

REVIEW PAPER

Vertical ecology of the pelagic ocean: classical patterns and new perspectives

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Applications of acoustic and optical sensing and intensive, discrete-depth sampling, in concert with collaborative international research programmes, have substantially advanced knowledge of pelagic ecosystems in the 17 years since the 1996 Deepwater Fishes Symposium of the Fisheries Society of the British Isles. Although the epipelagic habitat is the best-known, and remote sensing and high-resolution modelling allow near-synoptic investigation of upper layer biophysical dynamics, ecological studies within the mesopelagic and deep-demersal habitats have begun to link lower and upper trophic level processes. Bathypelagic taxonomic inventories are far from complete, but recent projects (*e.g.* MAR-ECO and CMarZ, supported by the Census of Marine Life programme) have quantitatively strengthened distribution patterns previously described for fishes and have provided new perspectives. Synthesis of net and acoustic studies suggests that the biomass of deep-pelagic fishes may be two to three orders of magnitude greater than the total global commercial fisheries landings. Discrete-depth net sampling has revealed relatively high pelagic fish biomass below 1000 m in some regions, and that gelatinous zooplankton may be key energy vectors for deep-pelagic fish production. Lastly, perhaps, the most substantive paradigm shift is that vertical connectivity among fishes across classical depth zones is prevalent— suggesting that a whole-water column approach is warranted for deep ocean conservation and management.

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INTRODUCTION

Edward Forbes' hypothesis presented to the British Association for the Advancement of Science in 1843 that the ocean below 300 fathoms (550 m) was 'azoic' (Forbes, 1844), despite extant evidence to the contrary (Ross, 1819), is often cited as one of the largest extrapolative missteps in the history of natural science. This hypothesis was rejected as new data became available, definitely so 30 years later, when the *Challenger* expedition discovered abundant life on the deep-sea floor. Less well-known is that the scientific leader of that expedition, Charles Wyville Thomson, made an equally egregious blunder in declaring the deep-pelagic zone azoic, stating '*there is every reason to believe that the fauna of deep water is confined principally to two belts, one at or near the surface and the other on or near the bottom; leaving*

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an intermediate zone in which larger animals, vertebrate and invertebrate, are nearly or entirely absent' (Thompson, 1878). Luckily, lest this be an extremely short paper, sampling in the ensuing 137 years has confirmed that the deep-pelagial hosts an amazingly diverse and adapted ichthyofauna, although the taxonomic inventory is far from complete (Webb *et al.*, 2010).

In this paper, the history of vertical distribution study will be reviewed briefly, primarily as related to deep-pelagic fishes, defined here as those fishes residing primarily below 200 m during the day. The classical (accepted) vertical zonation schema with respect to biophysical milieu and associated ichthyofauna will be summarized. Recent (*i.e.* since the 1996 Deepwater Fishes Symposium of the Fisheries Society of the British Isles) findings will then be discussed, some of which have altered perceptions of the structure and function of deep-pelagic ecosystems. Finally, a number of research advancements are discussed that will probably provide new insights in pelagic ecology.

