2022. "Poleward Distribution of Mesopelagic Fishes Is Constrained by Seasonality in Light." *Global Ecology and Biogeography* 31: 546–561. https://doi.org/10.1111/geb.13446.

Li, G., L. Cheng, J. Zhu, K. E. Trenberth, M. E. Mann, and J. P. Abraham. 2020. "Increasing Ocean Stratification Over the Past Half-Century." *Nature Climate Change* 10, no. 12: 1116–1123. https://doi.org/10.1038/s41558-020-00918-2.

Linkowsky, T. B., R. L. Radtke, and P. H. Lenz. 1993. "Otolith Microstructure, Age and Growth of Two Species of *Ceratoscopelus* (Osteichthyes: Myctophidae) From the Eastern North Atlantic." *Journal of Experimental Marine Biology and Ecology* 167: 237–260. https://doi.org/10.1016/0022-0981(93)90033-K.

Litchman, E., and C. A. Klausmeier. 2008. "Trait-Based Community Ecology of Phytoplankton." *Annual Review of Ecology, Evolution, and Systematics* 39, no. 1: 615–639. https://doi.org/10.1146/annurev.ecolsys.39.110707.173549.

Litchman, E., M. D. Ohman, and T. Kiørboe. 2013. "Trait-Based Approaches to Zooplankton Communities." *Journal of Plankton Research* 35, no. 3: 473–484. https://doi.org/10.1093/plankt/fbt019.

Locket, N. A. 1977. "Adaptations to the Deep-Sea Environment." In *Handbook of Sensory Physiology*, edited by F. Crescitelli, vol. VII/5, 67–192. Berlin, Heidelberg, New York: Springer.

Long, A. M., S. K. Jurgensen, A. R. Petchel, E. R. Savoie, and J. R. Brum. 2021. "Microbial Ecology of Oxygen Minimum Zones Amidst Ocean Deoxygenation." *Frontiers in Microbiology* 12: 748961. https://doi.org/10.3389/fmicb.2021.748961.

Lopes, A. R., K. Trubenbach, T. Teixeira, et al. 2013. "Oxidative Stress in Deep Scattering Layers: Heat Shock Response and Antioxidant Enzymes Activities of Myctophid Fishes Thriving in Oxygen Minimum Zones." *Deep-Sea Research Part I: Oceanographic Research Papers* 82: 10–16. https://doi.org/10.1016/j.dsr.2013.07.014.

Loutrage, L., A. Brind'Amour, T. Chouvelon, and J. Spitz. 2024a. "High Trophic Specialization Structures the Epi- To Bathypelagic Fish Community in the Bay of Biscay." *Deep-Sea Research Part I: Oceanographic Research Papers* 209: 104347. https://doi.org/10.1016/j.dsr.2024.104347.

Loutrage, L., A. Brind'Amour, T. Chouvelon, and J. Spitz. 2024b. "Ontogenetic Shift or Not? Different Foraging Trade-Offs Within the Meso- To Bathypelagic Fish Community." *Ecology and Evolution* 14: e11129. https://doi.org/10.1002/ece3.11129.

Loutrage, L., J. Spitz, S. P. Iglésias, and A. Brind'Amour. 2023. "The Nocturnal Distribution of Deep-Pelagic Fish on the Continental Slope of the Bay of Biscay." *Progress in Oceanography* 216: 103070. https://doi.org/10.1016/j.pocean.2023.103070.

Lowerre-Barbieri, S. K., K. Ganias, F. Saborido-Rey, H. Murua, and J. R. Hunter. 2011. "Reproductive Timing in Marine Fishes: Variability, Temporal Scales, and Methods." *Marine and Coastal Fisheries* 3: 71–91. https://doi.org/10.1080/19425120.2011.556932.

Luiz, O. J., J. D. Olden, M. J. Kennard, et al. 2019. "Trait-Based Ecology of Fishes: A Quantitative Assessment of Literature Trends and Knowledge Gaps Using Topic Modelling." *Fish and Fisheries* 20: 1100–1110. https://doi.org/10.1111/faf.12399.

Marchal, E., and A. Lebourges. 1996. "Acoustic Evidence for Unusual Diel Behaviour of a Mesopelagic Fish (*Vinciguerria nimbaria*) Exploited by Tuna." *ICES Journal of Marine Science* 53, no. 2: 443–447. https://doi.org/10.1006/jmsc.1996.0062.

Marranzino, A. N., and J. F. Webb. 2018. "Flow Sensing in the Deep Sea: The Lateral Line System of Stomiiform Fishes." *Zoological Journal of the Linnean Society* 183, no. 4: 945–965. https://doi.org/10.1093/zoolinnean/zlx090.

Marshall, N. B. 1954. *Aspects of Deep-Sea Biology*, 380. London: Hutchinson's Scientific and Technical Publications.

Marshall, N. B. 1967. "Olfactory Organs of Bathypelagic Fishes." *Symposia of the Zoological Society of London* 19: 57–70.

