Dining in the Deep: The Feeding Ecology of Deep-Sea Fishes

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Abstract

Deep-sea fishes inhabit ~75% of the biosphere and are a critical part of deep-sea food webs. Diet analysis and more recent trophic biomarker approaches, such as stable isotopes and fatty-acid profiles, have enabled the description of feeding guilds and an increased recognition of the vertical connectivity in food webs in a whole-water-column sense, including benthic-pelagic coupling. Ecosystem modeling requires data on feeding rates; the available estimates indicate that deep-sea fishes have lower per-individual feeding rates than coastal and epipelagic fishes, but the overall predation impact may be high. A limited number of studies have measured the vertical flux of carbon by mesopelagic fishes, which appears to be substantial. Anthropogenic activities are altering deep-sea ecosystems and their services, which are mediated by trophic interactions. We also summarize outstanding data gaps.

INTRODUCTION

The deep sea is the largest habitat on the planet. Water deeper than 200 m covers ~65% of the globe and constitutes a living volume of over a billion cubic kilometers, representing ~75% of the global biosphere (Angel 1997, Robison 2004). Abiotically, this ecosystem is typically characterized by high pressure, low temperatures, and reduced or absent sunlight. Such an enormous space cannot be thought of as a single ecosystem; rather, it comprises a diversity of benthic and pelagic habitats, including abyssal plains, trenches, seamounts, midocean ridges, marginal seas, gyres, upwelling zones, boundary currents, and oxygen minimum zones. All of these habitats differ from shallow waters in that primary production is absent (with the exception of some archaea and particular sites of chemoautotrophy, such as seeps and vents) and communities are supported through the passive sinking flux of detritus or the active migration of pelagic fauna to the surface at night (Smith et al. 2009).

Fishes are an important component of deep-sea ecosystems. They inhabit virtually all of the ocean except at depths greater than ~8,200 m (Linley et al. 2016, Yancey et al. 2014). The characteristics of the deep sea have resulted in a specialized fish fauna that is often dominated by taxa that are rare or absent in shallower waters (e.g., Myctophiformes, Stomiiformes, and Macrouridae). The abundance of fishes generally declines with increasing depth (Angel & Baker 1982, Wei et al. 2010), but because of the enormity of the ecosystem and the large amounts of biomass near abrupt topographies (Cook et al. 2013, Sutton et al. 2008), their overall abundance and biomass are extremely high. Recently, mesopelagic fish biomass has been estimated at 7–10 billion metric tons (Irigoien et al. 2014, Kaartvedt et al. 2012, Koslow et al. 1997), an order of magnitude higher than previous estimates (Gjosaeter & Kawaguchi 1980). Although the census of deep-sea fishes is far from complete (Webb et al. 2010), critical global ecosystem services are likely provided by deep-sea-fish biodiversity and interactions.

Fishes are critical in food webs as both intermediate trophic levels and top predators. Mesopelagic fishes provide a forage base for many commercially exploited species, such as tuna and swordfish (Choy et al. 2013, Young et al. 2015). Many demersal species are themselves commercially exploited (e.g., grenadiers, orange roughy, and Chilean sea bass; Koslow et al. 2000, Norse et al. 2012). Pelagic food-web models are now emphasizing the importance of mid-trophic-level species in overall oceanic ecology (Choy et al. 2016, Ruzicka et al. 2012). For example, in the California Current region, the biomass of mesopelagic fishes is an order of magnitude greater than the biomass of sardines and anchovies (Davison et al. 2015); mesopelagic fishes therefore consume approximately the same amount of zooplankton as sardines and anchovies do despite their lower metabolism (Koslow et al. 2014), and they can contribute significantly to vertical carbon flux through their vertical migrations (Davison et al. 2013). Recent research has also shown that the trophic interactions of deep-pelagic and deep-demersal fishes in slope ecosystems play an important role in the ocean carbon cycle, bypassing the detrital particle flux and transferring carbon to deep long-term storage. Global peaks in the biomass and diversity of deep-demersal fishes at midslope depths may be explained by mesopelagic organisms impinging on the slope and the competitive release of the deep-demersal fishes that feed on them (Trueman et al. 2014). In addition to their trophic significance, estimates suggest that marine fishes are important contributors of oceanic carbonate production (up to 15%, produced in their intestines; Wilson et al. 2009). Because fish carbonates are more soluble than those from other sources, they may make a major contribution (up to 26%) to the increase in titratable alkalinity in the top 1,000 m of the ocean, partially explaining a decades-old conundrum. Fish carbonate production may rise in response to rising environmental carbon dioxide, becoming an increasingly important part of the inorganic carbonate cycle (Wilson et al. 2009).

Studies of the trophic ecology of deep-sea fishes have progressed a great deal in the last ∼20 years. Earlier studies focused on diet, morphological specializations for feeding, and feeding guilds [e.g., the excellent review by Gartner et al. (1997)]. These approaches have been recently augmented by biomarker approaches, further elucidating food-web pathways and energy sources for deep-sea communities. Studies have focused on evaluating the connections between sources of food in surface waters and deep-sea fishes and on vertical connectivity in food webs between the epi-, meso-, and bathypelagic zones and between the pelagic and benthic realms. Recent studies have also attempted to estimate feeding rates and the flux of energy to assist in biogeochemical and food-web modeling, including modeling of vertical carbon flux. The focus of the community is increasingly turning to anthropogenic effects on deep-sea food webs, including fishes. Climate change, fishing, and deep-sea mining all have the potential to alter ecosystems and their food webs at a grand scale.

DEFINITIONS AND CLASSIFICATIONS OF DEEP-SEA FISHES

Deep-sea fishes are classified into many different subgroups based on their habitat and habits. The terms used in this review are those found throughout the literature:

- *Benthic*: Benthic fishes reside directly on the seafloor most of the time. Examples include flatfishes, many eelpouts, and tripod fishes.
- *Benthopelagic*: Benthopelagic fishes live in association with the seafloor but spend very little time in contact with it (Drazen & Seibel 2007, Gartner et al. 1997). Examples include grenadiers (Macrouridae), many rockfishes (Scorpaenidae), and cutthroat eels (Synaphobranchidae).
- *Demersal*: Demersal fishes live on or in association with the seafloor. We use this term to include both benthic and benthopelagic species.
- *Bathyal*: Bathyal fishes are demersal species living on the continental slope at depths of ∼200–3,000 m.
- *Abyssal*: Abyssal fishes are demersal species living largely on the abyssal seafloor at depths of ∼3,000–6,000 m.
- *Mesopelagic*: Mesopelagic fishes inhabit the dimly lit water bounded above by the euphotic zone and below by the lower boundary of visibly detectable light, typically at depths of 200–1,000 m. Examples include lanternfishes (Myctophidae) and dragonfishes (Stomiidae).
- *Bathypelagic*: Bathypelagic fishes inhabit the permanently dark zone below the mesopelagic, from depths of ∼1,000 m to >4,000 m. Examples include deep-sea anglerfishes, gulper eels, and whale fishes. It should be noted that the boundary between the mesopelagic and bathypelagic is far from precise, probably includes a broad transition zone, and varies regionally in depth (Sutton 2013).
- *Resident/migratory*: Resident fishes generally live in a pelagic habitat; migratory fishes undergo diel vertical migration, moving from deeper waters during the day to shallower waters, often near the surface, at night.

DEEP-SEA-FISH DIETS AND FEEDING GUILDS

Several aspects distinguish the feeding of deep-sea fishes from those in shallow waters. No herbivorous species live in the deep sea owing to the lack of primary producers in the ecosystem. One study found evidence of diatom consumption by a myctophid (Robison 1984), but it is unclear how common such feeding is. Earlier studies argued that a decreasing abundance of food with depth caused the diets of deep-sea fish to become more general, but more recent analyses of diet have shown that there can be specialization (discussed below), that niche partitioning occurs in fish assemblages (Hopkins & Gartner 1992, Mauchline & Gordon 1986), and that the diets of a number of shallow-water fishes can be quite general themselves. However, the deep sea is missing the narrow-diet specialists often found in shallow-water habitats, such as coral-polyp-feeding butterfly fishes. Rather than a trend of more generalized feeding habits with depth, there is a loss of the extreme end of the specialist-to-generalist continuum. Another difference between shallow- and deep-sea fishes is that deep-sea species are particularly tuned to finding prey in still environments that are either dark or dimly lit. Mesopelagic and bathyal species have greatly enhanced vision (Warrant & Locket 2004), and many species rely on mechanosensory and olfactory cues. Another adaptation of many deep-sea fishes, mostly those in the meso- and bathypelagic zones, is an enormous gape to consume a wide diversity of prey sizes (Ebeling & Cailliet 1974) (**Figure 1*b*,*c***), including some prey that are as large as the predator. Clearly, predator-to-prey size ratios can be much lower in the deep ocean than in shallow waters (Barnes et al. 2010), which has implications for the transfer of energy between trophic levels and the formulation of ecosystem models.

There is an extensive literature on the trophic ecology of deep-sea fishes. Gartner et al. (1997) presented a characterization of feeding guilds, and new studies have allowed us to amend the list of feeding guilds (**Table 1**). From the existing work, it is clear that the diversity of guilds is much greater in the benthic environment, likely because of the greater diversity of prey (i.e., benthic taxa). Below, we summarize previously described and recently corroborated patterns for demersal and pelagic species as well as their food sources and ecological processes (**Figure 2**). Note that ontogenetic changes in diet, particularly with regard to prey size, are common in fishes, so some species have juveniles in one guild and adults in another (e.g., *Coryphaenoides armatus* and *Coryphaenoides acrolepis*; Drazen et al. 2001) (**Figure 1*d***). Furthermore, diets can vary with changes in prey availability (Santos et al. 2013, Williams et al. 2001) or because of competitive interactions with other species (Lee et al. 2008).

Demersal Feeding Guilds

There are ten dietary guilds or subguilds for demersal species (**Table 1**). Piscivorous demersal fishes can be subdivided into mobile species (such as sharks) and more sedentary ambush predators (such as the deep-sea lizard fish *Bathysaurus*). At bathyal depths, and certainly over the abyss, where prey biomass is low, many mobile piscivores include scavenging in their trophic repertoire. The absence of sharks, rays, and chimaeras at abyssal depths (Priede et al. 2006) applies to a diverse range of taxa, not all of which are piscivores; it is unclear whether their absence is related to energetic constraints or a complex of energetic and physiological constraints (Laxson et al. 2011, Treberg & Speers-Roesch 2016).

The guilds that represent the majority of deep-demersal fish species are the micronektonivore, hyperbenthic crustacean feeder, and epifaunal browser guilds, the latter two of which largely overlap. The distinction is that hyperbenthic crustacean feeders, which include the tripod fishes (**Figure 1*f***), prey mostly on swimming copepods, amphipods, and mysids, whereas epifaunal browsers focus on truly benthic prey types, such as polychaetes, isopods, and crabs. Furthermore, the distinction between micronektonivores and hyperbenthic crustacean feeders is partly taxonomic (prey type) but largely functional (prey size). From the variety of diet studies (**Table 1**), it seems clear that these categories represent a continuum of the most common feeding modes of demersal fishes, and the commonness of hyperbenthic crustaceans clearly points to the importance of this food source (Carrasson & Cartes 2002, Fanelli & Cartes 2010).

Several of the guilds have only a few representatives. For instance, most fishes do not feed on infaunal organisms, despite early studies suggesting that grenadiers might use their snout "to