A BRIEF HISTORY OF THE STUDY OF THE VERTICAL DISTRIBUTION OF DEEP-PELAGIC FISHES

Prior to the mid-1960s, the depth distributions of meso and bathypelagic fishes were poorly known because of sampling limitations of the early, major oceanographic expeditions (*e.g.* *Challenger*, *Dana*, *Discovery*, *Galathea*, *Michael Sars* and Bermuda Oceanographic Expeditions); sampling depths were inaccurately determined by wire out and wire angle, and closing nets were rarely used. From these studies, only general characterizations of broad distribution patterns were possible. Murray & Hjort (1912) and later Marshall (1954) documented that darker fish species occupied deeper strata during daytime than silvery species. In the late 1940s to 1960s, sonar technology developed for fishing and naval warfare was increasingly used for research and deep-scattering layers (DSL) of deep-pelagic organisms were described (Balls, 1948; Kampa & Boden, 1954; Hersey & Backus, 1962). Diel vertical migrations were documented as discrete-depth midwater trawls were developed and implemented. Discrete-depth sampling revealed the restriction of adolescent forms to the shallower regions of a given species' distribution. Later work with opening and closing nets refined knowledge of the mesopelagial and provided taxonomic information on the major species comprising the DSL (Badcock & Merrett, 1976; Percy *et al.*, 1977). This period saw the seminal works of the legendary N. B. Marshall, whose study of the relationship between the distribution of deep-sea fishes and their general ecology, and the books derived from this study: *Aspects of Deep-sea Biology* (1954), *Explorations in the Life of Fishes* (1971) and *Developments in Deep-Sea Biology* (1979), still stand as benchmarks. Within this timeframe, Vinogradov (1968) introduced the concept of the 'ladder of vertical migration', whereby overlapping distributions of vertically migrating zooplankton could serve as an energy vector to support pelagic life far below the euphotic zone, a hypothesis that has been supported by recent findings of vertical migrations by bathypelagic taxa (Cook *et al.*, 2013).

The period from the 1970s to 1990s was one of dramatic change in the nature of deep-ocean research in general and deep-pelagic research in particular. Once formerly the domain of research institutes, deep-sea research saw increased involvement of academics from universities in the 1970s, although most research cruises were still

organized and staffed by the major oceanographic institutes such as Woods Hole Oceanographic Institute (WHOI, U.S.A.), Institute of Oceanographic Sciences (IOS, U.K.), Institut Français de Recherche Pour L'Exploitation de la Mer (IFREMER, France) (Tyler, 2013). Military interest in acoustical DSLs drove much of the seminal vertical distribution research at this time (Farquhar, 1970; Andersen & Zahuranec, 1977), as did interest in the biogeography (Backus *et al.*, 1977; Pierrot-Bults & van der Spoel, 1998), trophodynamics (Hopkins & Baird, 1977; Roe & Badcock, 1984), physiology (Childress & Nygaard, 1973; Torres *et al.*, 1979; Somero, *et al.*, 1983) and bioluminescence (Anctil, 1974; Young, 1983) of deep-pelagic organisms. In the 1970s, much research on the distribution of mesopelagic fishes resulted from interest shown by the Food and Agriculture Organization (FAO, Rome) in unexplored commercial resources, summarized by Gjøsæter & Kawaguchi (1980). This work produced the first accepted estimate of global mesopelagic fish biomass, *c.* 1 Gt (1×10^9 t wet mass), which exceeds the global commercial fish catch by an order of magnitude. In the 1980s and 1990s, many university students started going on deep-sea research cruises and as they graduated they began to extend the deep-sea community into institutions and universities that had no prior history of deep-sea research.

With respect to technological innovation, the 1980s and 1990s heralded the increased utilization of undersea vehicles for direct observation in the deep pelagial (Robison, 2000; National Research Council, 2003). Manned submersibles such as the Harbor Branch Oceanographic Institute (HBOI) *Johnson Sea-Link* enabled detailed studies of midwater ecology (Youngbluth, 1984), although logistical constraints and cost limited their availability to the research community. The increased portability and affordability of remotely operated vehicles enabled new insights into midwater ecology, behaviour, physiology and, most significantly, the underestimated importance of gelatinous organisms in deep-pelagic ecosystems (Robison, 1995; Hopcroft & Robison, 1999). In the 1990s, there was renewed interest in mesopelagic fishes in connection with large, multidisciplinary ecosystem studies [*e.g.* Joint Global Ocean Flux Study (JGOFS; <http://www.igbp.net/researchprojects/pastprojects/thejointglobaloceanfluxstudy.4.1b8ae20512db692f2a680009040.html>) and Global Ocean Ecosystem Dynamics (GLOBEC; www.globec.org)]. Further refinement of acoustical techniques to look at a larger size spectrum of organisms allowed remote observations of deep-pelagic biota on the same time and space scales of physical measurements (Holliday *et al.*, 1990; Foote & Stanton, 2000).