Marshall, N. B. 1971. *Explorations in the Life of Fishes*, 204. Harvard: Harvard University Press.

Marshall, N. B. 1980. *Deep-Sea Biology. Developments and Perspectives*, 566. New York: Garland STPM Press.

Marshall, N. J. 1996. "Vision and Sensory Physiology - The Lateral Line Systems of Three Deep-Sea Fish." *Journal of Fish Biology* 49: 239–258. https://doi.org/10.1111/j.1095-8649.1996.tb06079.x.

Martin, R. P., and M. P. Davis. 2020. "The Evolution of Specialized Dentition in the Deep-Sea Lanternfishes (Myctophiformes)." *Journal of Morphology* 281, no. 4–5: 536–555. https://doi.org/10.1002/jmor.21120.

Martin, R. P., M. P. Davis, and W. L. Smith. 2022. "The Impact of Evolutionary Trade-Offs Among Bioluminescent Organs and Body Shape in the Deep Sea: A Case Study on Lanternfishes." *Deep Sea Research Part I: Oceanographic Research Papers* 184: 103769. https://doi.org/10.1016/j.dsr.2022.103769.

Martin, R. P., and W. L. Smith. 2024. "First Evidence of Sexual Dimorphism in Olfactory Organs of Deep-Sea Lanternfishes (Myctophidae)." *PeerJ* 12: e17075. https://doi.org/10.7717/peerj.17075.

Martini, S., F. Larras, A. Boye, et al. 2021. "Functional Trait-Based Approaches as a Common Framework for Aquatic Ecologists." *Limnology and Oceanography* 66, no. 3: 965–994. https://doi.org/10.1002/lno.11655.

Maureaud, A., D. Hodapp, P. D. van Denderen, et al. 2019. "Biodiversity-Ecosystem Functioning Relationships in Fish Communities: Biomass Is Related to Evenness and the Environment, Not to Species Richness." *Proceedings of the Royal Society B: Biological Sciences* 286, no. 1906: 20191189. https://doi.org/10.1098/rspb.2019.1189.

McMonagle, H., J. K. Llopiz, R. Hilborn, and T. E. Essington. 2023. "High Uncertainty in Fish Bioenergetics Impedes Precision of Fish-Mediated Carbon Transport Estimates Into the ocean's Twilight Zone." *Progress in Oceanography* 217: 103078. https://doi.org/10.1016/j.pocean.2023.103078.

Ménard, F., and E. Marchal. 2003. "Foraging Behaviour of Tuna Feeding on Small Schooling *Vinciguerria nimbaria* in the Surface Layer of the Equatorial Atlantic Ocean." *Aquatic Living Resources* 16, no. 3: 231–238. https://doi.org/10.1016/S0990-7440(03)00040-8.

Miya, M., and T. Nemoto. 1991. "Comparative Life Histories of the Mesopelagic and Bathypelagic Fishes of the Genus *Cyclothone* (Pisces, Gonostomatidae) in Sagami Bay, Central Japan." *Deep Sea Research A: Oceanographic Research Papers* 38: 67–89. https://doi.org/10.1016/0198-0149(91)90055-k.

Morales-Nin, B., and J. Panfili. 2005. "Seasonality in the Deep Sea and Tropics Revisited: What Can Otoliths Tell Us?." *Marine and Freshwater Research* 56: 585–598. https://doi.org/10.1071/MF04150.

Moser, H. G., and E. H. Ahlstrom. 1970. "Development of Lanternfishes (Family Myctophidae) in the California Current. Part I. Species With Narrow-Eyed Larvae." *Bulletin of the Natural History Museum of Los Angeles County, Contributions in Science* 7: 1–145.

Moser, H. G., and E. H. Ahlstrom. 1996. "Myctophidae: Lanternfishes." In *The Early Stages of Fishes in the California Current Region*. CalCOFI Atlas No. 33, edited by H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall Jr., and S. L. Richardson, 387–475. Lawrence, KS: Allen Press.

Moser, H. G., E. H. Ahlstrom, and J. R. Paxton. 1984. "Myctophidae: Development." In *Ontogeny and Systematics of Fishes*, edited by H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall Jr., and S. L. Richardson, 218–239. New York: American Society of Ichthyologists and Herpetologists, Special Publication Number 1.

Munk, O. 1980. "Retinal Tapetum of the Deep-Sea Teleost *Diretmus argenteus*." *Videnskabelige Meddelelser Dansk Naturhistorisk Forening* 142: 179–186.

Musilova, Z., F. Cortesi, M. Matschiner, et al. 2019. "Vision Using Multiple Distinct Rod Opsins in Deep-Sea Fishes." *Science* 364: 588–592. https://doi.org/10.1126/science.aav4632.

Nakayama, S., K. A. Rose, and L. A. Fuiman. 2011. "Batch Spawning Decreases Competition Among Early Life Stages in Coastal Fishes: A Simulation Study Using Red Drum *Sciaenops ocellatus*." *Marine Ecology Progress Series* 441: 213–223.