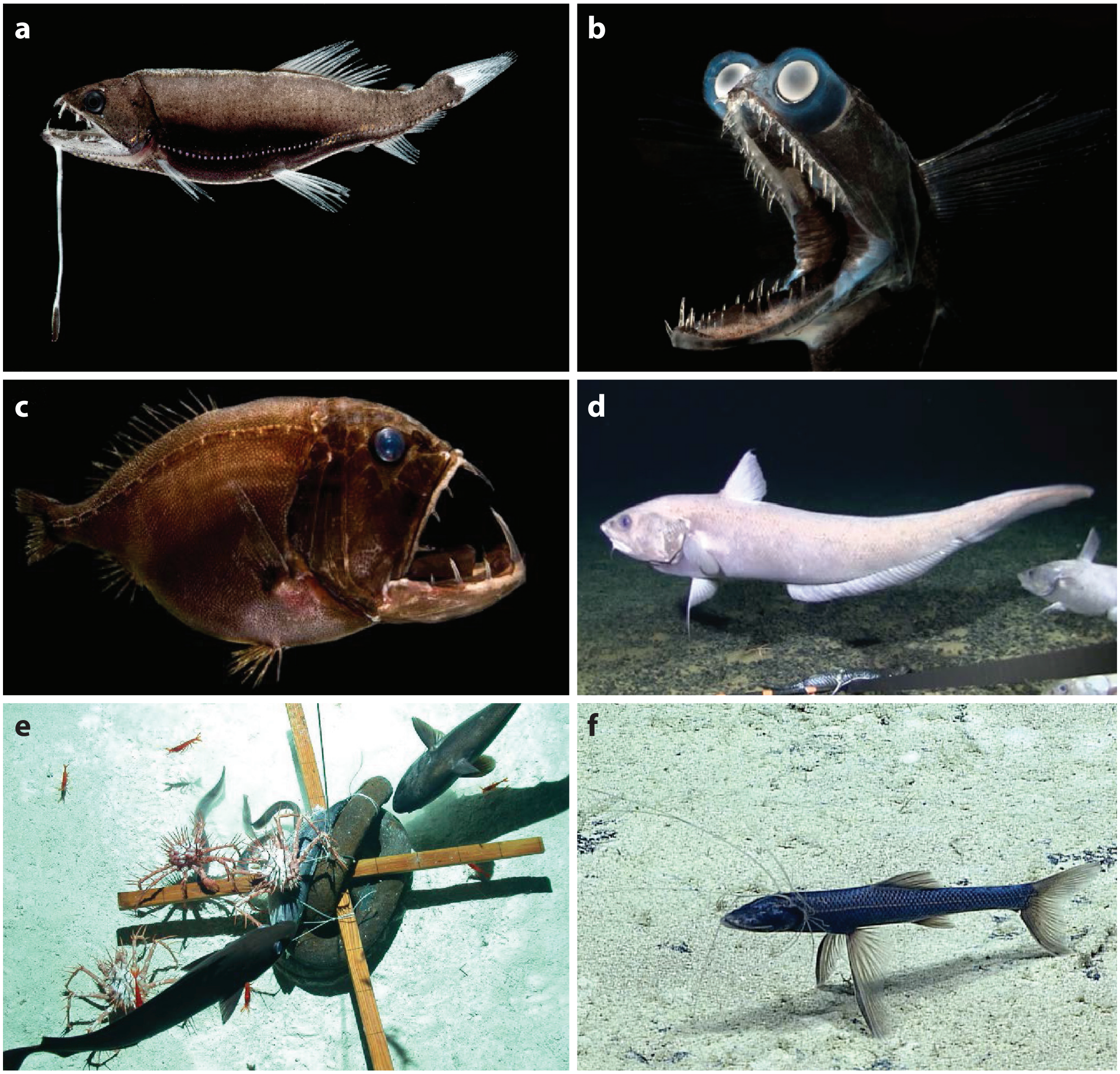

Figure 1

Deep-sea fishes and trophic adaptations. Mesopelagic species: (*a*) *Astronesthes gemmifer*, with a bioluminescent luring structure; (*b*) the telescopefish *Gigantura chuni*, with a flexible gape; and (*c*) the fangtooth *Anoplogaster cornuta*, a generalist with large teeth and a large gape. Demersal species: (*d*) the grenadier *Coryphaenoides armatus*, a globally distributed species that ontogenetically transitions from a hyperbenthic crustacean feeder/micronektonivore to a piscivore/facultative scavenger; (*e*) *Coryphaenoides rudis*, *Antimora microlepis*, *Simenchelys parasitica*, lithodid crabs, and aristeid shrimp attracted to a baited camera (a common tool for studying scavengers, shown here with the anchor and scale bars) at a depth of 1,500 m off the Hawaiian Islands; and (*f*) the tripod fish *Bathypterois* sp., which uses extended pelvic and anal fin rays to perch on the sediment and extended pectoral fin rays to form a sensory net to intercept hyperbenthic crustacean prey. Images courtesy of the Deep Pelagic Nekton Dynamics (DEEPEND) Consortium and Danté Fenolio (© 2015) (panels *a–c*); the Deep-Sea Fish Ecology Lab and the Abyssal Baseline (ABYSSLINE) project (panels *d* and *e*); and the National Oceanic and Atmospheric Administration's Office of Exploration and Research (panel *f*).

Table 1 Trophic guilds of deep-sea fishes (*sensu* Gartner et al. 1997)

Guild (subguild)	Prey consumed	Common characteristics	Examples	References
Demersal species				
Demersal piscivores (ambush)	Fish, large cephalopods and crustaceans	Large in size, muscular, sedentary, large gape, no gas bladder, often large eyes, large teeth	*Bathysaurus*, large *Helicolenus*, *Lophius*, *Reinhardtius*	Macpherson 1985, Madurell & Cartes 2005b, Solmundsson 2007, Sulak et al. 1985, Valentim et al. 2008
Demersal piscivores (active)	Fish, large cephalopods and crustaceans, frequently carrion	As above but with a gas bladder, active swimming, generally smaller sharp teeth (for teleosts)	*Synaphobranchus*, *Diastrobranchus*, *Antimora rostrata*, large *Coryphaenoides armatus*, *Raja hyperborean*, moderate- to large-sized squaloid sharks	Anderson 2005b, Bjelland et al. 2000, Carrasson et al. 1992, Churchill et al. 2015b, Gordon & Mauchline 1996, Jones & Breen 2014, Martin & Christiansen 1997, Mauchline & Gordon 1984, Navarro et al. 2014, Pearcy & Ambler 1974, Saldanha et al. 1995
Demersal micronektonivores[a]	Small midwater fishes, mysids, euphausiids, decapods, cephalopods, often some epibenthic invertebrates	Active swimming, some schooling, forays into the pelagic (for many taxa), moderate to large in size, moderate gape, well-developed gill rakers, large eyes	Many moderate- to large-sized grenadiers (*Coryphaenoides*, *Malacocephalus*, *Albatrossia*), *Alepocephalus*, *Bassozetus*, *Hoplostethus*, *Bothrocara brunneum*, *Antigonia*, *Zenopsis*, *Beryx splendens*, many skates (*Bathyraja*), small- to moderate-sized squaloid sharks	Anderson 2005a, Bergstad et al. 2010, Boyle et al. 2012, Bulman & Koslow 1992, Crabtree et al. 1991, Drazen et al. 2001, Ebert & Bizzarro 2007, Fanelli & Cartes 2010, Ferry 1997, Fock et al. 2002, Horn et al. 2010, Jones 2008a, Madurell & Cartes 2005a
Hyperbenthic crustacean feeders[b]	Small hyperbenthic crustaceans, some epibenthic invertebrates (e.g., polychaetes and crustaceans)	Small to moderate in size, terminal but often subterminal mouths, often small eyes	Small- to moderate-sized codlings, many small grenadiers (e.g., *Coelorinchus*, *Coryphaenoides*, *Hymenocephalus*, *Nezumia*), *Halosauropsis*, *Aldrovandia*, *Bathypterois*, *Cataetyx alleni*, *Antigonia*, deepwater notothenioids	Anderson 2005a; Bergstad et al. 2012; Carrasson & Matallanas 2001, 2002a; Carrasson et al. 1997; Drazen et al. 2001; Hoff et al. 2000; Jones 2008b; Lee et al. 2008; Mauchline & Gordon 1980, 1984; Würzberg et al. 2011
Epifaunal browsers	Polychaetes, isopods, crabs, gastropods, some echinoderms and hyperbenthic prey	Small to moderate in size, terminal but often subterminal mouths, often small eyes	*Hydrolagus*, *Polyacanthonotus*, *Notacanthus*	Anderson 2005b, Carrasson & Matallanas 2002b, Dunn et al. 2010

(*Continued*)

Table 1 *(Continued)*

Guild (subguild)	Prey consumed	Common characteristics	Examples	References
Demersal species				
Infaunal predators	Bivalves, polychaetes, tanaids, gastropods, often sediment as well	Small to moderate in size, various body forms, some with crushing palatine teeth or beaklike jaws	Eelpouts, *Glyptocephalus*, *Microstomus*, *Laemonema barbatula*, several chimaerids	Bjelland et al. 2000, Buckley et al. 1999, Dunn et al. 2010, Saldanha et al. 1995, Sedberry & Musick 1978
Megafaunal croppers	Sponges, anemones, corals, echinoderms	No distinct unifying characters	*Notacanthus chemnitzii*, *Barathrites parri*, several chimaerids	Crabtree et al. 1991, Dunn et al. 2010, Mauchline & Gordon 1983b
Necrophages (scavengers)	Dead fish, elasmobranchs, whales, jellies	Many species facultative; specialists mostly eel-like with small mouths full of stout teeth or rasping surfaces	Hagfishes (*Myxine*, *Eptatretus*), *Simenchelys parasitica*	Anderson 2005b, Tamburri & Barry 1999, Zintzen et al. 2011
Necrophagivores	Mostly amphipods that are attracted to carrion	Variety of bait-attending fishes, small to large in size, variety of body forms	*Paraliparis bathybius*, *Notoliparis kermadecensis*, *Pachycara*, *Bassozetus*	M.E. Gerringer, B.N. Popp, T.D. Linley, A.J. Jamieson & J.C. Drazen, manuscript in review; Jamieson et al. 2009; Lampitt et al. 1983
Both demersal and pelagic species				
Gelativores	Medusae, ctenophores, salps, pyrosomes, often micronekton prey as a supplement	Often large eyes, grinding structure at back of throat, some with long intestinal tract	*Helicolenus percoides*, *Neocyttus rhomboidalis*, *Alepocephalus*, *Conocara*, large bigscales (Melamphaidae), deep-sea smelts (Bathylagidae), most Stromateoidei (driftfishes and medusafishes)	Blaber & Bulman 1987, Carrasson & Matallanas 1998, Crabtree & Sulak 1986, Haedrich 1967, Hopkins et al. 1996, Jones & Breen 2013, Mauchline & Gordon 1983a
Pelagic species				
Zooplanktivores	Diverse zooplankton (nauplii, copepods, ostracods, euphausiids, etc.)	Small meso- and bathypelagic fishes with small- to moderate-sized mouths and teeth, often vertically migrating	Most larval teleosts, lanternfishes, deep-sea smelts, hatchetfishes, lightfishes, many smaller bristlemouths, *Cyclothone*	Bernal et al. 2013, 2015; Hopkins & Baird 1985; Hopkins et al. 1996; Moser & Ahlstrom 1996; Van Noord et al. 2013
Pelagic micronektonivores	Most commonly fishes, but also shrimps, larger mysids, and occasionally cephalopods	Many small to moderate in size, often with bioluminescent lures, large mouths, and fanglike teeth	Dragonfishes, ceratioid anglerfishes, nemichthyid and serrivomerid eels, sabertooths (Evermannellidae), barracudinas (Paralepididae)	Clarke 1982, Feagans-Bartow & Sutton 2014, Hopkins et al. 1996, Sutton & Hopkins 1996

(Continued)

Table 1 *(Continued)*

Guild (subguild)	Prey consumed	Common characteristics	Examples	References
Pelagic species				
Pelagic generalists	A diversity of zooplankton and micronekton	Possibly mostly bathypelagic, enormous gape, reduced musculature, reduced visual predation (small eyes)	Saccopharyngiformes (gulper eels), fangtooths, smaller anglerfishes, telescopefishes (Giganturidae), smaller dragonfishes	Gartner et al. 1997, Hopkins et al. 1996

Example species and studies are meant as representatives only and are not comprehensive lists. For additional examples, see Gartner et al. (1997).

[a]This guild represents Gartner et al.'s (1997) macronektonivores but is renamed here for consistency with the pelagic guilds.

[b]This guild represents Gartner et al.'s (1997) micronektonivores.

turn over the surface of the oozes" (Marshall 1965, p. 305). This guild has representatives that include some eelpouts (Zoarcidae), a few chimaerids, and several flatfishes that feed on polychaetes and ophiuroids. The lack of a diverse infaunal guild suggests that this foraging mode is not very profitable in the deep sea. Megafaunal croppers feeding on sessile benthic invertebrates such as sponges, corals, and anemones—which are common potential prey in regions with hard substrates—are probably uncommon because these types of prey have low caloric values and often have chemical defenses (Loh & Pawlik 2014). Notably, echinoderms are not frequently consumed by deep-sea fishes, although they are commonly the most abundant epibenthic megafauna on the seafloor. Brittle stars are most commonly eaten, and urchins are eaten by some chimaerids, but sea cucumbers are consumed infrequently. Shallow-water urchins and sea cucumbers are frequently toxic or distasteful in order to deter predators (Stonik et al. 1999). The same may be true in deepwater environments.

Specialist necrophages appear to be rare among deep-sea fishes, perhaps because carrion, although an important food source, is only sporadically available (Stockton & DeLaca 1982). Hagfishes can rapidly mass at fish, whale, and even jelly carcasses (e.g., Yeh & Drazen 2011) and exude copious mucus, which can deter other scavengers and predators. However, even hagfish are unlikely to be obligate scavengers, and diet studies have found that they also eat infaunal animals (Martini 1998) and small burrowing fishes (Zintzen et al. 2011). Energetic modeling, balancing the time required to find carrion and use up energy stores, has found obligate scavenging in deep-sea fishes feasible using *C. armatus* as a model scavenger (Ruxton & Bailey 2005), but these fish scavengers are also clearly capable of predation.

Whereas obligate scavenging in deep-sea fishes is debatable (Britton & Morton 1994), facultative scavenging is a common and important foraging mode (King et al. 2007) for taxa such as hagfish, eelpouts, cusk eels (Ophidiidae), grenadiers, codlings (Moridae), cutthroat eels, and sharks (**Figure 1**). Indeed, such species make up ∼20% of demersal fish species in the eastern North Atlantic (Priede et al. 2010) and eastern North Pacific (Yeh & Drazen 2011) and up to 46% of the demersal fish species in the North Pacific at 3,000 m. Carrion identified in the stomachs of fishes has included surface-dwelling species, parts of large animals, and fishery discards (Bjelland et al. 2000, Drazen et al. 2008, Jones & Breen 2014). Even kitchen scraps (broccoli, cantaloupe rind, and onion peels) have been noted in some fishes (Drazen et al. 2001). Carrion can make up 20–50% (by biomass) of the diets of some species. Scavenging fishes tend to be larger taxa, and in some cases