The 1990s also saw increased cooperation and organization of deep-pelagic research at the international level, with long-established programmes in Russia and Japan joining those of Europe and North America, and emergent programmes in Australia, Brazil, Chile, India and New Zealand (to name a few), opening a new era of recognition of the open ocean as the true global commons. The early 1990s saw the genesis of open-ocean management efforts, although not often including the deep pelagial. The 1990s also saw the inception of the Census of Marine Life (Grassle *et al.*, 1991), a landmark 10-year project that included several deep-pelagic projects [*e.g.* MAR-ECO (www.mar-eco.no), Census of Marine Zooplankton (CMarZ; www.cmarz.org) and Arctic Ocean Diversity (ArcOD; <http://www.coml.org/projects/arctic-ocean-diversity-arcod>)] among its historical run (McIntyre, 2010).

VERTICAL ZONATION OF THE PELAGIC OCEAN: THE CLASSICAL SCHEMA

Characterizations of the pelagic oceanic habitat can be found in Angel (1993, 1997), Herring (2002) and Robison (2004), and a brief summary of the classical (accepted) schema is presented here. The deep-pelagic zone contains almost 95% of the ocean's volume (Horn, 1972). A comparison of relevant spatial scales of pelagic assemblages reveals that the vertical scale of distributions is finer by three to five orders of magnitude than the horizontal scale (*i.e.* 10–10³ m *v.* >10³ m, respectively; Angel, 1993). It is not surprising then that the global pelagic habitat is subdivided primarily by depth, with each stratum defined in some way by the penetration of sunlight, a covariant of depth, and by the associated biota.

The epipelagic (euphotic) biome, 0–200 m, is defined as the depth zone in which there is enough sunlight during daytime to support primary production, the rate of which is controlled abiotically by the availability of nutrients and turbulent mixing (Reid *et al.*, 1978). Although the primary production per unit area is lower in the epipelagic biome than on land, and the epipelagic zone constitutes <4% of the ocean's volume, its vast surface area accounts for *c.* 50% of the annual global fixation of carbon, and the majority of the total CO₂ flux from the atmosphere due to solubility effects (W. O. Smith, pers. comm.). The epipelagic biome has greater spatiotemporal variability, both hydrographically and biotically, than deeper strata owing to the near-surface circulation patterns established by planetary forcing and the much greater effect of seasonality on surface temperature (*i.e.* stability) and primary production (Longhurst, 1995). The epipelagic also contains a specialized habitat at the sea–air interface in which a specialized neustonic fauna is associated (Watanabe *et al.*, 2002). As a consequence of the distribution of phytoplankton production in the epipelagic biome, the majority of oceanic zooplankton production and biomass is found within this biome. For example, 75% of net-caught zooplankton individuals between the surface and 1000 m in the eastern Gulf of Mexico occur in the top 200 m, both at day and night (Hopkins, 1982).

The mesopelagic biome (also called the dysphotic or twilight zone), extending from 200 to 1000 m depth, is defined as that stratum of the ocean that receives enough solar illumination for the fauna to differentiate diurnal and nocturnal cycles, but not enough to support photosynthesis (*i.e.* below 1% surface light level). The main thermocline is found within this stratum. The highly variable biophysical conditions of the epipelagic are muted at mesopelagic depths and conditions become more stable over space and time. A further synopsis of the mesopelagic biome is presented in the study by Robinson *et al.* (2010).