Neighbors, M. A., and B. G. Nafpaktitis. 1982. "Lipid Compositions, Water Contents, Swimbladder Morphologies and Buoyancies of Nineteen Species of Midwater Fishes (18 Myctophids and 1 Neoscopelid)." *Marine Biology* 66: 207–215. https://doi.org/10.1007/BF00397024.

Netburn, A. N., and J. A. Koslow. 2015. "Dissolved Oxygen as a Constraint on Daytime Deep Scattering Layer Depth in the Southern California Current Ecosystem." *Deep-Sea Research Part I* 104: 149–158. https://doi.org/10.1016/j.dsr.2015.06.006.

Nielsen, J. G., E. Bertelsen, and Å. Jespersen. 1989. "The Biology of *Eurypharynx pelecanoides* (Pisces, Eurypharyngidae)." *Acta Zoologica* 70, no. 3: 187–197. https://doi.org/10.1111/j.1463-6395.1989.tb01069.x.

Nock, C. A., R. J. Vogt, and B. E. Beisner. 2016. *Functional Traits*. Chichester: John Wiley & Sons, Ltd. https://doi.org/10.1002/9780470015902.a0026282.

Olivar, M. P., T. Contreras, P. A. Hulley, et al. 2018. "Variation in the Diel Vertical Distributions of Larvae and Transforming Stages of Oceanic Fishes Across the Tropical and Equatorial Atlantic." *Progress in Oceanography* 160: 83–100. https://doi.org/10.1016/j.pocean.2017.12.005.

Olivar, M. P., J. I. González-Gordillo, J. Salat, et al. 2016. "The Contribution of Migratory Mesopelagic Fishes to Neuston Fish Assemblages Across the Atlantic, Indian and Pacific Oceans." *Marine and Freshwater Research* 67, no. 8: 1114–1127. https://doi.org/10.1071/MF14391.

Olivar, M. P., P. A. Hulley, A. Castellón, et al. 2017. "Mesopelagic Fishes Across the Tropical and Equatorial Atlantic: Biogeographical and Vertical Patterns." *Progress in Oceanography* 151: 116–137. https://doi.org/10.1016/j.pocean.2016.12.001.

Olivar, M. P., P. Rubiés, and J. Salat. 1992. "Horizontal and Vertical Distribution Patterns of Ichthyoplankton Under Intense Upwelling Regimes off Namibia." *South African Journal of Marine Science* 12: 71–82. https://doi.org/10.2989/02577619209504692.

Olla, B. L., M. W. Davis, C. H. Ryer, and S. M. Sogard. 1996. "Behavioural Determinants of Distribution and Survival in Early Stages of Walleye Pollock, *Theragra chalcogramma*: Synthesis of Experimental Studies." *Fisheries Oceanography* 5, no. Suppl. 1: 167–178. https://doi.org/10.1111/j.1365-2419.1996.tb00090.x.

Osse, J. W. M., and J. G. M. van den Boogaart. 1995. "Fish Larvae, Development, Allometric Growth and the Aquatic Environment." *ICES Marine Science Symposia* 201: 21–34. https://doi.org/10.17895/ices.pub.19271519.

Paoletti, S., J. R. Nielsen, C. R. R. Sparrevohn, F. Bastardie, and B. M. J. Vastenhoud. 2021. "Potential for Mesopelagic Fishery Compared to Economy and Fisheries Dynamics in Current Large Scale Danish Pelagic Fishery." *Frontiers in Marine Science* 08: 720897. https://doi.org/10.3389/fmars.2021.720897.

Parin, N. V. 1971. "The Family Swallowers (Chiasmodontidae)." In *Zhizn' zhivotnykh, t. 4. Rybi (The Life of Animals, vol. 1. Fishes)*, edited by T. S. Rass, 497. Moscow: Prosveshcheniye.

Patrick, S. C., D. Réale, J. R. Potts, et al. 2022. "Differences in the Temporal Scale of Reproductive Investment Across the Slow-Fast Continuum in a Passerine." *Ecology Letters* 25, no. 5: 1139–1151. https://doi.org/10.1111/ele.13982.

Pecuchet, L., M. Lindegren, M. Hidalgo, et al. 2017. "From Traits to Life History Strategies: Deconstructing Fish Community Composition Across European Seas." *Global Ecology and Biogeography* 26: 812–822. https://doi.org/10.1111/geb.12587.

Péron, C., H. Weimerskirch, and C.-A. Bost. 2012. "Projected Poleward Shift of King penguins' (*Aptenodytes patagonicus*) Foraging Range at the Crozet Islands, Southern Indian Ocean." *Proceedings of the Royal Society B: Biological Sciences* 279: 2515–2523. https://doi.org/10.1098/rspb.2011.2705.

Pianka, E. R. 1970. "On r- and K-Selection." *American Naturalist* 104: 592–597.

Pietsch, T. W. 2009. *Oceanic Anglerfishes, Extraordinary Diversity in the Deep Sea*. Berkeley: University of California Press. https://doi.org/10.1525/9780520942554.