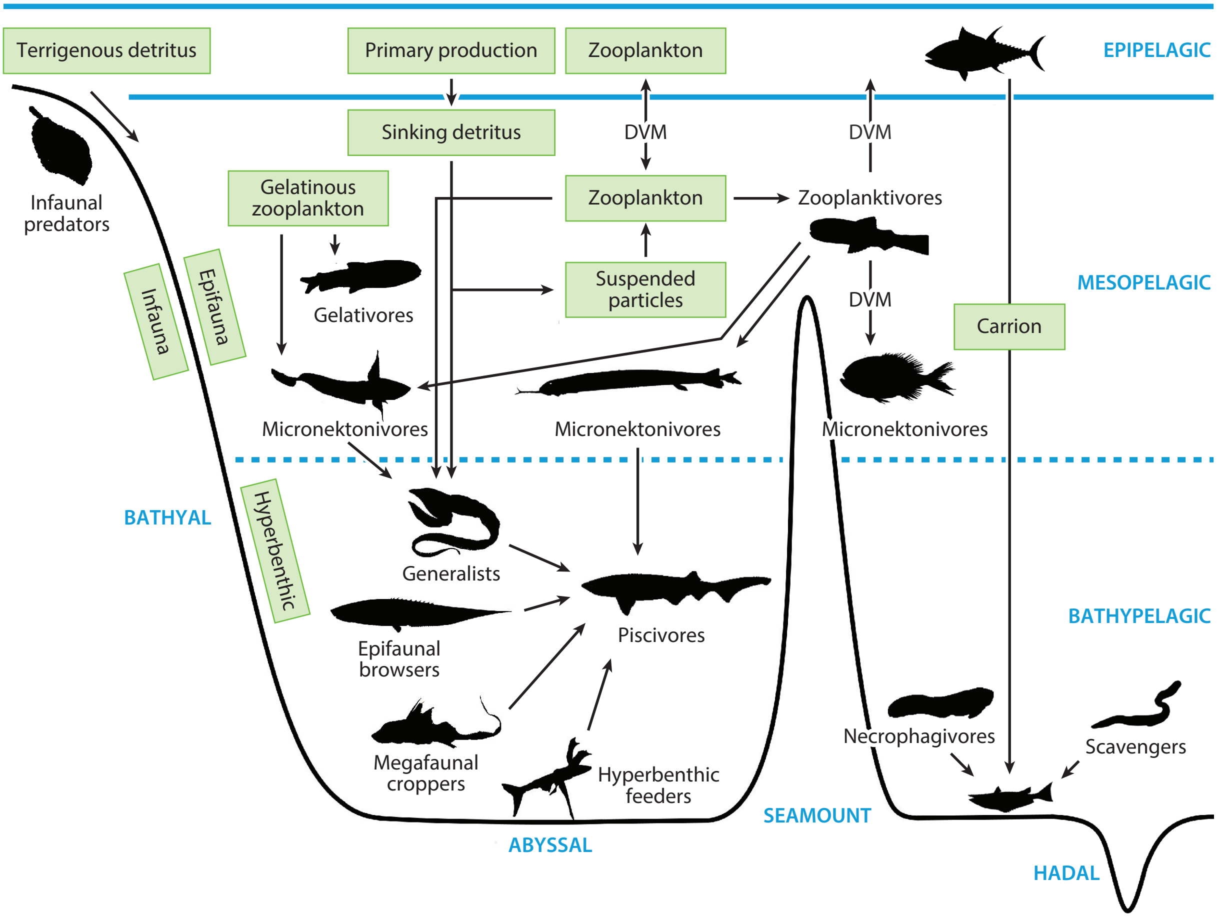

Figure 2

Trophic diagram illustrating the various sources of food for fishes (*boxes*) and the primary feeding guilds. Some arrows have been removed for clarity. Well-described trophic pathways include the sinking of detritus and fecal pellets, terrigenous inputs, and diel vertical migration (DVM) of zooplanktivores and some micronektonivores toward the surface at night. Pathways that have less information available and are therefore of uncertain importance include carrion flux, gelatinous zooplankton, and the recycling of primary production through suspended or slowly sinking particles. Graphics created by Matthew Johnston (Nova Southeastern University).

scavenging develops only at larger size classes (Drazen et al. 2008, Martin & Christiansen 1997). The pattern of increased size with depth in some species correlates to scavenging (Collins et al. 2005, Yeh & Drazen 2011), theoretically because the larger energy reserves, lower mass-specific metabolic rates, and greater swimming speeds associated with a larger size facilitate competition for sporadic food resources (Collins et al. 2005). At a time-series station under the California Current, long-term changes in populations of *Coryphaenoides* spp. covaried with the relative abundance of surface-dwelling Pacific hake spawners, an important carrion source in their diets (Drazen et al. 2012). Increases in fish abundance and size occurred rather rapidly, and given the longevity of macrourids (25–73 years; Drazen & Haedrich 2012), Drazen et al. (2012) proposed that the population changes reflected migration into and out of the study site, following interannual variations in the location and strength of hake spawning aggregations. Thus, it seems clear that carrion is a significant foodstuff for deep-sea species and represents an important, though sometimes overlooked, trophic link between top trophic levels in the epipelagic and those in the deep sea. Further study of carrion sources for demersal fishes would be most profitable under nekton migration routes and at times when nekton are concentrated for either feeding or reproduction.

The necrophagivore (feeding on animals attracted to carrion) feeding guild was first recognized through baited camera observations of a small snailfish, *Paraliparis bathybius*. This species came to a baited camera, but instead of consuming the dead fish, it fed on the abundant small amphipods that were also attracted (Lampitt et al. 1983). Subsequent studies have found similar behavior in eelpouts, hadal snailfishes, some grenadiers, and the abyssal cusk eek *Bassozetus* sp. (Jamieson et al. 2009). In the past, many baited camera studies employed still imagery, and the regular use of videography in recent years should shed more light on the behavioral interactions at carrion falls and on the abundance of necrophagivores.

Pelagic Feeding Guilds

Among the mesopelagic fishes, three major feeding guilds have been reported (**Table 1**). Zooplanktivores represent the majority of mesopelagic species, individuals, and biomass. The term planktivory is fairly broad and includes both herbivores and carnivores as well as filter feeders and particulate feeders. With regard to herbivory, although at least one deep-pelagic fish consumes plant material as part of its diet (*Ceratoscopelus warmingii*; Robison 1984), carnivory is basically the rule. With regard to feeding mode, Herring (2002) pointed out that particulate organic carbon levels of at least 25 $\mu g\ L^{-1}$ are required for filter feeding to be energetically feasible, a value exceeded in neritic environments but rarely met in the deep sea. Thus, filter feeding and herbivory are excluded among the deep-pelagic ichthyofauna. This energetic constraint is one of several that explains the overall lower trophic guild diversity of deep-pelagic fishes relative to their neritic and deep-demersal counterparts.

The zooplanktivorous feeding guild includes all larval deep-sea teleost (bony) fishes, including pelagic, demersal, and benthic taxa. A large literature base has established that most deep-sea teleost larvae are distributed in the upper 200 m (Moser & Ahlstrom 1996) and feed during daylight, with increased light intensity provoking feeding responses (Conley & Hopkins 2004). Recently hatched fish larvae consume primarily copepod eggs and nauplii, whereas older, more mobile larvae consume primarily calanoid copepodites (e.g., Sassa & Kawaguchi 2005). Elongate-eyed lanternfish larvae (subfamily Myctophini) have a broader diet, ostensibly enabled by better visual prey detection (Sabatés et al. 2003). Adult lanternfishes and other vertically migrating taxa feed primarily in the epipelagic at night (e.g., Hopkins et al. 1996), although daytime feeding has been reported for some species (Kinzer & Schulz 1985, Paxton 1967). Adults tend to select for larger zooplankton species (large copepods and euphausiids; Bernal et al. 2015, Hopkins & Baird 1985), thereby likely exerting top-down control over the composition of oceanic zooplankton communities (Hopkins & Gartner 1992, Van Noord et al. 2013).

In contrast to the vertically migrating lanternfishes, bristlemouths (Gonostomatidae), hatchetfishes (Sternoptychidae), and lightfishes (Phosichthyidae), there is a numerically large, zooplanktivorous component of the deep-pelagic fish fauna (e.g., the genus *Cyclothone* and the sternoptychid *Argyropelecus hemigymnus*) that does not vertically migrate. This fauna appears to feed at various times throughout the day and night, and on a wider spectrum of prey (Bernal et al. 2015). The low average prey number (one or two prey per positive stomach) and high vacuity index (33–90%) of the genus *Cyclothone* (Bernal et al. 2015, Palma 1990) appears to be an end point in the evolution of fishes in the deep-ocean interior—a neotenic existence with infrequent feeding and very low metabolic requirements (Smith & Laver 1981).

One of the outstanding information gaps in deep-sea-fish trophic ecology is quantitative data regarding the consumption and cycling of gelatinous zooplankton (Sutton 2013). Many authors have reported that estimates of the occurrence of soft-bodied taxa (e.g., larvaceans and gelatinous zooplankton) may be artificially low owing to low detection success (i.e., rapid digestion) relative to hard-bodied prey (Arai et al. 2003, Purcell & Arai 2001). Nevertheless, in some regions this pathway appears to be quite important. For example, biomass estimates of deep-pelagic fishes over the northern Mid-Atlantic Ridge suggest that gelativory may be a dominant trophic pathway: Fish families known or suspected to be gelativorous (Bathylagidae, larger species of Melamphaidae, and Platytroctidae; Balanov et al. 1995, Gartner & Musick 1989, Sutton et al. 1998) ranked first, third, and fifth in total biomass of the 58 families sampled between the surface and depths of >3,000 m, and in total, the wet-weight biomass of these families equaled that of all other families combined (Sutton et al. 2008). Gelativores are also present among benthopelagic species such as the slickheads (Alepocephalidae), which possess specialized grinding organs (analogous to those in pelagic stromateoids) used to masticate rubbery prey and discharge noxious nematocysts (Gartner et al. 1997). Medusae and salps can also periodically bloom and fall to the seafloor (Billett et al. 2006, Smith et al. 2014, Sweetman et al. 2014), providing a large but episodic food source. The importance of such events to fishes is not known.

The deep-pelagic environment, which is generally characterized by large nearest-neighbor distances of potential prey, is the primary domain of the sit-and-wait micronektonivore (**Figure 2**). Energetic constraints require energy savings at the potential expense of prey encounter for the majority of species. It is therefore not surprising that the archetypical predators of the meso- and bathypelagic zones—the dragonfishes and deep-sea anglerfishes, respectively—are characterized by luring appendages and/or an enhanced mechanosensory capability (**Figure 1*a***). Enlarged teeth and a large relative gape size, in combination with highly flexible jaws and neurocranial attachments (**Figure 1*b*,*c***), are thought to be adaptations that ensure higher capture-per-encounter rates in food-limited environments (Kenaley 2012, Schnell et al. 2010). The utility of these characters is exemplified by the success of these predators; dragonfishes consume as much as 53–230% of the annual standing stock of their fish prey (Clarke 1982, Davison et al. 2013, Sutton & Hopkins 1996). Where and when these dragonfishes feed (i.e., in the epipelagic zone at night) can be inferred from the faunal composition of their diets, as dragonfishes consume the majority of vertically migratory fish biomass but very little of the nonmigratory fish biomass (Clarke 1982, Sutton & Hopkins 1996). This finding emphasizes the energetic connections among the epi-, meso-, and bathypelagic zones.

The vast majority of micronektonivorous deep-pelagic fishes are strictly or nearly strictly piscivorous (Sutton & Hopkins 1996). Predation primarily centered on macrocrustaceans (e.g., shrimps and mysidaceans) appears to be fairly restricted in the open pelagic but a major trophic linkage in some outer continental shelf environments [e.g., snipe eels (Nemichthyidae) of the Northwest Atlantic; Feagans-Bartow & Sutton 2014]. If very large euphausiids (>1.5 cm) are included as micronekton prey, then large, cold-water myctophids can be included in this guild. For example, the three dominant lanternfishes of the northern California Current system (*Tarletonbeania crenularis*, *Diaphus theta*, and *Stenobrachius leucopsarus*) all consume the dominant euphausiid, *Euphausia pacifica* (Suntsov & Brodeur 2008). As with macrocrustacean predation, cephalopod predation appears to be restricted to a relatively small number of deep-pelagic fish taxa (e.g., Evermannellidae), although the gear selectivity of standard rectangular midwater trawls may prevent the collection of fishes large and mobile enough to prey on oceanic cephalopods (Vecchione & Roper 1991).

The final pelagic feeding guild is that of generalists. Although the majority of deep-pelagic feeding studies have focused on mesopelagic taxa, there are few examples that truly corroborate the "eat anything you see in a food-poor environment" hypothesis, with most taxa being fairly predictable in their primary prey. True generalism may be more prevalent in bathypelagic depths, where adaptations to food limitation reach their end point: an enormous gape, reduced musculature, and reduced visual predation (inferred from decreased eye/head length ratios). These adaptations are exemplified by the Saccopharyngiformes (gulper eels), in which a wide variety of prey, even benthic forms, have been reported (Gartner et al. 1997). The meso-to-bathypelagic fangtooth *Anoplogaster cornuta* (**Figure 1*c***) likely fits in this category, with scant records indicating a wide prey spectrum (Hopkins et al. 1996). Much more diet analysis is needed for the bathypelagic fishes.

FEEDING RATES

Assessments of the impacts of predators on their prey populations, the flux of carbon, and the connectivity between neighboring ecosystems all require estimates of feeding rates, which are sorely lacking. For demersal species, two approaches have been employed. First, feeding rates have been estimated by integrating estimates of stomach fullness and measurements of the rates of gastric evacuation (Bromley 1994, Heroux & Magnan 1996), which requires extrapolation from data for shallow-water species. Second, bioenergetic modeling approaches have been used that sum the measured energy needs of an animal, metabolism, growth, reproduction, and so on, which is assumed to be equivalent, on average, to the feeding rate. This approach is quite data intensive and has been applied only a few times for deep-sea fishes (**Table 2**).

In general, the data available for demersal species suggest very low feeding rates (**Table 2**) compared with those of shallow-water species, for which the daily ration is often 2–5% of body weight at temperatures of 5–10°C (Bromley 1994, Livingston & Goiney 1984). From the available rates, a few general conclusions can be made. First, most of the values come from fishes in the warm (13–15°C) Mediterranean, where a long-term study of the slope food web has been carried out. Temperature is one of the most important determinants of feeding rates in fishes (Bromley 1994), so the generality of the results across all deep habitats is questionable. Rates for species living at cooler temperatures come from one study of gastric evacuation in *Hoplostethus atlanticus* and one study of several macrourids that used energy budget methods. *H. atlanticus* is a very active fish, but it exhibits a daily ration of ∼1% of its body weight, much lower than the rations of some of the fishes from the Mediterranean, as would be expected based solely on temperature differences. The macrourids have an incredibly low daily ration (∼0.1% of body weight), at the low end of all the measurements, but this is not entirely unexpected given that they have slow growth rates and metabolic rates that are approximately one-tenth of those of shallow-living cods at similar temperatures (Drazen & Seibel 2007). It is not yet clear whether differences among species are the result of different methods, ecologies, temperatures, or other factors, and more studies of species using both approaches for comparison are needed. This will be a great challenge because the energy budget approaches require direct measurements of metabolic rate and validated growth rates with which to estimate energy requirements (Drazen 2002).