The bathypelagic biome, depths below 1000 to *c.* 100 m from the seafloor, is defined by the apparent absence of diel variation in sunlight, and the relative invariance of temperature and salinity. In most places and times, the upper limit of the bathypelagic coincides with the base of the permanent thermocline, and in some places underlies the lower limit of an oxygen minimum zone. At these depths, pressure begins to affect organisms' ability to develop skeletal carbonate. There is limited evidence of a possible subdivision of the bathypelagic biome further at around 2500 m, the abyssopelagic zone, characterized primarily by dramatic decreases in deep-pelagic fish abundance (Angel, 1993; Sutton *et al.*, 2010a), although this boundary is equivocal and not universally accepted. In this treatment, the abyssopelagic

zone is subsumed within the bathypelagic biome for purposes of discussion. A hadalpelagic ichthyofauna within the deepest trenches may exist, but is unknown at this time. Fishes may be excluded from the deepest hadal depths (*i.e.* >9000 m) by the physiological balance of osmoregulation and pressure-counteracting osmolytes (piezolytes) such as trimethylamine oxide (TMAO; Yancey *et al.*, 2001; Yancey, 2005; Jamieson & Yancey, 2012). Taken as a whole, the bathypelagic biome is by far the planet's largest biome; 79% of the volume occupied by life on earth lies at depths >1000 m (Childress, 1983).

A fourth vertical zone, the benthic boundary layer (BBL), is defined relative to the sea floor instead of the sea surface. The BBL is a physically homogenous stratum of water generally found within 100 m of the sea floor, but can be much more, up to 1000 m, if turbulent mixing occurs near the seafloor (Weatherly & Kelly, 1985). A nepheloid layer of suspended particulate matter is sometimes observed within the BBL. BBL bottom currents are often accelerated over abrupt topography relative to the same depths over bathyal or abyssal plains.

ICHTHYOFAUNAL CHARACTERISTICS OF THE MAJOR DEPTH ZONES

The vertical spatial scale of pelagic habitat variability is much finer than the horizontal, as previously mentioned, and this is reflected in the nature of oceanic ichthyofaunal distributions. For example, a multivariate analysis of pelagic fish assemblage structure of the mid-North Atlantic (Iceland to the Azores), from the surface to 3000 m, revealed that depth was by far the primary factor determining pelagic fish assemblage composition (Sutton *et al.*, 2008), despite a horizontal study transect length of over 3000 km that spanned several major water masses. Each of the major depth biomes listed above contains a characteristic ichthyofauna, albeit with regional variation, and these are described below.

EPIPELAGIAL

The epipelagic, particularly within warm-water regions (*i.e.* between 40° N and 40° S), hosts a specialized, holoepipelagic fauna with limited connectivity to deeper waters. Members of this ichthyofauna include the flyingfishes (Exocoetidae) and their relatives (Belonidae and Hemirhamphidae), flotsam and jetsam associated fishes (*e.g.* Monacanthidae, Balistidae, Coryphaenidae and juvenile Carangidae), baitfishes (*e.g.* Clupeidae, Engraulidae, Stromateoidei and some Carangidae). This biome is also host to larval and juvenile fishes of astounding variety (*e.g.* Anguilliformes, Gadiformes, Pleuronectiformes and deepwater Perciformes) and a limited number of large, highly migratory species (*e.g.* Lamniformes, Scombridae, Istiophoridae and Coryphaenidae).

At night-time, the epipelagic hosts an influx of vertically migrating fishes from below, the nyctoepipelagic diel vertical migrators (*e.g.* Myctophidae, Gonostomatidae, Sternoptychidae, Phosichthyidae and Stomiidae), which either feed on zooplankton or on organisms feeding on zooplankton (Merrett & Roe, 1974; Hopkins & Baird, 1977; Clarke, 1978; Gorelova, 1983; Roe & Badcock, 1984; Hopkins *et al.*, 1996; Sutton *et al.*, 1998). Other taxa undertaking nocturnal vertical migrations into