Pinti, J., T. DeVries, T. Norin, et al. 2023. "Model Estimates of Metazoans' Contributions to the Biological Carbon Pump." *Biogeosciences* 20: 997–1009. https://doi.org/10.5194/bg-20-997-2023.

Pitcher, G. C., A. Aguirre-Velarde, D. Breitburg, et al. 2021. "System Controls of Coastal and Open Ocean Oxygen Depletion." *Progress in Oceanography* 197: 102613. https://doi.org/10.1016/j.pocean.2021.102613.

Porteiro, F. M., and T. Sutton. 2007. "Midwater Fish Assemblages and Seamounts." In *Seamounts: Ecology, Fisheries & Conservation*, edited by T. J. Pitcher, T. Morato, P. J. B. Hart, M. R. Clark, N. Haggan, and R. S. Santos. Hoboken: Blackwell Publishing. https://doi.org/10.1002/9780470691953.ch6.

Potier, M., F. Marsac, Y. Cherel, et al. 2007. "Forage Fauna in the Diet of Three Large Pelagic Fishes (Lancetfish, Swordfish and Yellowfin Tuna) in the Western Equatorial Indian Ocean." *Fisheries Research* 83, no. 1: 60–72. https://doi.org/10.1016/J.FISHRES.2006.08.020.

Prellezo, R., X. Corrales, E. Andonegi, et al. 2024. "Economic Trade-Offs of Harvesting the Ocean Twilight Zone: An Ecosystem Services Approach." *Ecosystem Services* 67: 101633. https://doi.org/10.1016/j.ecoser.2024.101633.

Priede, I. G. 2017. *Deep-Sea Fishes: Biology, Diversity, Ecology and Fisheries*. Cambridge: Cambridge University Press.

Priede, I. G., and R. Froese. 2013. "Colonization of the Deep Sea by Fishes." *Journal of Fish Biology* 83: 1528–1550. https://doi.org/10.1111/jfb.12265.

Quang, G. T., M. Kourantidou, and D. Jin. 2024. "Assessing the Potential Economic Effects of Mesopelagic Fisheries as a Novel Source of Fishmeal." *Natural Resource Modeling* 37: e12398. https://doi.org/10.1111/nrm.12398.

Quimbayo, J. P., F. C. D. Silva, T. C. Mendes, et al. 2021. "Life-History Traits, Geographical Range, and Conservation Aspects of Reef Fishes From the Atlantic and Eastern Pacific." *Ecology* 102: e03298. https://doi.org/10.1002/ecy.3298.

Reimchen, T. E., and N. F. Temple. 2004. "Hydrodynamic and Phylogenetic Aspects of the Adipose Fin in Fishes." *Canadian Journal of Zoology* 82: 910–916. https://doi.org/10.1139/z04-069.

Reygondeau, G., L. Guidi, G. Beaugrand, et al. 2018. "Global Biogeochemical Provinces of the Mesopelagic Zone." *Journal of Biogeography* 45, no. 2: 500–514. https://doi.org/10.1111/jbi.13149.

Robertson, D. A. 1977. "Planktonic Eggs of the Lanternfish *Lampanyctodes hectoris* (Family Myctophidae)." *Deep-Sea Research* 24: 849–850. https://doi.org/10.1016/0146-6291(77)90476-3.

Robinson, C., D. K. Steinberg, T. R. Anderson, et al. 2010. "Mesopelagic Zone Ecology and Biogeochemistry – A Synthesis." *Deep Sea Research Part II: Topical Studies in Oceanography* 57: 1504–1518. https://doi.org/10.1016/j.dsr2.2010.02.018.

Robison, B. H. 1984. "Herbivory by the Myctophid Fish *Ceratoscopelus warmingii*." *Marine Biology* 84: 119–123. https://doi.org/10.1007/BF00392995.

Roe, H. S. J., and J. Badcock. 1984. "The Diel Migrations and Distributions Within a Mesopelagic Community in the North East Atlantic. 5. Vertical Migrations and Feeding of Fish." *Progress in Oceanography* 13: 389–424. https://doi.org/10.1016/0079-6611(84)90014-4.

Röpke, A. 1993. "Do Larvae of Mesopelagic Fishes in the Arabian Sea Adjust Their Vertical Distribution to Physical and Biological Gradients?." *Marine Ecological Progress Series* 101: 223–235. https://doi.org/10.3354/meps101223.

Rosland, R., and J. Giske. 1994. "A Dynamic Optimization Model of the Diel Vertical Distribution of a Pelagic Planktivorous Fish." *Progress in Oceanography* 34: 1–43. https://doi.org/10.1016/0079-6611(94)90025-6.

Ross, S. W., A. M. Quattrini, A. Y. Roa-Varon, and J. P. McClain. 2010. "Species Composition and Distributions of Mesopelagic Fishes Over the Slope of the North-Central Gulf of Mexico." *Deep-Sea Research Part II: Topical Studies in Oceanography* 57: 1926–1956. https://doi.org/10.1016/j.dsr2.2010.05.008.