It seems clear that deep-sea demersal fishes have relatively low feeding rates, but some caution is required in using the data quantitatively. For the energy budget approaches, metabolic expenditures often represent resting or routine rates; active metabolic requirements would increase the feeding-rate estimates. For the gastric evacuation methods, the rates of evacuation are a critical input. For example, Bulman & Koslow (1992) sampled a single fish population every 3 h over a period of 42 h and found a peak in fullness near midnight followed by a dramatic decline. Other studies (Madurell & Cartes 2005b, 2006) found no regular declines in stomach fullness across multiple times of sampling, so they pooled data across days to average declines or used published relationships between gastric evacuation rates and temperatures from shallow-water fishes. A few consumption-to-biomass rates have been reported in the literature (Trueman et al. 2014), but

Table 2 Estimated feeding rates (daily ration as a percentage of body weight) for demersal deep-sea fishes

Species	Depth (m)	Temp. (°C)	Length (cm)[a]	Method	DR (% bw)	Reference(s)
Alepocephalus rostratus	984–2,169	13.0	10–37	GE	0.17–0.40	Modica et al. 2014
Coelorhynchus coelorhynchus	473–603	14.5	3–9 (PAL)	GE	2.08–2.92	Madurell & Cartes 2005b, 2006
Coelorhynchus fasciatus	300–350	9.5	15–29	GE	0.55–2.15	Macpherson 1985
Coryphaenoides acrolepis	700–2,000[b]	2–5[c]	NA	EB	0.10	Koslow 1996
	700–2,000[b]	2–5[c]	3–27 (PAL)	EB	0.07–0.31	Drazen 2002
Coryphaenoides armatus	2,000–4,100[b]	1–3[c]	3–34 (PAL)	EB	0.02–0.12	Drazen 2002
Coryphaenoides guentheri	1,409–2,202	13.0	5–20	GE	0.10–0.32	Modica et al. 2014
Coryphaenoides mediterraneus	1,468–2,251	13.0	8–29	GE	0.62	Modica et al. 2014
Coryphaenoides rupestris	400–1,500[b]	NA	NA	EB	0.05	Koslow 1996
Etmopterus spinax	473–603	14.5	9–35	GE	2.11–4.27	Madurell & Cartes 2005b
Galeus melastomus	473–603	14.5	12–48	GE	1.49–3.65	Madurell & Cartes 2005b
Helicolenus dactylopterus	300–350	9.5	15–29	GE	0.16–0.68	Macpherson 1985
	473–603	14.5	9–30	GE	0.28–0.86	Madurell & Cartes 2005b
Hoplostethus atlanticus	700–1,200	3.7–6.5[c]	<30	GE	0.91	Bulman & Koslow 1992
	700–1,200	3.7–6.5[c]	>30	GE	1.15	Bulman & Koslow 1992, Koslow 1996
Hoplostethus mediterraneus	473–603	14.5	7–23	GE	0.14–0.39	Madurell & Cartes 2005a
Hymenocephalus italicus	473–603	14.5	2–4 (PAL)	GE	1.47–1.51	Madurell & Cartes 2005b, 2006
Lepidion lepidion	986–2,024	13.0	4–29	GE	0.65–0.91	Modica et al. 2014
Lepidorhombus boscii	473–603	14.5	13–38	GE	0.76–0.77	Madurell & Cartes 2005b
Lophius upsicephalus	300–350	9.5	30–59	GE	0.55–1.60	Macpherson 1985
Nezumia sclerorhynchus	473–603	14.5	2–5 (PAL)	GE	0.42–0.72	Madurell & Cartes 2005b, 2006
Polyacanthonotus rissoanus	984–2,251	13.0	11–21	GE	0.05–0.25	Modica et al. 2014

Abbreviations: DR (% bw), daily ration as a percentage of body weight; EB, energy budget; GE, gastric evaluation; NA, not available from the reference; PAL, preanal fin length; temp., temperature.

[a] Lengths are total lengths except for those labeled with "(PAL)," which are preanal fin lengths.

[b] Values are approximates from depth ranges of species where most energy terms were determined.

[c] Temperatures were not reported in the study; these values are based on depth range and location extracted from Locarnini et al. (2013).

these are also based on extrapolations from shallow-water species. Although it is admirable and useful that these authors produced these estimates, the estimates must be applied with some caution. Energetic processes such as metabolic rates decline with depth faster than would be expected from temperature changes alone (Drazen & Seibel 2007). There is no information on whether digestive rates of deep-sea fishes deviate from empirical temperature relationships derived from shallow-water species, but lower gastric evacuation rates seem reasonable. Given the need to place demersal fishes into an ecosystem context, much more work on estimates of feeding rates is needed.

Many more feeding-rate estimates are available for pelagic species, largely because more direct methodologies are applicable to their ecology. Specifically, regurgitation is less of a problem, and these smaller fishes, many of which are migratory, often exhibit diel feeding periodicity, which provides a time element for rate estimation. The most common method involves quantitative gut content analysis, with the ration [(prey weight) · (predator weight)$^{-1}$, usually expressed as dry-weight ratio] standardized per day via diel gastric evacuation estimation (see references in **Table 3**). Bioenergetics models have also been used to estimate the expected daily ration requirement based on metabolic and biochemical parameters (Childress et al. 1980, Davison et al. 2013). Although all methods of estimating feeding rates make inherent assumptions, the results overall suggest that most mesopelagic fishes consume somewhere between 0.5% and 5.0% of their body weight daily, higher than for most demersal species, ostensibly because mesopelagic fishes are smaller and often occupy warmer waters, at least at night. Although no data on this aspect exist, it is logical that the rations for bathypelagic species would be smaller owing to decreases in metabolism relative to mesopelagic fishes. Given the enormity of the bathypelagic realm and relatively high bathypelagic fish biomass reported for some regions (e.g., midocean ridge systems; Sutton et al. 2008), this represents another primary data gap in deep-sea research.

TROPHIC BIOMARKERS

Many of the challenges of stomach content analysis in deep-sea fishes (**Figure 3**), such as barotrauma-associated regurgitation, the short temporal representation of gut contents, and differential digestion of potentially important prey taxa (e.g., gelata), are being addressed using alternative methods. Historically, indirect methods have included the use of functional morphology, endoparasites and knowledge of their intermediate hosts (Campbell et al. 1980), and cross-reacting antisera to identify digested prey in stomach and intestinal fluids (Feller et al. 1985).

In the last ~15 years, the application of biochemical trophic biomarkers, notably stable isotopes and fatty acids (FAs), to the trophic ecology of deep-sea fishes has rapidly expanded. Nitrogen stable-isotope compositions ($\delta^{15}N$) can be highly effective tools for determining trophic position because animals fractionate the nitrogen in their diets, preferentially retaining the heavier isotope and becoming higher in $\delta^{15}N$ relative to their prey by 2–4‰ (Post 2002). Carbon isotopes ($\delta^{13}C$) fractionate much less with each trophic step and have been used to infer basal sources of nutrition. Furthermore, both $\delta^{15}N$ and $\delta^{13}C$ values of primary producers change because of different physiologies and primary molecular pools (Peterson & Fry 1987). Deep-sea fishes have nitrogen-containing osmolytes and high lipid contents that can affect $\delta^{15}N$ and $\delta^{13}C$, respectively, but these can be accounted for with proper sample preparation (Churchill et al. 2015a, Hoffman & Sutton 2010). FA biomarkers are based on the principles that organisms have unique FA and sterol profiles and that many of these lipid biomarkers are transferred from predator to prey without modification. Animals typically have 30 or more FAs and 10–20 sterols, which can be used to infer trophic connections. An advantage of stable isotopes and FA biomarkers is that they integrate the feeding history of the animal over long timescales (weeks to months or more). Stable isotopes and FA biomarkers are widely used, and we refer readers to other reviews for more information on this topic (e.g., Dalsgaard et al. 2003, Peterson & Fry 1987).

Trophic biomarkers have been used successfully to elucidate trophic level, important prey types, and trophic niche breadth. Many isotope studies (e.g., Boyle et al. 2012, Pethybridge et al. 2012) have identified ~3–5 trophic levels, with benthic fishes often having a greater number of trophic levels, corresponding to a greater number of trophic guilds. Interestingly, in some cases benthic

Table 3 Estimated feeding rates (daily ration as a percentage of body weight) for pelagic deep-sea fishes

Species	Depth (m)	Method	DR (% bw)	Location	Reference
Astronesthes spp.	200–1,000	GCA	4.2	Gulf of Mexico	Sutton & Hopkins 1996
Ceratoscopelus warmingii	0–1,500	GCA	2.4–3.8	Off Hawaii	Clarke 1978
Danophos oculatus	450–650	GCA	1.9	Off Hawaii	Clarke 1978
Danophos oculatus (est.)	0–550	EB	1.1	NA	Childress et al. 1980
Diaphus hudsoni	0–300	GCA	2.1	Off South Africa	Pakhomov et al. 1996
Diaphus schmidti	0–1,000	GCA	1.3–1.7	Off Hawaii	Clarke 1978
Diaphus taaningi	0–250	GCA	0.8	Cariaco Trench	Hopkins & Baird 1977
Diaphus theta	0–500	GCA	1.5–3.2	Northwest Pacific	Kosenok et al. 2006
Electrona carlsbergi	0–300	GCA	1.6–2.9	Off South Africa	Pakhomov et al. 1996
Gonostoma atlanticum	0–1,000	GCA	2.4–3.2	Off Hawaii	Clarke 1978
Gonostoma elongatum	0–1,000	GCA	3.3–4.9	Off Hawaii	Clarke 1978
Gymnoscopelus bolini	0–300	GCA	1.8–3.3	Off South Africa	Childress et al. 1980
Gymnoscopelus nicholsi	0–300	GCA	0.8–1.3	Off South Africa	Childress et al. 1980
Hygophum hanseni	700–1,500	GCA	1.9	Off Australia	Williams et al. 2001
Hygophum hygomii	0–400	GCA	0.98	Great Meteor Seamount	Pusch et al. 2004
Hygophum proximum	0–1,000	GCA	5.7	Off Hawaii	Clarke 1978
Hygophum proximum (est.)	0–550	EB	5.0	NA	Childress et al. 1980
Lampanyctus niger	0–2,000	GCA	0.7–1.9	Off Hawaii	Clarke 1978
Myctophum asperum	0–86	GCA	1.9	Northwest Pacific	Takagi et al. 2009
Protomyctophum normani	0–300	GCA	2.3–4.3	Off South Africa	Childress et al. 1980
Stenobrachius leucopsaras	20–701	GCA	0.8–1.1	Off Japan	Moku et al. 2000
Stenobrachius nannochir	20–701	GCA	0.07–0.11	Off Japan	Moku et al. 2000
Tarletonbeania crenularis	30–50	GCA	2.2–3.7	California Current	Suntsov & Brodeur 2008
Triphoturus nigrescens	0–1,000	GCA	4.3–4.5	Off Hawaii	Clarke 1978
Valenciennellus tripunctulatus	180–580	GCA	1.4–3.9	Gulf of Mexico	Baird & Hopkins 1981
Vinciguerria nimbaria	0–1,000	GCA	2.6–5.6	Off Hawaii	Clarke 1978

Abbreviations: DR (% bw), daily ration as a percentage of body weight; EB, energy budget; est., estimated using a proxy taxon; GCA, gut content analysis; NA, not applicable.

fishes do not have the highest δ^{15}N values, but sea stars and predatory polychaetes were interpreted as occupying the highest trophic levels (Bergmann et al. 2009, Iken et al. 2001, Polunin et al. 2001), a finding discussed below. FA signatures or profiles provide more taxon-specific information than isotopes do. For instance, Stowasser et al. (2009) found two trophic guilds of Southern Ocean myctophids, with one having FA profiles that suggested feeding on euphausiids and amphipods and the other having FA profiles that suggested a diet predominantly of copepods. Species with unknown diets grouped with these two guilds, providing new trophic classifications. Pethybridge et al. (2011) applied FA signature analysis across a suite of slope-dwelling sharks in Australia and found that the profiles could be used to classify chimaeras as benthic consumers; dogfish as predators on micronekton; cat sharks as predominantly cephalopod predators; and deeper-living, larger dogfish as micronektonivores and scavengers on marine mammals.

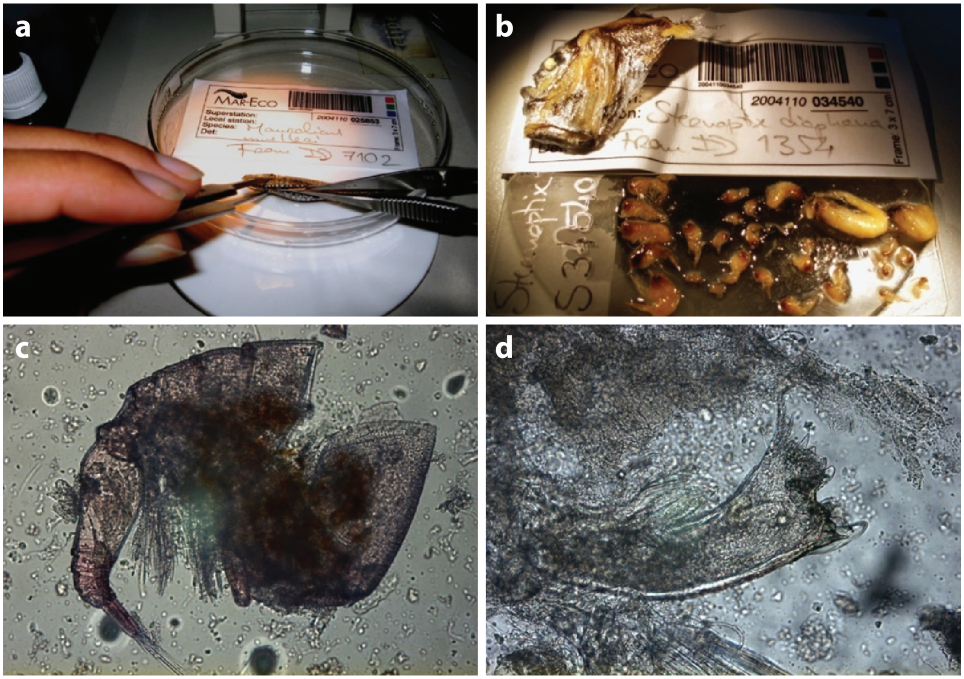

Figure 3

Stomach content analysis. (*a*) Dissection of a mesopelagic hatchetfish. (*b*) Dissected fish with stomach prey items displayed on a glass slide. After dissection, prey items are preserved in vials (for whole animals) or glass slides (for body parts and unidentifiable material) for further identification to the lowest possible taxonomic level. (*c*,*d*) Microscope pictures of a copepod (panel *c*) and a mandible (panel *d*) on glass slides. Hard body parts, such as crustacean mandibles, polychaete setae, uropods, fish eye lenses, and otoliths, can be used to identify prey items.