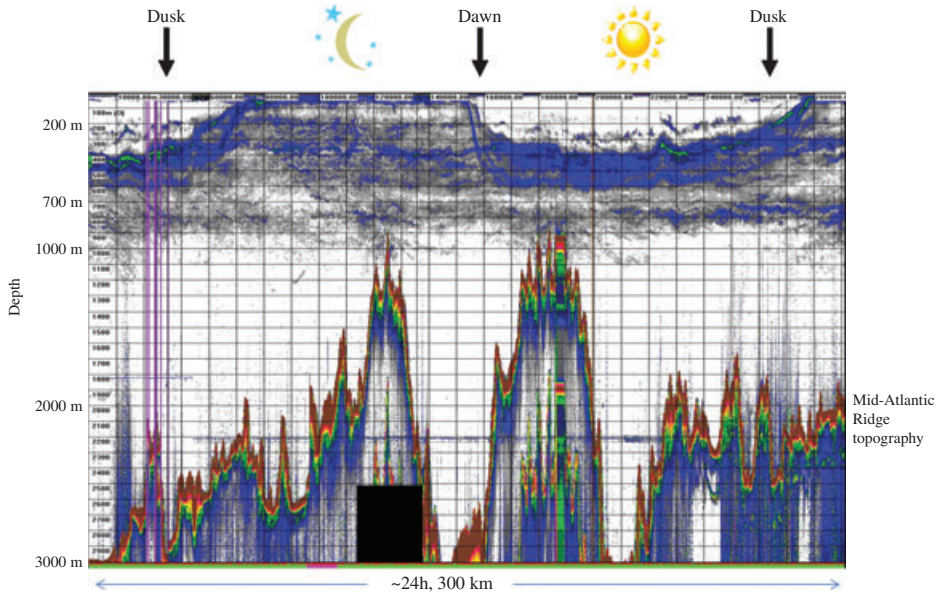


FIG. 1. Mean backscatter (S_v) data (18 kHz SIMRAD EK60 echosounder) during a cross-ridge transect (west–east) in the Azorean region of the Mid-Atlantic Ridge (topography shown at bottom, ■). The transect distance and duration equalled *c.* 300 km and *c.* 24 h. Vertical displacement of the main deep-scattering layer due to diel vertical migration can be seen from left (dusk) to right (dawn). Redrawn with permission from Sutton *et al.*, 2010b.

the epipelagial include Crustacea and Cephalopoda, which, when combined with the deep-pelagic fishes, constitute the micronekton, a functional grouping of actively swimming oceanic organisms with body sizes generally between 2 and 20 cm. Diel vertical migration as a phenomenon has received much attention, as it represents Earth's largest animal migration when taken *in toto*. The stimulus for diel vertical migration is thought to be the rapid change in light intensity at dawn and dusk (Clarke & Backus, 1964; Frank & Widder, 1997), while the benefits for migrating zooplankton and nekton are enhanced food supply at night-time and reduced predation risk during the day (Hays, 2003). The micronekton are the primary components of the DSLs observed with 18–36 kHz hydroacoustics (Fig. 1), particularly mesopelagic fishes, whose intricate swimbladders have evolved to secrete and resorb gas efficiently in order to facilitate rapid vertical migration (Marshall, 1960).

MESOPELAGIAL

Diel vertical migration, mentioned above, is ubiquitous across taxa in the mesopelagic biome, as is bioluminescence; at least 90% of its inhabitants produce light (Widder, 2010). In many oceanic regions, the mesopelagial can be further divided into upper and lower zones at around 600–700 m. Most vertically migrating fish species inhabiting the upper mesopelagial during daytime have reflective sides and large ventral photophores, adaptations for avoiding predators in dimly lit waters (Denton *et al.*, 1985). These adaptations would be a liability if these fishes were in either shallower or deeper water (Marshall, 1979). Characteristic fishes of the

upper mesopelagic zone include the Myctophidae, some Gonostomatidae (*Gonostoma* and *Margrethia*), some Sternoptychidae (*Maurolicus* and *Argyropelecus*), Phosichthyidae, Paralepididae and smaller Gempylidae.