Røstad, A., S. Kaartvedt, and D. L. Aksnes. 2016a. "Light Comfort Zones of Mesopelagic Acoustic Scattering Layers in Two Contrasting Optical Environments." *Deep-Sea Research Part I: Oceanographic Research Papers* 113: 1–6. https://doi.org/10.1016/j.dsr.2016.02.020.

Røstad, A., S. Kaartvedt, and D. L. Aksnes. 2016b. "Erratum to "Light Comfort Zones of Mesopelagic Acoustic Scattering Layers in Two Contrasting Optical Environments" [Deep-Sea Res. I 113 (2016) 1–6]." *Deep Sea Research Part I: Oceanographic Research Papers* 114: 162–164. https://doi.org/10.1016/j.dsr.2016.05.001.

Ruxton, G., and D. Bailey. 2005. "Combining Motility and Bioluminescent Signalling Aids Mate Finding in Deep-Sea Fish: A Simulation Study." *Marine Ecology Progress Series* 293: 235–241. https://doi.org/10.3354/meps293253.

Saba, G. K., A. B. Burd, J. P. Dunne, et al. 2021. "Toward a Better Understanding of Fish-Based Contribution to Ocean Carbon Flux." *Limnology and Oceanography* 66, no. 5: 1639–1664. https://doi.org/10.1002/lno.11709.

Sabatés, A. 2004. "Diel Variability of Fish Larvae Distribution During the Winter Mixing Period in the NW Mediterranean." *ICES Journal of Marine Science* 61: 1243–1252. https://doi.org/10.1016/j.icesjms.2004.07.022.

Sabatés, A., A. Bozzano, and I. Vallvey. 2003. "Feeding Pattern and the Visual Light Environment in Myctophid Fish Larvae." *Journal of Fish Biology* 63, no. 6: 1476–1490. https://doi.org/10.1111/j.1095-8649.2003.00259.x.

Salvanes, A. G. V., and J. B. Kristoffersen. 2001. "Mesopelagic Fishes." In *Encyclopedia of Ocean Sciences*, edited by J. H. Steele, S. A. Thorpe, and K. K. Turekian, vol. 3, 1711–1717. New York: Academic Press.

Sarmiento-Lezcano, A. N., M. P. Olivar, M. J. Caballero, et al. 2023. "Swimbladder Properties of *Cyclothone* Spp. in the Northeast Atlantic Ocean and the Western Mediterranean Sea." *Frontiers in Marine Science* 10: 1093982. https://doi.org/10.3389/fmars.2023.1093982.

Sassa, C., K. Kawaguchi, Y. Hirota, and M. Ishida. 2007. "Distribution Depth of the Transforming Stage Larvae of Myctophid Fishes in the Subtropical–Tropical Waters of the Western North Pacific." *Deep-Sea Research, Part I: Oceanographic Research Papers* 54: 2181–2193. https://doi.org/10.1016/j.dsr.2007.09.006.

Sassa, C., K. Kawaguchi, T. Kinoshita, and C. Watanabe. 2002. "Assemblages of Vertical Migratory Mesopelagic Fish in the Transitional Region of the Western North Pacific." *Fisheries Oceanography* 11, no. 4: 193–204. https://doi.org/10.1046/j.1365-2419.2002.00199.

Saunders, R. A., M. A. Collins, E. Foster, et al. 2014. "The Trophodynamics of Southern Ocean *Electrona* (Myctophidae) in the Scotia Sea." *Polar Biology* 37, no. 6: 789–807. https://doi.org/10.1007/s00300-014-1480-3.

Saunders, R. A., M. A. Collins, G. Stowasser, and G. A. Tarling. 2017. "Southern Ocean Mesopelagic Fish Communities in the Scotia Sea Are Sustained by Mass Immigration." *Marine Ecology Progress Series* 569: 173–185. https://doi.org/10.3354/meps12093.

Saunders, R. A., S. Fielding, S. E. Thorpe, and G. A. Tarling. 2013. "School Characteristics of Mesopelagic Fish at South Georgia." *Deep-Sea Research Part I: Oceanographic Research Papers* 81: 62–77. https://doi.org/10.1016/j.dsr.2013.07.007.

Schaber, M., S. Gastauer, B. Cisewski, et al. 2022. "Extensive Oceanic Mesopelagic Habitat Use of a Migratory Continental Shark Species." *Scientific Reports* 12, no. 1: 2047. https://doi.org/10.1038/s41598-022-05989-z.

Schembri, F. 2018. "First Direct Observation of Hunting Pelican Eel Reveals Bizarre Fish With Inflatable Head." Science. https://www.science.org/content/article/first-direct-observation-hunting-pelican-eel-reveals-bizarre-fish-inflatable-head.

Seibel, B. A. 2011. "Critical Oxygen Levels and Metabolic Suppression in Oceanic Oxygen Minimum Zones." *Journal of Experimental Biology* 214, no. 2: 326–336. https://doi.org/10.1242/jeb.049171.