Biomarkers have also been useful in evaluating ontogenetic and seasonal diet shifts, where large-sample-size requirements for gut content analysis were difficult to meet. For instance, *Antimora rostrata* has size-related increases in δ^{15}N and δ^{13}C values, suggestive of ontogenetic increases in trophic level (Reid et al. 2013). Antarctic deep-sea notothenioid fishes exhibited declining amounts of monounsaturated FAs with size, suggesting a shifting reliance away from pelagic zooplankton (Würzberg et al. 2011). Polunin et al. (2001) did not find seasonal shifts in isotopic values of bathyal fishes and proposed that their long tissue turnover times prevented such signals from being incorporated. However, Fanelli & Cartes (2010) did find seasonal signals in demersal fishes that consumed pelagic prey, and Valls et al. (2014a) found seasonal isotopic shifts in mesopelagic fishes, suggesting that fishes more closely tied to surface food webs may be more likely to exhibit seasonal changes in feeding ecology.

One of the most useful applications of isotopic biomarker techniques is the identification of different general food sources. Because the carbon signature of primary production can vary (i.e., between macroalgae and phytoplankton), food webs that show a linear relationship between δ^{15}N and δ^{13}C values are suggestive of a single food source (Polunin et al. 2001). Work in the Mediterranean has shown that regions with terrestrial inputs of carbon from rivers show a large scatter in the relationship, whereas sites away from such inputs show a linear relationship (Fanelli et al. 2011). Inshore-to-offshore changes in δ^{13}C values are apparent in epipelagic fishes (Miller et al.

2008) but have not been evaluated in deep-sea species. Regional differences in δ^{15}N values, caused by changes in oceanographic processes and nitrogen sources for primary producers, are apparent in some epi- and mesopelagic fishes and could be used to infer the importance of different regions or types of production for mobile species (Flynn & Kloser 2012). Chemosynthetic production has strong δ^{13}C and δ^{34}S signatures, which have been used to determine that resident fishes make strong use of cold-seep biomass, whereas more mobile species make limited or no use of this biomass (MacAvoy et al. 2002, Zapata-Hernandez et al. 2014).

It is also now apparent that the longer benthic food web supported by microbially degraded phytodetritus results in higher isotopic values of nitrogen and carbon compared with the pelagic food web (Papiol et al. 2013, Romero-Romero et al. 2016). δ^{15}N values of sinking phytodetritus increase with depth along with those of the zooplankton (Hannides et al. 2013), benthic suspension feeders (Mintenbeck et al. 2007), some fishes, and other taxa (Valls et al. 2014b). These patterns have been successfully used to identify pelagic sources of nutrition. For instance, the isotopic composition of pelagic-derived carrion was lower in δ^{15}N compared with potential benthic invertebrate prey of abyssal Pacific macrourids. Isotopic mixing models illustrated that the carrion was a substantial food source for the fishes (Drazen et al. 2008), a finding corroborated by stomach content and FA biomarker techniques (Drazen et al. 2009). In the North Atlantic, Trueman et al. (2014) used the isotopic signatures of the demersal fish community along with community survey data to illustrate the depth-varying importance of vertically migrating prey. In this case, benthopelagic fishes feeding on pelagic migrants had lower δ^{15}N values that did not change with depth, but the benthic fishes, which rely on a microbially reworked benthic food web, had increasing δ^{15}N with depth. Where the isotopic values of the groups diverged, there was a peak in benthopelagic fish biomass arguably caused by reduced competition with benthic fishes. There are clearly important isotopic enrichments with depth that have not been fully explored but have great potential for advancing our understanding of vertical food-web coupling.

Compound-specific approaches are helping to refine isotopic and FA techniques to great effect. Compound-specific isotopic analysis of amino acids has proven to be an excellent tool for evaluating both trophic positions and general food sources (Chikaraishi et al. 2009). One group of source amino acids does not fractionate with trophic steps and reflects the basal isotopic signature of the food web, whereas another group of trophic amino acids fractionates 7‰ on average. Thus, the difference between the source and trophic amino acids can be used to estimate the trophic level of the animals without the need for samples of detritus or phytoplankton to determine the isotopic baseline. Choy et al. (2012) used these methods to find that large differences (~6‰ within a taxon) in the δ^{15}N of myctophids and stomiids across ocean basins were the result of shifting isotopic baselines and not changes in trophic position. Furthermore, source-amino-acid values of mesopelagic fishes increase with depth, becoming closer to values of small suspended or slowly sinking particles (Choy et al. 2015), which suggests possible links to this poorly understood food source.

Further refinements are also required for FA approaches because the underlying assumption of "you are what you eat" is not proving to be straightforward. Fishes can synthesize a variety of FAs, and essential FAs may be preferentially routed to particular tissues and retained. FA analysis of the abyssal macrourid *C. armatus* has shown considerable consistency across regions and between studies spanning ocean basins, which suggests a strong physiologically generated or conserved component of the fishes' FA profiles (Mayor et al. 2013). Storage lipids differ from membrane-bound phospholipids in physiological function, so future studies reporting lipid-class composition and employing lipid-class-specific FA analysis will be profitable.

Other exciting but barely used trophic biomarkers in deep-sea fishes are molecular prey identification and mercury isotopes. The DNA of individual prey or perhaps even intestinal fluids has now been used to identify digested prey (Paquin et al. 2014) and might be very effective with gelatinous prey. Mercury concentrations increase with depth in fishes (Choy et al. 2009). Methylmercury is microbially formed in deeper, lower-oxygen waters (Blum et al. 2013), and thus mercury likely enters the food web at mesopelagic depths, providing a potential tracer for depth of forage.

VERTICAL CARBON FLUX

The concentration of carbon dioxide in the atmosphere would be 50% higher without the mitigating effects of the oceanic biological carbon pump (Parekh et al. 2006). Evidence for vertical migrations contributing to export of organic material has been well documented (e.g., Steinberg et al. 2000). Metazoan feeding in surface waters followed by migration to depth, with concomitant evacuation, is called active or migratory vertical flux. It is thought to account for sediment trap observations of flux maxima at mesopelagic depths (Robinson et al. 2010). Given their ubiquity, high biomass, and moderate feeding rates, mesopelagic fishes contribute substantially to this biological carbon pump. As mentioned above, global estimates of mesopelagic fish biomass have recently increased by an order of magnitude. The efficiency of energy transferred from primary producers to higher trophic levels through midwater fishes also appears to be higher than previously thought, with mesopelagic fishes respiring an estimated 10% of primary production at depth globally (Irigoien et al. 2014). Hopkins et al. (1996) estimated that mesopelagic fishes in the eastern Gulf of Mexico consume 5–10% of daily zooplankton production, an estimate based on trawl-derived fish abundance and biomass. If this estimate is scaled up, as suggested by recent works, then it appears that mesopelagic fishes (and likely shrimps) consume the majority of zooplankton production in this low-latitude system, a finding corroborated by the carbon flux modeling of Rowe (2013). In other ecosystems, deep-pelagic fishes play a significant role in vertical carbon flux, accounting for 10–20% at depths near 200 m in the North Pacific (Davison et al. 2013) and perhaps as much as 70% at depths of 750–1,000 m in the North Atlantic (Hudson et al. 2014). Davison et al. (2013) estimated that the carbon export by mesopelagic fishes in the California Current is 15–17% of the total export. A model of the Antarctic pelagic subsystem suggested that ~23% of total primary production may be indirectly ingested by pelagic fishes and squid (Huntley et al. 1991), thus accounting for a substantial export of organic carbon from the euphotic zone in this region.

Also poorly studied is the vertical transport of carbon by demersal fishes, which could be substantial along continental margins, seamounts, and ridges, where vertically migrating micronekton impinge on the seafloor and are consumed. Demersal micronektonivores are a substantial component of the fauna at midslope depths (between ~500 and 1,500 m), which coincides with maxima in fish diversity and often abundance (Fanelli et al. 2013, Trueman et al. 2014). The consumption of vertical migrants provides a direct link between the epi- and mesopelagic and the benthic environment (Mauchline & Gordon 1991). Although this flux is incorporated into the epipelagic export flux estimates discussed above through the model's mortality terms, it is important to consider in terms of the energy pathways leading to demersal fish production (**Figure 2**). Trueman et al. (2014) suggested that this link supports as much as 50% of benthic fish production at midslope depths. Similar trophic links are found on seamounts, where many species are micronektonivores (**Figure 2**, **Table 1**), and the interception of laterally advected prey or those impinging on the seafloor during downward migrations at dawn leads to high biomass of demersal and large pelagic fishes (Hirch & Christiansen 2010, Morato & Clarke 2007).

ANTHROPOGENIC EFFECTS

Deep-sea ecosystems are increasingly threatened by anthropogenic activities. Fisheries have extended to depths of ~1,400 m (Morato et al. 2006), although their impacts may extend appreciably deeper (Bailey et al. 2009), and deep-sea fishing has been widespread in both national and international waters (e.g., Clark et al. 2007). The interest in mining deep-sea minerals has grown rapidly in the last decade (Ramirez-Llodra et al. 2011, Wedding et al. 2015). The spatial scale of these activities may be unprecedented. The area already claimed for mining in the abyssal Clarion-Clipperton Fracture Zone is equivalent to 80% of the area of the continental United States. The number of mining exploration claims granted by the International Seabed Authority has jumped from 8 to 26 in the last five years (Wedding et al. 2015). The deep ocean will also be affected by global climate change through effects such as acidification (Barry et al. 2013, Ramirez-Llodra et al. 2011); expansion of oxygen minimum zones (Gilly et al. 2013); and, in many areas, reductions in surface-water production and thus food supply to deep-pelagic and seafloor communities (Jones et al. 2014, Smith et al. 2013). Additionally, pollutants (often bioaccumulated through food webs) and the increasingly obvious pervasion of plastics in the marine environment stand to alter the structure and function of these ecosystems.

Many of these anthropogenic perturbations have or will alter species abundances, distributions, and community composition and thus food-web structures. More difficult to observe are actual long-term changes in ecosystem function, particularly in the diets of species and the strength of food-web linkages. Fishes have evolved physiologically and morphologically to fill a particular trophic niche. For example, most piscivores are probably incapable of becoming gelativores. But trophic changes with regard to certain prey species within a prey group could certainly occur and—depending on their nutritional value, ease of capture, and other factors—could greatly affect the success and productivity of deep-sea fishes. Such changes are likely to be nuanced. Large programs working with commercially harvested species are beginning to document diet changes over decades in response to changing environmental conditions (e.g., Olson et al. 2014). For example, the diet of a myctophid changed over decades in the North Pacific in response to changes in prey availability, notably sardine larvae (Watanabe & Kawaguchi 2003). Similar studies, augmented with biomarkers, might be possible for a number of deep-sea fishes where long-term monitoring has been performed. These types of studies could inform and ground-truth ecosystem models.

Plastics are present throughout the marine environment, including the deep ocean (Schlining et al. 2013, Woodall et al. 2014), and are directly consumed by deep-sea fishes (Boerger et al. 2010, Choy & Drazen 2013, Davison & Asch 2011), so they represent a different class of anthropogenic effect on trophic ecology. Plastics are likely mistaken for regular prey, perhaps because they have bioluminescent biofilms or in some cases mimic translucent prey, such as salps. Plastics can cause gut blockages and can adsorb contaminants from the water, which are then delivered to the fish when they are solubilized in an acidic stomach (Rochman et al. 2013). Future stomach content work should evaluate plastic ingestion quantitatively so that we can develop a better appreciation for what species consume it, why they do so, and ultimately what effects this will have on deep-sea-fish populations.

SUMMARY POINTS

1. Rather than being generalists that eat whatever they come across, deep-sea fishes can be placed in feeding guilds. Demersal species have more guilds than deep-pelagic species.

2. Feeding on pelagic micronekton is a dominant feeding mode among demersal fishes, and the consumption of vertically migrating prey at bathyal depths links deep-pelagic and bathyal communities.
3. Scavenging is an important facultative foraging mode for many demersal fishes, and the availability of epipelagic carrion, a major diet component, likely affects the distribution and abundance of demersal fishes.
4. Gelatinous plankton provide a food resource for both demersal and pelagic species, and its importance as a nutritional source has likely been underestimated.
5. The feeding rates of deep-sea fishes are generally lower than those of coastal and epipelagic fishes. The feeding rates of deep-pelagic fishes exceed those of demersal fishes by up to an order of magnitude, likely owing to their smaller size and the higher temperatures of the waters in which they live. Feeding rates for demersal species have been calculated largely from the vital rates of shallow-water species and therefore may have been overestimated.
6. Trophic biomarkers have proven very useful in establishing trophic positions, identifying important prey, and describing ontogenetic diet changes of deep-sea fishes, which has helped overcome several methodological obstacles. Analysis of stable isotopes has proven particularly useful in identifying food sources such as chemosynthetic production, carrion, and benthic versus pelagic prey.
7. The historic underestimation of the biomass of mesopelagic fishes, and likely that of bathypelagic fishes, emphasizes the need for trophic research on the fauna and its role in the vertical transport of carbon to depth.
8. Anthropogenic effects such as climate change, oxygen minimum zone expansion, fishing, and mining will broadly alter deep-sea ecosystems. The resulting effects on the trophic ecology of deep-sea fishes will occur through major changes in community composition and thus alteration of food-web structures.

FUTURE ISSUES

1. The diets of bathypelagic fishes are almost entirely unknown, yet their biomass and importance to the vertical connectivity of food webs are likely large. More study of this ecosystem is warranted, and investigation of the trophic ecology of these fishes should be included.
2. Studies of mesopelagic assemblages and bathyal communities are usually conducted separately. However, it is clear that bathyal micronektonivores, through their consumption of vertically migrating prey, may transport significant amounts of organic matter into benthic environments. Surface-to-seafloor studies should be conducted to better parameterize these connections.
3. Given the importance of rate information to ecosystem and biogeochemical models, which can elucidate the importance of the feeding of deep-sea fishes in a global context, much more work is needed on estimating the feeding rates of deep-sea fishes. In particular,

more estimates are needed for demersal and bathypelagic fishes. This work will be challenging and will depend on measuring or estimating appropriate vital rates, such as metabolism and growth.

4. Compound-specific approaches (e.g., amino-acid-specific isotopes and lipid-class-specific fatty-acid signatures) will greatly improve the usefulness of biomarkers, particularly with regard to identifying important prey and primary food-web pathways leading to deep-sea-fish production. Molecular approaches to prey identification could greatly expand the detail of deep-sea food webs if libraries of prey species sequence data can be amassed.
5. Many biogeochemical models do not consider active flux; thus, the role of mesopelagic fishes in exporting carbon to depth is a major outstanding issue with respect to the biological carbon pump and its parameterization. Quantifying active flux by fishes and including active flux in models should be a priority for international biogeochemical research.
6. More effort is needed to integrate knowledge of deep-sea-fish feeding ecology into ecosystem models, particularly to evaluate the effects of climate change and other anthropogenic activities. Such efforts could be accompanied by long-term studies of the trophic ecology of fishes in the deep sea, where time-series studies are already under way.