Snoeijs-Leijonmalm, P., H. Flores, S. Sakinan, et al. 2022. "Unexpected Fish and Squid in the Central Arctic Deep Scattering Layer." *Science Advances* 8: eabj7536. https://doi.org/10.1126/sciadv.abj7536.

Somero, G. N., and J. J. Childress. 1980. "A Violation of the Metabolism-Size Scaling Paradigm: Activities of Glycolytic Enzymes in Muscle Increase in Larger-Size Fish." *Physiological Zoology* 53, no. 3: 322–337.

Spitz, J., E. Mourocq, J. P. Leauté, J. C. Quéro, and V. Ridoux. 2010. "Prey Selection by the Common Dolphin: Fulfilling High Energy Requirements With High Quality Food." *Journal of Experimental Marine Biology and Ecology* 390, no. 2: 73–77. https://doi.org/10.1016/j.jembe.2010.05.010.

Spitz, J., V. Ridoux, and A. Brind'Amour. 2014. "Let's Go Beyond Taxonomy in Diet Description: Testing a Trait-Based Approach to Prey–Predator Relationships." *Journal of Animal Ecology* 83, no. 5: 1137–1148. https://doi.org/10.1111/1365-2656.12218.

St John, M. A., A. Borja, G. Chust, et al. 2016. "A Dark Hole in Our Understanding of Marine Ecosystems and Their Services: Perspectives From the Mesopelagic Community." *Frontiers in Marine Science* 3: 31. https://doi.org/10.3389/fmars.2016.00031.

Stearns, S. C. 1992. *The Evolution of Life Histories*, 249. Oxford: Oxford University.

Stefanescu, C., and J. E. Cartes. 1992. "Benthopelagic Habits of Adult Specimens of *Lampanyctus crocodilus* (Risso, 1810) (Osteichthyes, Myctophidae) in the Western Mediterranean Deep Slope." *Scientia Marina* 56: 69–74.

Suding, K. N., S. Lavorel, F. S. Chapin III, et al. 2008. "Scaling Environmental Change Through the Community-Level: A Trait-Based Response-And-Effect Framework for Plants." *Global Change Biology* 14: 1125–1140. https://doi.org/10.1111/j.1365-2486.2008.01557.x.

Sutton, T. T. 2005. "Trophic Ecology of the Deep-Sea Fish *Malacosteus niger* (Pisces: Stomiidae): An Enigmatic Feeding Ecology to Facilitate a Unique Visual System?." *Deep Sea Research Part I: Oceanographic Research Papers* 52, no. 11: 2065–2076. https://doi.org/10.1016/J.DSR.2005.06.011.

Sutton, T. T. 2013. "Vertical Ecology of the Pelagic Ocean: Classical Patterns and New Perspectives." *Journal of Fish Biology* 83, no. 6: 1508–1527. https://doi.org/10.1111/jfb.12263.

Sutton, T. T., M. R. Clark, D. C. Dunn, et al. 2017. "A Global Biogeographic Classification of the Mesopelagic Zone." *Deep Sea Research Part I: Oceanographic Research Papers* 126: 85–102. https://doi.org/10.1016/j.dsr.2017.05.006.

Sutton, T. T., and T. L. Hopkins. 1996. "Species Composition, Abundance, and Vertical Distribution of the Stomiid (Pisces: Stomiiformes) Fish Assemblage of the Gulf of Mexico." *Bulletin of Marine Science* 59: 530–542.

Sutton, T. T., T. B. Letessier, and B. Bardarson. 2013. "Midwater Fishes Collected in the Vicinity of the Sub-Polar Front, Mid-North Atlantic Ocean, During ECOMAR Pelagic Sampling." *Deep Sea Research Part II: Topical Studies in Oceanography* 98: 292–300. https://doi.org/10.1016/j.dsr2.2013.08.001.

Thorson, J. T., A. A. Maureaud, R. Frelat, et al. 2023. "Identifying Direct and Indirect Associations Among Traits by Merging Phylogenetic Comparative Methods and Structural Equation Models." *Methods in Ecology and Evolution* 14: 1259–1275. https://doi.org/10.1111/2041-210X.14076.

Tont, S. 1976. "Deep Scattering Layers: Patterns in the Pacific." *CalCOFI Report* 18: 112–117.

Torgersen, T., and S. Kaartvedt. 2001. "In Situ Swimming Behaviour of Individual Mesopelagic Fish Studied by Split-Beam Echo Target

Tracking." *ICES Journal of Marine Science* 58: 346–354. https://doi.org/10.1006/jmsc.2000.1016.

Torres, J. J., and G. N. Somero. 1988. "Metabolism, Enzymic Activities and Cold Adaptation in Antarctic Mesopelagic Fishes." *Marine Biology* 98: 169–180. https://doi.org/10.1007/BF00391192.

Trueman, C. N., G. Johnston, B. O'Hea, and K. M. MacKenzie. 2014. "Trophic Interactions of Fish Communities at Midwater Depths Enhance Long-Term Carbon Storage and Benthic Production on Continental Slopes." *Proceedings of the Royal Society B: Biological Sciences* 281, no. 1787: 20140669. https://doi.org/10.1098/rspb.2014.0669.

Turner, J. R., E. M. White, M. A. Collins, J. C. Partridge, and R. H. Douglas. 2009. "Vision in Lanternfish (Myctophidae): Adaptations for Viewing Bioluminescence in the Deep-Sea." *Deep Sea Research Part I: Oceanographic Research Papers* 56: 1003–1017. https://doi.org/10.1016/j.dsr.2009.01.007.

Urmy, S. S., and K. J. Benoit-Bird. 2021. "Fear Dynamically Structures the Ocean's Pelagic Zone." *Current Biology* 31: 5086–5092.e3. https://doi.org/10.1016/j.cub.2021.09.003.

Van de Putte, A., H. Flores, F. Volckaert, and J. A. van Franeker. 2006. "Energy Content of Antarctic Mesopelagic Fishes: Implications for the Marine Food Web." *Polar Biology* 29, no. 12: 1045–1051. https://doi.org/10.1007/s00300-006-0148-z.

van Denderen, P. D., C. M. Petrik, C. A. Stock, and K. H. Andersen. 2021. "Emergent Global Biogeography of Marine Fish Food Webs." *Global Ecology and Biogeography* 30: 1822–1834. https://doi.org/10.1111/geb.13348.

van der Meer, J., M. Callier, G. Fabi, L. van Hoof, J. R. Nielsen, and S. Raicevich. 2023. "The Carrying Capacity of the Seas and Oceans for Future Sustainable Food Production: Current Scientific Knowledge Gaps." *Food and Energy Security* 12, no. 4: e464. https://doi.org/10.1002/fes3.464.

van Netten, S. M., and M. J. McHenry. 2014. "The Biophysics of Neuromasts." In *Springer Handbook of Auditory Research 48: The Lateral Line*, edited by S. Coombs, H. Bleckmann, R. R. Fay, and A. N. Popper. New York: Springer. https://doi.org/10.1007/2506_2013_14.

Vastenhoud, B. M. J., F. Bastardie, K. H. Andersen, D. C. Speirs, and J. R. Nielsen. 2023. "Economic Viability of a Large Vessel Mesopelagic Fishery Under Ecological Uncertainty." *Frontiers in Marine Science* 10: 1285793. https://doi.org/10.3389/fmars.2023.1285793.

Velasco-Hogan, A., D. D. Deheyn, M. Koch, B. Nothdurft, E. Arzt, and M. A. Meyers. 2019. "On the Nature of the Transparent Teeth of the Deep-Sea Dragonfish, *Aristostomias scintillans*." *Matter* 1, no. 1: 235–249. https://doi.org/10.1016/j.matt.2019.05.010.

Villéger, S., S. Brosse, M. Mouchet, D. Mouillot, and M. J. Vanni. 2017. "Functional Ecology of Fish: Current Approaches and Future Challenges." *Aquatic Sciences* 79: 783–801. https://doi.org/10.1007/s00027-017-0546-z.

Violle, C., M.-L. Navas, D. Vile, et al. 2007. "Let the Concept of Trait Be Functional!" *Oikos* 116, no. 5: 882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x.

Wagner, H.-J. 2001. "Brain Areas in Abyssal Demersal Fishes." *Brain, Behaviour and Evolution* 57: 301–316. https://doi.org/10.1159/000047249.

Wang, X. L., J. Zhang, X. Y. Zhao, et al. 2019. "Vertical Distribution and Diel Migration of Mesopelagic Fishes on the Northern Slope of the South China Sea." *Deep Sea Research Part II: Topical Studies in Oceanography* 167: 128–141. https://doi.org/10.1016/j.dsr2.2019.05.009.

Warrant, E. J., S. P. Collin, and N. A. Locket. 2003. "Eye Design and Vision in Deep-Sea Fishes." In *Sensory Processing in Aquatic Environments*, edited by S. P. Collin and N. J. Marshall, 303–322. New York, NY: Springer. https://doi.org/10.1007/978-0-387-22628-6_16.

Warrant, E. J., and N. A. Locket. 2004. "Vision in the Deep Sea." *Biological Reviews* 79, no. 3: 671–712. https://doi.org/10.1017/S1464793103006420.

Watanabe, H., M. Moku, K. Kawaguchi, K. Ishimaru, and A. Ohno. 1999. "Diel Vertical Migration of Myctophid Fishes (Family Myctophidae) in the Transitional Waters of the Western North Pacific." *Fisheries Oceanography* 8: 115–127. https://doi.org/10.1046/j.1365-2419.1999.00103.x.

Watson, W. 1996. "Gonostomatidae: Bristlemouths." In *The Early Stages of Fishes in the California Current Region*. California Cooperative Oceanic Fisheries Investigations (CalCOFI) Atlas No. 33, edited by H. G. Moser, 247–267. Lawrence, KS: Allen Press.