DISCLOSURE STATEMENT

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LITERATURE CITED

Anderson M. 2005a. Food habits of some deep-sea fish off South Africa's west coast and Agulhas Bank. 1. The grenadiers (Teleostei: Macrouridae). *Afr. J. Mar. Sci.* 27:409–25

Anderson M. 2005b. Food habits of some deep-sea fish off South Africa's west coast and Agulhas Bank. 2. Eels and spiny eels. *Afr. J. Mar. Sci.* 27:557–66

Angel MV. 1997. What is the deep sea? In *Deep-Sea Fishes*, ed. DJ Randall, AP Farrell, pp. 1–41. San Diego, CA: Academic

Angel MV, Baker AC. 1982. Vertical distribution of the standing crop of plankton and micronekton at three stations in the northeast Atlantic. *Biol. Oceanogr.* 2:1–30

Arai MN, Welch DW, Dunsmuir AL, Jacobs MC, Ladouceur AR. 2003. Digestion of pelagic Ctenophora and Cnidaria by fish. *Can. J. Fish. Aquat. Sci.* 60:825–29

Bailey DM, Collins MA, Gordon JDM, Zuur AF, Priede IG. 2009. Long-term changes in deep-water fish populations in the northeast Atlantic: a deeper reaching effect of fisheries? *Proc. R. Soc. B* 276:1965–69

Baird RR, Hopkins TL. 1981. Trophodynamics of the fish *Valenciennellus tripunctulatus*. III. Energetics, resources and feeding strategy. *Mar. Ecol. Prog. Ser.* 5:21–28

Balanov AA, Gorbatenko KM, Efimkin A. 1995. Foraging dynamics of mesopelagic fishes in the Bering Sea during summer and autumn. *J. Ichthyol.* 35:65–77

Barnes C, Maxwell D, Reuman DC, Jennings S. 2010. Global patterns in predator-prey size relationships reveal size dependency of trophic transfer efficiency. *Ecology* 91:222–32

Barry JP, Buck KR, Lovera C, Brewer PG, Seibel BA, et al. 2013. The response of abyssal organisms to low pH conditions during a series of CO_2-release experiments simulating deep-sea carbon sequestration. *Deep-Sea Res. I* 92:249–60

Bergmann M, Dannheim J, Bauerfeind E, Klages M. 2009. Trophic relationships along a bathymetric gradient at the deep-sea observatory HAUSGARTEN. *Deep-Sea Res. I* 56:408–24

Bergstad OA, Clark L, Hansen HØ, Cousins N. 2012. Distribution, population biology, and trophic ecology of the deepwater demersal fish *Halosauropsis macrochir* (Pisces: Halosauridae) on the Mid-Atlantic Ridge. *PLOS ONE* 7:e31493

Bergstad OA, Gjelsvik G, Schander C, Høines ÅS. 2010. Feeding ecology of *Coryphaenoides rupestris* from the Mid-Atlantic Ridge. *PLOS ONE* 5:e10453

Bernal A, Olivar MP, Fernández de Puelles ML. 2013. Feeding patterns of *Lampanyctus pusillus* (Pisces: Myctophidae) throughout its ontogenetic development. *Mar. Biol.* 160:81–95

Bernal A, Olivar MP, Maynou F, de Puelles MLF. 2015. Diet and feeding strategies of mesopelagic fishes in the western Mediterranean. *Prog. Oceanogr.* 135:1–17

Billett DSM, Bett BJ, Jacobs CL, Rouse IP, Wigham BD. 2006. Mass deposition of jellyfish in the deep Arabian Sea. *Limnol. Oceanogr.* 51:2077–83

Bjelland O, Bergstad OA, Skjaeraasen JE, Meland K. 2000. Trophic ecology of deep-water fishes associated with the continental slope of the eastern Norwegian Sea. *Sarsia* 85:101–17

Blaber SJM, Bulman CM. 1987. Diets of fishes of the upper continental slope of eastern Tasmania: content, calorific values, dietary overlap and trophic relationships. *Mar. Biol.* 95:345–56

Blum JD, Popp BN, Drazen JC, Choy CA, Johnson MW. 2013. Methylmercury production below the mixed layer in the North Pacific Ocean. *Nat. Geosci.* 6:879–84

Boerger CM, Lattin GL, Moore SL, Moore CJ. 2010. Plastic ingestion by planktivorous fishes in the North Pacific Central Gyre. *Mar. Pollut. Bull.* 60:2275–78

Boyle MD, Ebert DA, Cailliet GM. 2012. Stable-isotope analysis of a deep-sea benthic-fish assemblage: evidence of an enriched benthic food web. *J. Fish Biol.* 80:1485–507

Britton JC, Morton B. 1994. Marine carrion and scavengers. In *Oceanography and Marine Biology: An Annual Review*, Vol. 32, ed. AD Ansell, RN Gibson, M Barnes, pp. 369–434. London: UCL Press

Bromley PJ. 1994. The role of gastric evacuation experiments in quantifying the feeding rates of predatory fish. *Rev. Fish Biol. Fish.* 4:36–66

Buckley TW, Tyler GE, Smith DM, Livingston PA. 1999. *Food habits of some commercially important groundfish off the coasts of California, Oregon, Washington, and British Columbia*. NOAA Tech. Memo. NMFS-AFSC-102, Natl. Ocean. Atmos. Adm., US Dep. Commer., Springfield, VA

Bulman CM, Koslow JA. 1992. Diet and food consumption of a deep-sea fish, orange roughy *Hoplostethus atlanticus* (Pisces: Trachichthyidae), off southeastern Australia. *Mar. Ecol. Prog. Ser.* 82:115–29

Campbell RA, Haedrich RL, Munroe TA. 1980. Parasitism and ecological relationships among deep-sea benthic fishes. *Mar. Biol.* 57:301–13

Carrasson M, Cartes JE. 2002. Trophic relationships in a Mediterranean deep-sea fish community: partition of food resources, dietary overlap and connections within the benthic boundary layer. *Mar. Ecol. Prog. Ser.* 241:41–55

Carrasson M, Matallanas J. 1998. Feeding habits of *Alepocephalus rostratus* (Pisces: Alepocephalidae) in the western Mediterranean Sea. *J. Mar. Biol. Assoc. UK* 78:1295–306

Carrasson M, Matallanas J. 2001. Feeding ecology of the Mediterranean spiderfish, *Bathypterois mediterraneus* (Pisces: Chlorophthalmidae), on the western Mediterranean slope. *Fish. Bull.* 99:266–74

Carrasson M, Matallanas J. 2002a. Feeding habits of *Cataetyx alleni* (Pisces: Bythitidae) in the deep western Mediterranean. *Sci. Mar.* 66:417–21

Carrasson M, Matallanas J. 2002b. Feeding strategies of *Polyacanthonotus rissoanus* (Pisces: Notacanthidae) in the deep western Mediterranean. *J. Mar. Biol. Assoc. UK* 82:665–71

Carrasson M, Matallanas J, Casadevall M. 1997. Feeding strategies of deep-water morids on the western Mediterranean slope. *Deep-Sea Res. I* 44:1685–99

Carrasson M, Stefanescu C, Cartes JE. 1992. Diets and bathymetric distributions of two bathyal sharks of the Catalan deep sea (western Mediterranean). *Mar. Ecol. Prog. Ser.* 82:21–30

Chikaraishi Y, Ogawa NO, Kashiyama Y, Takano Y, Suga H, et al. 2009. Determination of aquatic food-web structure based on compound-specific nitrogen isotopic composition of amino acids. *Limnol. Oceanogr. Methods* 7:740–50

Childress JJ, Taylor SM, Cailliet GM, Price MH. 1980. Patterns of growth, energy utilization and reproduction in some meso- and bathypelagic fishes off southern California. *Mar. Biol.* 61:27–40

Choy CA, Davison PC, Drazen JC, Flynn A, Gier EJ, et al. 2012. Global trophic position comparison of two dominant mesopelagic fish families (Myctophidae, Stomiidae) using amino acid nitrogen isotopic analyses. *PLOS ONE* 7:e50133

Choy CA, Drazen JC. 2013. Plastic for dinner? Frequent debris ingestion by large pelagic fishes from the central North Pacific subtropical gyre. *Mar. Ecol. Prog. Ser.* 485:155–63

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

Choy CA, Popp BN, Kaneko JJ, Drazen JC. 2009. The influence of depth on mercury levels in pelagic fishes and their prey. *PNAS* 106:13865–69

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

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

Churchill DA, Heithaus MR, Grubbs RD. 2015a. Effects of lipid and urea extraction on δ^{15}N values of deep-sea sharks and hagfish: Can mathematical correction factors be generated? *Deep-Sea Res. II* 115:103–8

Churchill DA, Heithaus MR, Vaudo JJ, Grubbs RD, Gastrich K, Castro JI. 2015b. Trophic interactions of common elasmobranchs in deep-sea communities of the Gulf of Mexico revealed through stable isotope and stomach content analysis. *Deep-Sea Res. II* 115:92–102

Clark MR, Vinnichenko VI, Gordon JDM, Beck-Bulat GZ, Kukharev NN, Kakora AF. 2007. Large-scale distant-water trawl fisheries on seamounts. In *Seamounts: Ecology, Fisheries and Conservation*, ed. TJ Pitcher, T Morato, PJB Hart, MR Clark, N Haggan, RS Santos, pp. 361–99. Oxford, UK: Blackwell

Clarke TA. 1978. Diel feeding patterns of 16 species of mesopelagic fishes from Hawaiian waters. *Fish. Bull.* 76:495–513

Clarke TA. 1982. Feeding habits of stomiatoid fishes from Hawaiian waters. *Fish. Bull.* 80:287–304

Collins MA, Bailey DM, Ruxton GD, Priede IG. 2005. Trends in body size across an environmental gradient: a differential response in scavenging and non-scavenging demersal deep-sea fish. *Proc. R. Soc. B* 272:2051–57

Conley WJ, Hopkins TL. 2004. Feeding ecology of lanternfish (Pisces: Myctophidae) larvae: prey preferences as a reflection of morphology. *Bull. Mar. Sci.* 75:361–79

Cook AB, Sutton TT, Galbraith JK, Vecchione M. 2013. Deep-pelagic (0–3000 m) fish assemblage structure over the Mid-Atlantic Ridge in the area of the Charlie-Gibbs Fracture Zone. *Deep-Sea Res. II* 98:279–91

Crabtree RE, Carter J, Musick JA. 1991. The comparative feeding ecology of temperate and tropical deep-sea fishes from the western North Atlantic. *Deep-Sea Res. A* 38:1277–98

Crabtree RE, Sulak KJ. 1986. A contribution to the life history and distribution of Atlantic species of the deep-sea fish genus *Conocara* (Alepocephalidae). *Deep-Sea Res. A* 33:1183–201

Dalsgaard J, St. John M, Kattner G, Müller-Navarra D, Hagen W. 2003. Fatty acid trophic markers in the pelagic marine environment. In *Advances in Marine Biology*, Vol. 46, ed. AJ Southward, PA Tyler, CM Young, LA Fuiman, pp. 225–340. San Diego, CA: Academic

Davison PC, Asch RG. 2011. Plastic ingestion by mesopelagic fishes in the North Pacific Subtropical Gyre. *Mar. Ecol. Prog. Ser.* 432:173–80

Davison PC, Checkley DM Jr., Koslow JA, Barlow J. 2013. Carbon export mediated by mesopelagic fishes in the northeast Pacific Ocean. *Prog. Oceanogr.* 116:14–30

Davison PC, Lara-Lopez A, Koslow JA. 2015. Mesopelagic fish biomass in the southern California Current ecosystem. *Deep-Sea Res. II* 112:129–42

Drazen JC. 2002. Energy budgets and feeding rates of *Coryphaenoides acrolepis* and *C. armatus*. *Mar. Biol.* 140:677–86

Drazen JC, Bailey DM, Ruhl H, Smith KL Jr. 2012. The role of carrion supply in the abundance of deep-water fish off California. *PLOS ONE* 7:e49332

Drazen JC, Buckley TW, Hoff GR. 2001. The feeding habits of slope dwelling macrourid fishes in the eastern North Pacific. *Deep-Sea Res. I* 48:909–35

Drazen JC, Haedrich RL. 2012. A continuum of life histories in deep-sea demersal fishes. *Deep-Sea Res. I* 61:34–42

Drazen JC, Phleger CF, Guest MA, Nichols PD. 2009. Lipid compositions and diet inferences in abyssal macrourids of the eastern North Pacific. *Mar. Ecol. Prog. Ser.* 387:1–14

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

Drazen JC, Seibel BA. 2007. Depth-related trends in metabolism of benthic and benthopelagic deep-sea fishes. *Limnol. Oceanogr.* 52:2306–16

Dunn MR, Griggs L, Forman J, Horn P. 2010. Feeding habits and niche separation among the deep-sea chimaeroid fishes *Harriotta raleighana*, *Hydrolagus bemisi* and *Hydrolagus novaezealandiae*. *Mar. Ecol. Prog. Ser.* 407:209–25

Ebeling AW, Cailliet GM. 1974. Mouth size predator strategy of midwaters fishes. *Deep-Sea Res. Oceanogr. Abstr.* 21:959–68

Ebert DA, Bizzarro JJ. 2007. Standardized diet compositions and trophic levels of skates (Chondrichthyes: Rajiformes: Rajoidei). *Environ. Biol. Fishes* 80:221–37

Fanelli E, Cartes JE. 2010. Temporal variations in the feeding habits and trophic levels of three deep-sea demersal fishes from the western Mediterranean Sea, based on stomach contents and stable isotope analyses. *Mar. Ecol. Prog. Ser.* 402:213–32

Fanelli E, Cartes JE, Papiol V. 2011. Food web structure of deep-sea macrozooplankton and micronekton off the Catalan slope: insight from stable isotopes. *J. Mar. Syst.* 87:79–89

Fanelli E, Cartes JE, Papiol V, López-Pérez C. 2013. Environmental drivers of megafaunal assemblage composition and biomass distribution over mainland and insular slopes of the Balearic Basin (Western Mediterranean). *Deep-Sea Res. I* 78:79–94

Feagans-Bartow JN, Sutton TT. 2014. Ecology of the oceanic rim: pelagic eels as key ecosystem components. *Mar. Ecol. Prog. Ser.* 502:257–66

Feller RJ, Zagursky G, Day EA. 1985. Deep-sea food web analysis using cross-reacting antisera. *Deep-Sea Res. A* 32:485–97

Ferry LA. 1997. Food habits of the two-line eelpout (*Bothrocara brunneum*: Zoarcidae) at two deep-sea sites in the eastern North Pacific. *Deep-Sea Res. I* 44:521–31

Flynn AJ, Kloser RJ. 2012. Cross-basin heterogeneity in lanternfish (family Myctophidae) assemblages and isotopic niches (δ^{13}C and δ^{15}N) in the southern Tasman Sea abyssal basin. *Deep-Sea Res. I* 69:113–27

Fock H, Matthiessen B, Zidowitz H, von Westernhagen H. 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. *Mar. Ecol. Prog. Ser.* 244:219–33

Gartner JV, Crabtree RE, Sulak KJ. 1997. Feeding at depth. In *Deep-Sea Fishes*, ed. DJ Randall, AP Farrell, pp. 115–93. San Diego, CA: Academic

Gartner JV, Musick JA. 1989. Feeding habits of the deep-sea fish *Scopelogadus beanii* (Pisces: Melamphaidae), in the western North Atlantic. *Deep-Sea Res. I* 36:1457–68

Gilly WF, Beman JM, Litvin SY, Robison BH. 2013. Oceanographic and biological effects of shoaling of the oxygen minimum zone. *Annu. Rev. Mar. Sci.* 5:393–420

Gjosaeter J, Kawaguchi K. 1980. *A review of the world resources of mesopelagic fish*. Fish. Tech. Paper 193, Food Agric. Organ. UN, Rome

Gordon JDM, Mauchline J. 1996. The distribution and diet of the dominant, slope-dwelling eel, *Synaphobranchus kaupi*, of the Rockall Trough. *J. Mar. Biol. Assoc. UK* 76:493–503

Haedrich RL. 1967. The stromateoid fishes: systematics and a classification. *Bull. Mus. Comp. Zool. Harv. Coll.* 135:31–139

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

Heroux D, Magnan P. 1996. In situ determination of food daily ration in fish: review and field evaluation. *Environ. Biol. Fishes* 46:61–74

Herring PJ. 2002. *The Biology of the Deep Ocean*. Oxford, UK: Oxford Univ. Press

Hirch S, Christiansen B. 2010. The trophic blockage hypothesis is not supported by the diets of fishes on Seine Seamount. *Mar. Ecol.* 31:107–20

Hoff GR, Buckley TW, Drazen JC, Duncan KM. 2000. Biology and ecology of *Nezumia liolepis* and *N. stelgidolepis* from the west coast of North America. *J. Fish Biol.* 57:662–80

Hoffman JC, Sutton TT. 2010. Lipid correction for carbon stable isotope analysis of deep-sea fishes. *Deep-Sea Res. I* 57:956–64

Hopkins TL, Baird RC. 1977. Aspects of the feeding ecology of oceanic midwater fishes. In *Oceanic Sound Scattering Prediction*, ed. NR Andersen NR, BJ Zahuranec, pp. 325–60. New York: Plenum

Hopkins TL, Baird RC. 1985. Aspects of the trophic ecology of the mesopelagic fish *Lampanyctus alatus* (Family Myctophidae) in the eastern Gulf of Mexico. *Biol. Oceanogr.* 3:285–313

Hopkins TL, Gartner JV Jr. 1992. Resource-partitioning and predation impact of a low-latitude myctophid community. *Mar. Biol.* 114:185–97

Hopkins TL, Sutton TT, Lancraft TM. 1996. The trophic structure and predation impact of a low latitude midwater fish assemblage. *Prog. Oceanogr.* 38:205–39

Horn PL, Forman J, Dunn MR. 2010. Feeding habits of alfonsino *Beryx splendens*. *J. Fish Biol.* 76:2382–400

Hudson JM, Steinberg DK, Sutton TT, Graves JE, Latour RJ. 2014. Myctophid feeding ecology and carbon transport along the northern mid-Atlantic ridge. *Deep-Sea Res. I* 93:104–16

Huntley ME, Lopez MDG, Karl DM. 1991. Top predators in the Southern Ocean: a major leak in the biological carbon pump. *Science* 253:64–66

Iken K, Brey T, Wand U, Voight J, Junghans P. 2001. Food web structure of the benthic community at the Porcupine Abyssal Plain (NE Atlantic): a stable isotope analysis. *Prog. Oceanogr.* 50:383–405

Irigoien X, Klevjer TA, Røstad A, Martinez U, Boyra G, et al. 2014. Large mesopelagic fishes biomass and trophic efficiency in the open ocean. *Nat. Commun.* 5:3271

Jamieson A, Fujii T, Solan M, Matsumoto AK, Bagley PM, Priede IG. 2009. Liparid and macrourid fishes of the hadal zone: in situ observations of activity and feeding behaviour. *Proc. R. Soc. B* 276:1037–45

Jones DOB, Yool A, Wei C-L, Henson SA, Ruhl HA, et al. 2014. Global reductions in seafloor biomass in response to climate change. *Glob. Change Biol.* 20:1861–72

Jones MRL. 2008a. Biology and diet of *Coryphaenoides subserrulatus* and *Etmopterus baxteri* from the Puysegur region, southern New Zealand. *N.Z. J. Mar. Freshw. Res.* 42:333–37

Jones MRL. 2008b. Dietary analysis of *Coryphaenoides serrulatus*, *C. subserrulatus* and several other species of macrourid fish (Pisces: Macrouridae) from northeastern Chatham Rise, New Zealand. *N.Z. J. Mar. Freshw. Res.* 42:73–84

Jones MRL, Breen BB. 2013. Food and feeding relationships of three sympatric slickhead species (Pisces: Alepocephalidae) from northeastern Chatham Rise, New Zealand. *Deep-Sea Res. I* 79:1–9

Jones MRL, Breen BB. 2014. Role of scavenging in a synaphobranchid eel (*Diastobranchus capensis*, Barnard, 1923), from northeastern Chatham Rise, New Zealand. *Deep-Sea Res. I* 85:118–23

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

Kenaley CP. 2012. Exploring feeding behaviour in deep-sea dragonfishes (Teleostei: Stomiidae): jaw biomechanics and functional significance of a loosejaw. *Biol. J. Linn. Soc.* 106:224–40

King NJ, Bailey DM, Priede IG. 2007. Role of scavengers in marine ecosystems: introduction. *Mar. Ecol. Prog. Ser.* 350:175–78

Kinzer J, Schulz K. 1985. Vertical distribution and feeding patterns of midwater fish in the central equatorial Atlantic. *Mar. Biol.* 85:313–22

Kosenok SN, Chuchukalo VI, Savinykh VF. 2006. The characteristics of feeding of *Diaphus theta* (Myctophidae) in the northwestern part of the Pacific Ocean in the summer–autumn period. *J. Ichthyol.* 46:606–12

Koslow JA. 1996. Energetic and life-history patterns of deep-sea benthic, benthopelagic and seamount-associated fish. *J. Fish Biol.* 49(Suppl. A):54–74

Koslow JA, Boehlert GW, Gordon JD, Haedrich RL, Lorance P, Parin N. 2000. Continental slope and deep-sea fisheries: implications for a fragile ecosystem. *ICES J. Mar. Sci.* 57:548–57

Koslow JA, Davison P, Lara-Lopez A, Ohman MD. 2014. Epipelagic and mesopelagic fishes in the southern California Current System: ecological interactions and oceanographic influences on their abundance. *J. Mar. Syst.* 138:20–28

Koslow JA, Kloser RJ, Williams A. 1997. Pelagic biomass and community structure over the mid-continental slope off southeastern Australia based upon acoustic and midwater trawl sampling. *Mar. Ecol. Prog. Ser.* 146:21–35

Lampitt RS, Merrett NR, Thurston MH. 1983. Inter-relations of necrophagous amphipods, a fish predator, and tidal currents in the deep sea. *Mar. Biol.* 74:73–78

Laxson CJ, Condon NE, Drazen JC, Yancey PH. 2011. Decreasing urea:trimethylamine N-oxide ratios with depth in chondrichthyes: a physiological depth limit? *Physiol. Biochem. Zool.* 84:494–505

Lee CC, Chen HW, Shao KT, Hsu CC. 2008. Feeding ecology of three congeneric grenadiers in waters of northeastern Taiwan. In *Grenadiers of the World Oceans: Biology, Stock Assessment, and Fisheries*, ed. AM Orlov, T Iwamoto, pp. 185–201. Bethesda, MD: Am. Fish. Soc.

Linley TD, Gerringer ME, Yancey PH, Drazen JC, Weinstock CL, Jamieson AJ. 2016. Fishes of the hadal zone including new species, in situ observations and depth records of Liparidae. *Deep-Sea Res. I* 114 99–110

Livingston PA, Goiney BJ. 1984. *Bibliography on daily food ration of fishes*, NOAA Tech. Memo. NMFS F/NWC-63, Natl. Ocean. Atmos. Adm., US Dep. Commer., Springfield, VA

Locarnini RA, Mishonov AV, Antonov JI, Boyer TP, Garcia HE, et al. 2013. *World Ocean Atlas 2013*, Vol. 1: *Temperature*. Ed. S Levitus, Tech. Ed. A Mishonov. NOAA Atlas NESDIS 73. Washington, DC: Natl. Ocean. Atmos. Adm.

Loh T-L, Pawlik JR. 2014. Chemical defenses and resource trade-offs structure sponge communities on Caribbean coral reefs. *PNAS* 111:4151–56

MacAvoy SE, Carney RS, Fisher CR, Macko SA. 2002. Use of chemosynthetic biomass by large, mobile, benthic predators in the Gulf of Mexico. *Mar. Ecol. Prog. Ser.* 225:65–78

Macpherson E. 1985. Daily ration and feeding periodicity of some fishes off the coast of Namibia. *Mar. Ecol. Prog. Ser.* 26:253–60

Madurell T, Cartes JE. 2005a. Temporal changes in feeding habits and daily rations of *Hoplostethus mediterraneus* in the bathyal Ionian Sea (eastern Mediterranean). *Mar. Biol.* 146:951–62

Madurell T, Cartes JE. 2005b. Trophodynamics of a deep-sea demersal fish assemblage from the bathyal eastern Ionian Sea (Mediterranean Sea). *Deep-Sea Res. I* 52:2049

Madurell T, Cartes JE. 2006. Trophic relationships and food consumption of slope dwelling macrourids from the bathyal Ionian Sea (eastern Mediterranean). *Mar. Biol.* 148:1325

Marshall NB. 1965. Systematic and biological studies of the macrourid fishes (Anacanthini-Teleostii). *Deep-Sea Res. Oceanogr. Abstr.* 12:299–322

Martin B, Christiansen B. 1997. Diets and standing stocks of benthopelagic fishes at two bathymetrically different midoceanic localities in the Northeast Atlantic. *Deep-Sea Res. I* 44:541–58

Martini FH. 1998. The ecology of hagfishes. In *The Biology of Hagfishes*, ed. JM Jørgensen, JP Lomholt, RE Weber, H Malte, pp. 57–77. London: Chapman & Hall

Mauchline J, Gordon JDM. 1980. The food and feeding of the deep-sea morid fish *Lepidion eques* (Gunther, 1887) in the Rockall Trough. *J. Mar. Biol. Assoc. UK* 60:1053–59

Mauchline J, Gordon JDM. 1983a. Diets of clupeoid, stomiatoid and salmonoid fish of the Rockall Trough, northeastern Atlantic Ocean. *Mar. Biol.* 77:67–78

Mauchline J, Gordon JDM. 1983b. Diets of the sharks and chimaeroids of the Rockall Trough, northeastern Atlantic Ocean. *Mar. Biol.* 75:269–78

Mauchline J, Gordon JDM. 1984. Feeding and bathymetric distribution of the gadoid and morid fish of the Rockall Trough. *J. Mar. Biol. Assoc. UK* 64:657–65

Mauchline J, Gordon JDM. 1986. Foraging strategies of deep-sea fish. *Mar. Ecol. Prog. Ser.* 27:227–38

Mauchline J, Gordon JDM. 1991. Oceanic pelagic prey of benthopelagic fish in the benthic boundary layer of a marginal oceanic region. *Mar. Ecol. Prog. Ser.* 74:109–15

Mayor DJ, Sharples CJ, Webster L, Walsham P, Lacaze J-P, Cousins NJ. 2013. Tissue and size-related changes in the fatty acid and stable isotope signatures of the deep sea grenadier fish *Coryphaenoides armatus* from the Charlie-Gibbs Fracture Zone region of the Mid-Atlantic Ridge. *Deep-Sea Res. II* 98:421–30

Miller TW, Brodeur RD, Rau GH. 2008. Carbon stable isotopes reveal relative contribution of shelf-slope production to the northern California Current pelagic community. *Limnol. Oceanogr.* 53:1493–503

Mintenbeck K, Jacob U, Knust R, Arntz WE, Brey T. 2007. Depth-dependence in stable isotope ratio δ^{15}N of benthic POM consumers: the role of particle dynamics and organism trophic guild. *Deep-Sea Res. I* 54:1015–23

Modica L, Cartes JE, Carrassón M. 2014. Food consumption of five deep-sea fishes in the Balearic Basin (western Mediterranean Sea): Are there daily feeding rhythms in fishes living below 1000 m? *J. Fish Biol.* 85:800–20

Moku M, Kawaguchi K, Watanabe H, Ohno A. 2000. Feeding habits of three dominant myctophid fishes, *Diaphus theta*, *Stenobrachius Leucopsarus* and *S. nannochir*, in the subarctic and transitional waters of the western North Pacific. *Mar. Ecol. Prog. Ser.* 207:129–40

Morato T, Clarke MR. 2007. Seamount fishes: ecology and life histories. In *Seamounts: Ecology, Fisheries and Conservation*, ed. TJ Pitcher, T Morato, PJB Hart, MR Clark, N Haggan, RS Santos, pp. 170–88. Oxford, UK: Blackwell

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

Moser HG, Ahlstrom EH. 1996. Myctophidae: lanternfishes. In *The Early Stages of Fishes in the California Current Region*, ed. HG Moser, pp. 387–475. CalCOFI Atlas 33. Lawrence, KS: Allen