Webb, P. W., and D. Weihs. 1986. "Functional Locomotor Morphology of Early-Life-History Stages of Fishes." *Transactions of the American Fisheries Society* 115: 115–127. https://doi.org/10.1577/1548-8659(1986)115%3C115:FLMOEL%3E2.0.CO;2.

Webb, T. J., E. Vanden Berghe, and R. O'Dor. 2010. "Biodiversity's Big Wet Secret: The Global Distribution of Marine Biological Records Reveals Chronic Under-Exploration of the Deep Pelagic Ocean." *PLoS One* 5, no. 8: e10223. https://doi.org/10.1371/journal.pone.0010223.

Weihs, D. 1974. "Energetic Advantages of Burst Swimming of Fish." *Journal of Theoretical Biology* 48: 215–229. https://doi.org/10.1016/0022-5193(74)90192-1.

Weihs, D. 1980. "Respiration and Depth Control as Possible Reasons for Swimming of Northern Anchovy, *Engraulis mordax*, Yolk-Sac Larvae." *Fishery Bulletin* 78: 109–117.

Weihs, D., and H. G. Moser. 1981. "Stalked Eyes as an Adaptation Towards More Efficient Foraging in Marine Fish Larvae." *Bulletin of Marine Science* 31: 31–36.

Whiteman, E. A., and I. M. Côté. 2004. "Monogamy in Marine Fishes." *Biological Reviews* 79: 351–375. https://doi.org/10.1017/s1464793103006304.

Widder, E. A. 2010. "Bioluminescence in the Ocean: Origins of Biological, Chemical, and Ecological Diversity." *Science* 328, no. 5979: 704–708. https://doi.org/10.1126/science.1174269.

Widder, E. A., M. I. Latz, P. J. Herring, and J. F. Case. 1984. "Far Red Bioluminescence From Two Deep-Sea Fishes." *Science* 225, no. 4661: 512–514. https://doi.org/10.1126/science.225.4661.512.

Wiedmann, M. A., R. Primicerio, A. Dolgov, C. A. M. Ottesen, and M. Aschan. 2014. "Life History Variation in Barents Sea Fish: Implications for Sensitivity to Fishing in a Changing Environment." *Ecology and Evolution* 4, no. 18: 3596–3611. https://doi.org/10.1002/ece3.1203.

Williams, A., J. Koslow, A. Terauds, and K. Haskard. 2001. "Feeding Ecology of Five Fishes From the Mid-Slope Micronekton Community Off Southern Tasmania, Australia." *Marine Biology* 139: 1177–1192. https://doi.org/10.1007/s002270100671.

Williams, R., C. Erbe, A. Duncan, K. Nielsen, T. Washburn, and C. Smith. 2022. "Noise From Deep-Sea Mining May Span Vast Ocean Areas." *Science* 377, no. 6602: 157–158. https://doi.org/10.1126/science.abo2804.

Winemiller, K. 2005. "Life History Strategies, Population Regulation, and Implications for Fisheries Management." *Canadian Journal of Fisheries and Aquatic Sciences* 62, no. 4: 872–885. https://doi.org/10.1139/f05-040.

Winemiller, K. O., and K. A. Rose. 1992. "Patterns of Life-History Diversification in North-American Fishes - Implications for Population Regulation." *Canadian Journal of Fisheries and Aquatic Sciences* 49, no. 10: 2196–2218. https://doi.org/10.1139/f92-242.

Yancey, P. H., R. Lawrenceberrey, and M. D. Douglas. 1989. "Adaptations in Mesopelagic Fishes. 1. Buoyant Glycosaminoglycan Layers in Species Without Diel Vertical Migrations." *Marine Biology* 103, no. 4: 453–459. https://doi.org/10.1007/bf00399577.

Yosef, T. G., and J. M. Casselman. 1995. "A Procedure for Increasing the Precision of Otolith Age Determination of Tropical Fish by Differentiating Biannual Recruitment." In *Recent Developments in Fish Otolith Research*, edited by D. H. Secor, J. M. Dean, and S. E. Campana, 247–269. Columbia, SC: University of South Carolina Press.

Young, J. W., C. M. Bulman, S. J. M. Blaber, and S. E. Wayte. 1988. "Age and Growth of the Lanternfish *Lampanyctodes hectoris* (Myctophidae) From Eastern Tasmania, Australia." *Marine Biology* 99: 569–576. https://doi.org/10.1007/BF00392564.

Young, R. E., E. M. Kampa, S. D. Maynard, F. M. Mencher, and C. F. Roper. 1980. "Counterillumination and the Upper Depth Limits of Midwater Animals." *Deep Sea Research Part A: Oceanographic Research Papers* 27: 671–691. https://doi.org/10.1016/0198-0149(80)90022-9.

Zakharova, L., K. M. Meyer, and M. Seifan. 2019. "Trait-Based Modelling in Ecology: A Review of Two Decades of Research." *Ecological Modelling* 407: 108703. https://doi.org/10.1016/j.ecolmodel.2019.05.008.