Navarro J, López L, Coll M, Barría C, Sáez-Liante R. 2014. Short- and long-term importance of small sharks in the diet of the rare deep-sea shark *Dalatias licha*. *Mar. Biol.* 161:1697–707

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

Olson RJ, Duffy LM, Kuhnert PM, Galván-Magaña F, Bocanegra-Castillo N, Alatorre-Ramírez V. 2014. Decadal diet shift in yellowfin tuna *Thunnus albacares* suggests broad-scale food web changes in the eastern tropical Pacific Ocean. *Mar. Ecol. Prog. Ser.* 497:157–78

Pakhomov EA, Perissinotto R, McQuaid CD. 1996. Prey composition and daily rations of myctophid fishes in the Southern Ocean. *Mar. Ecol. Prog. Ser.* 134:1–14

Palma S. 1990. Feeding ecology of *Cyclothone braueri* Jesperseng and Taning, 1926 (Gonostomatidae), Ligurian Sea, western Mediterranean. *J. Plankton Res.* 12:519–34

Papiol V, Cartes JE, Fanelli E, Rumolo P. 2013. Food web structure and seasonality of slope megafauna in the NW Mediterranean elucidated by stable isotopes: relationship with available food sources. *J. Sea Res.* 77:53–69

Paquin MM, Buckley TW, Hibpshman RE, Canino MF. 2014. DNA-based identification methods of prey fish from stomach contents of 12 species of eastern North Pacific groundfish. *Deep-Sea Res. I* 85:110–17

Parekh P, Dutkiewicz S, Follows MJ, Ito T. 2006. Atmospheric carbon dioxide in a less dusty world. *Geophys. Res. Lett.* 33:L03610

Paxton JR. 1967. Biological notes on southern California lanternfishes (family Myctophidae). *Calif. Fish Game* 53:214–17

Pearcy WG, Ambler JW. 1974. Food habits of deep-sea fishes off the Oregon coast. *Deep-Sea Res. Oceanogr. Abstr.* 21:745–59

Peterson BJ, Fry B. 1987. Stable isotopes in ecosystem studies. *Annu. Rev. Ecol. Syst.* 18:293–320

Pethybridge H, Butler ECV, Cossa D, Daley R, Boudou A. 2012. Trophic structure and biomagnification of mercury in an assemblage of deepwater chondrichthyans from southeastern Australia. *Mar. Ecol. Prog. Ser.* 451:163–74

Pethybridge H, Daley RK, Nichols PD. 2011. Diet of demersal sharks and chimaeras inferred by fatty acid profiles and stomach content analysis. *J. Exp. Mar. Biol. Ecol.* 409:290–99

Polunin NVC, Morales-Nin B, Pawsey WE, Cartes JE, Pinnegar JK, Moranta J. 2001. Feeding relationships in Mediterranean bathyal assemblages elucidated by stable nitrogen and carbon isotope data. *Mar. Ecol. Prog. Ser.* 220:13–23

Post DM. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83:703–18

Priede IG, Froese R, Bailey DM, Bergstad OA, Collins MA, et al. 2006. The absence of sharks from abyssal regions of the world's oceans. *Proc. R. Soc. B* 273:1435–41

Priede IG, Godbold JA, King NJ, Collins MA, Bailey DM, Gordon JDM. 2010. Deep-sea demersal fish species richness in the Porcupine Seabight, NE Atlantic Ocean: global and regional patterns. *Mar. Ecol.* 31:247–60

Purcell JE, Arai MN. 2001. Interactions of pelagic cnidarians and ctenophores with fish: a review. *Hydrobiologia* 451:27–44

Pusch C, Hulley PA, Kock K-H. 2004. Community structure and feeding ecology of mesopelagic fishes in the slope waters of King George Island (South Shetland Islands, Antarctica). *Deep-Sea Res. I* 51:1685–708

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

Reid WDK, Sweeting CJ, Wigham BD, McGill RAR, Polunin NVC. 2013. High variability in spatial and temporal size-based trophodynamics of deep-sea fishes from the Mid-Atlantic Ridge elucidated by stable isotopes. *Deep-Sea Res. II* 98:412–20

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

Robison BH. 1984. Herbivory by the myctophid fish *Ceratoscopelus warmingii*. *Mar. Bio*l. 84:119–23

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

Rochman CM, Hoh E, Kurobe T, Teh SJ. 2013. Ingested plastic transfers hazardous chemicals to fish and induces hepatic stress. *Sci. Rep.* 3:1–7

Romero-Romero S, Molina-Ramírez A, Höfer J, Acuña JL. 2016. Body size-based trophic structure of a deep marine ecosystem. *Ecology* 97:171–81

Rowe GT. 2013. Seasonality in deep-sea food webs—a tribute to the early works of Paul Tyler. *Deep-Sea Res. II*'92:9–17

Ruxton GD, Bailey DM. 2005. Searching speeds and the energetic feasibility of an obligate whale-scavenging fish. *Deep-Sea Res. I* 52:1536

Ruzicka JJ, Brodeur RD, Emmett RL, Steele JH, Zamon JE, et al. 2012. Interannual variability in the Northern California Current food web structure: changes in energy flow pathways and the role of forage fish, euphausiids, and jellyfish. *Prog. Oceanogr.* 102:19–41

Sabatés A, Bozzano A, Vallvey I. 2003. Feeding pattern and the visual light environment in myctophid fish larvae. *J. Fish Biol.* 63:1476–90

Saldanha L, Almeida AJ, Andrade F, Guerreiro J. 1995. Observations on the diet of some slope dwelling fishes of southern Portugal. *Int. Rev. Gesamten Hydrobiol.* 80:217–34

Santos AR, Trueman C, Connolly P, Rogan E. 2013. Trophic ecology of black scabbardfish, *Aphanopus carbo* in the NE Atlantic—assessment through stomach content and stable isotope analyses. *Deep-Sea Res. I* 77:1–10

Sassa C, Kawaguchi K. 2005. Larval feeding habits of *Diaphus theta*, *Protomyctophum thompsoni*, and *Tarletonbeania taylori* (Pisces: Myctophidae) in the transition region of the western North Pacific. *Mar. Ecol. Prog. Ser.* 298:261–76

Schlining K, von Thun S, Kuhnz L, Schlining B, Lundsten L, et al. 2013. Debris in the deep: using a 22-year video annotation database to survey marine litter in Monterey Canyon, central California, USA. *Deep-Sea Res. I* 79:96–105

Schnell NK, Britz R, Johnson GD. 2010. New insights into the complex structure and ontogeny of the occipito-vertebral gap in barbeled dragonfishes (Stomiidae, Teleostei). *J. Morphol.* 271:1006–22

Sedberry GR, Musick JA. 1978. Feeding strategies of some demersal fishes of the continental slope and rise off the Mid-Atlantic coast of the USA. *Mar. Biol.* 44:357–75

Smith KL Jr., Laver MB. 1981. Respiration of the bathypelagic fish *Cyclothone* acclinidens. *Mar. Biol.* 61:261–66

Smith KL Jr., Ruhl HA, Bett BJ, Billett DSM, Lampitt RS, Kaufman RS. 2009. Climate, carbon cycling, and deep-ocean ecosystems. *PNAS* 106:19211–18

Smith KL Jr., Ruhl HA, Kahru M, Huffard CL, Sherman AD. 2013. Deep ocean communities impacted by changing climate over 24 y in the abyssal northeast Pacific Ocean. *PNAS* 110:19838–41

Smith KL Jr., Sherman AD, Huffard CL, McGill PR, Henthorn R, et al. 2014. Large salp bloom export from the upper ocean and benthic community response in the abyssal northeast Pacific: day to week resolution. *Limnol. Oceanogr.* 59:745–57

Solmundsson J. 2007. Trophic ecology of Greenland halibut (*Reinhardtius hippoglossoides*) on the Icelandic continental shelf and slope. *Mar. Biol. Res.* 3:231–42

Steinberg DK, Carlson CA, Bates NR, Goldthwait SA, Madin LP, Michaels AF. 2000. Zooplankton vertical migration and the active transport of dissolved organic and inorganic carbon in the Sargasso Sea. *Deep-Sea Res. I* 47:137–58

Stockton WL, DeLaca TE. 1982. Food falls in the deep sea: occurrence, quality, and significance. *Deep-Sea Res. A* 29:157–69

Stonik VA, Kalinin VI, Avilov SA. 1999. Toxins from sea cucumbers (holothuroids): chemical structures, properties, taxonomic distribution, biosynthesis and evolution. *J. Nat. Toxins* 8:235–48

Stowasser G, Pond D, Collins M. 2009. Using fatty acid analysis to elucidate the feeding habits of Southern Ocean mesopelagic fish. *Mar. Biol.* 156:2289–302

Sulak KJ, Wenner CA, Sedberry GR, Van Guelpen L. 1985. The life history and systematics of deep-sea lizard fishes, genus *Bathysaurus* (Synodontidae). *Can. J. Zool.* 63:623–42

Suntsov AV, Brodeur RD. 2008. Trophic ecology of three dominant myctophid species in the northern California Current region. *Mar. Ecol. Prog. Ser.* 373:81–96

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

Sutton TT, Hopkins TL. 1996. Species composition, abundance, and vertical distribution of the stomiid (Pisces: Stomiiformes) fish assemblage of the Gulf of Mexico. *Bull. Mar. Sci.* 59:530–42

Sutton TT, Hopkins TL, Lancraft TM. 1998. Trophic diversity of a midwater fish community. In *Pelagic Biogeography ICoPB II: Proceedings of the 2nd International Conference*, ed. AC Pierrot-Bults, S van der Spoel, pp. 353–57 IOC Workshop Rep. 142. Paris: UN Educ. Sci. Cult. Organ.

Sutton TT, Porteiro FM, Heino M, Byrkjedal I, Langhelle G, et al. 2008. Vertical structure, biomass and topographic association of deep-pelagic fishes in relation to a mid-ocean ridge system. *Deep-Sea Res. II* 55:161–84

Sweetman AK, Smith CR, Dale T, Jones DOB. 2014. Rapid scavenging of jellyfish carcasses reveals the importance of gelatinous material to deep-sea food webs. *Proc. R. Soc. B* 281:20142210

Takagi K, Yatsu A, Itoh H, Moku M, Nishida H. 2009. Comparison of feeding habits of myctophid fishes and juvenile small epipelagic fishes in the western North Pacific. *Mar. Biol.* 156:641–59

Tamburri MN, Barry JP. 1999. Adaptations for scavenging by three diverse bathyal species, *Eptatretus stouti*, *Neptunea amianta* and *Orchomene obtusus*. *Deep-Sea Res. I* 46:2079–93

Treberg JR, Speers-Roesch B. 2016. Does the physiology of chondrichthyan fishes constrain their distribution in the deep sea? *J. Exp. Biol.* 219:615–25

Trueman CN, Johnston G, O'Hea B, MacKenzie KM. 2014. Trophic interactions of fish communities at midwater depths enhance long-term carbon storage and benthic production on continental slopes. *Proc. R. Soc. B* 281:20140669

Valentim MFM, Caramaschi EP, Vianna M. 2008. Feeding ecology of monkfish *Lophius gastrophysus* in the south-western Atlantic Ocean. *J. Mar. Biol. Assoc. UK* 88:205–12

Valls M, Olivar MP, Fernández de Puelles ML, Molí B, Bernal A, Sweeting CJ. 2014a. Trophic structure of mesopelagic fishes in the western Mediterranean based on stable isotopes of carbon and nitrogen. *J. Mar. Syst.* 138:160–70

Valls M, Sweeting CJ, Olivar MP, Fernández de Puelles ML, Pasqual C, et al. 2014b. Structure and dynamics of food webs in the water column on shelf and slope grounds of the western Mediterranean. *J. Mar. Syst.* 138:171–81

Van Noord JE, Olson RJ, Redfern JV, Kaufmann RS. 2013. Diet and prey selectivity in three surface-migrating myctophids in the eastern tropical Pacific. *Ichthyol. Res.* 60:287–90

Vecchione M, Roper CF. 1991. Cephalopods observed from submersibles in the western North Atlantic. *Bull. Mar. Sci.* 49:433–45

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

Watanabe H, Kawaguchi K. 2003. Decadal change in the diets of the surface migratory myctophid fish *Myctophum nitidulum* in the Kuroshio region of the western North Pacific: predation on sardine larvae by myctophids. *Fish. Sci.* 69:716–21

Webb TJ, Berghe EV, O'Dor R. 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:e10223

Wedding LM, Reiter SM, Smith CR, Gjerde KM, Kittinger JN, et al. 2015. Managing mining of the deep seabed. *Science* 349:144–45

Wei C-L, Rowe GT, Escobar-Briones E, Boetius A, Soltwedel T, et al. 2010. Global patterns and predictions of seafloor biomass using random forests. *PLOS ONE* 5:e15323

Williams A, Koslow JA, Terauds A, Haskard K. 2001. Feeding ecology of five fishes from the mid-slope micronekton community off southern Tasmania, Australia. *Mar. Biol.* 139:1177–92

Wilson RW, Millero FJ, Taylor JR, Walsh PJ, Christensen V, et al. 2009. Contribution of fish to the marine inorganic carbon cycle. *Science* 323:359–62

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

Würzberg L, Peters J, Flores H, Brandt A. 2011. Demersal fishes from the Antarctic shelf and deep sea: a diet study based on fatty acid patterns and gut content analyses. *Deep-Sea Res. II* 58:2036–42

Yancey PH, Gerringer ME, Drazen JC, Rowden AA, Jamieson AJ. 2014. Are marine fish biochemically constrained from inhabiting the deepest ocean depths? *PNAS* 111:4461–65

Yeh J, Drazen JC. 2011. Baited-camera observations of deep-sea megafaunal scavenger ecology on the California slope. *Mar. Ecol. Prog. Ser.* 424:145–56

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

Zapata-Hernandez G, Sellanes J, Thurber AR, Levin LA, Chazalon F, Linke P. 2014. New insights on the trophic ecology of bathyal communities from the methane seep area off Concepcion, Chile (36°S). *Mar. Ecol.* 35:1–21

Zintzen V, Roberts CD, Anderson MJ, Stewart AL, Struthers CD, Harvey ES. 2011. Hagfish predatory behaviour and slime defence mechanism. *Sci. Rep.* 1:131

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Errata

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