An overall feature of fishes inhabiting the lower mesopelagial is a reduction in reflectivity, a trend that continues into the bathypelagial. Characteristic fishes of this stratum include the Stomiidae, Melamphaidae, Bathylagidae, the ubiquitous gonostomatid genus *Cyclothone*, some Myctophidae (e.g. *Nannobranchium*, *Hygophum* and *Taaningichthys*), the sternoptychid genus *Sternoptyx* and the pelagic eels (Nemichthyidae, Serrivomeridae, Derichthyidae and Nessorhamphidae). Parallel changes in body colouration are exhibited by mesopelagic decapod shrimps in many regions. The Sergestidae, for example, are predominantly half red (*Sergestes* spp.) above 700 m and all red (*Sergia* spp.) below 700 m (Hopkins *et al.*, 1994). The inverse relationship between reflectivity and depth exhibited by mesopelagic fishes, well-described by Marshall (1954), is also mirrored by the decrease in musculoskeletal robustness with increasing depth of occurrence (Salvanes & Kristoffersen, 2001). This relationship is ostensibly linked to ambient light. Fishes from deeper waters with reduced light availability probably have less need for locomotion associated with visually triggered predator and prey responses. Ancillary evidence exists in the finding that at bathypelagic depths, where light is absent, depth-related declines in metabolic rate cease (Childress, 1995; Seibel *et al.*, 1997, 2000). Moku *et al.* (2000) found a direct relationship between food consumption rate and vertical migratory capacity in three dominant mesopelagic myctophid species [*Diaphus theta* Eigenmann & Eigenmann 1890, *Stenobranchius leucopsarus* (Eigenmann & Eigenmann 1890) and *Stenobranchius nannochir* (Gilbert 1890)] in the western North Pacific Ocean, exemplifying the pattern of reduced metabolic demand with depth amongst deep-pelagic fishes (Torres *et al.*, 1979; Torres & Somero, 1988). This pattern can be seen clearly in echograms taken across a 24 h cycle (Fig. 1), where the fauna of the upper mesopelagic zone undertake extensive diel migrations into the well-mixed surface layers, whereas the lower mesopelagic fauna appears to undertake little or no diel vertical migration.

BATHYPELAGIAL

There is a well-documented logarithmic decline of food energy available with increasing depth (Haedrich, 1996; Angel, 1997). In the North Atlantic Ocean, investigations with an rectangular midwater trawl (RMT) 8 (<http://blog.antarctica.ac.uk/mscieng/main/available-equipment/rectangular-midwater-trawl-rmt/>) revealed a decline in fish biomass with depth below 1000 m (Angel & Baker, 1982; Angel, 1989a), although recent studies with larger gear have reported bathypelagic fish biomass figures considerably higher than previously reported (Sutton *et al.*, 2008; Fock & Ehrich, 2010; Cook *et al.*, 2013). Depths around 1000 m often contain the species richness maxima of both the deep-pelagic and megabenthic faunas (Angel, 1993). The bathypelagial hosts a unique assortment of highly modified holobathypelagic fishes, most of which are extremely rare in ichthyological collections. These include the ceratioid anglerfishes (11 families), whalefishes (Cetomimidae), gulpers (Eurypharyngidae), swallowers (Saccopharyngidae) and tubeshoulders (Platyroctidae) (Matsui & Rosenblatt, 1984; Bertelsen & Nielsen, 1986; Paxton, 1989; Nelson, 1994; Sutton *et al.*, 2008, 2010a; Pietsch, 2009). Morphological

adaptations of primarily bathypelagic fishes, relative to primarily mesopelagic taxa, include a reduction in relative eye size; loss or reduction in photophores; replacement of reflective and silvery pigmentation with black, brown or red pigment; replacement of dense muscle mass with watery tissues having less metabolic demand; and reduction or loss of swimbladders (Marshall, 1979). Sexual dimorphism is pronounced among many of the primarily bathypelagic fishes, with some taxa (*e.g.* ceratioid anglerfishes and cetomimid whalefishes) representing the most extreme examples of dimorphism amongst all vertebrates (Pietsch, 2005; Johnson *et al.*, 2009). This would appear to be a form of ecological bet-hedging in a food-limited environment; taxa invest the majority of their species' biomass in females, ostensibly to facilitate greater fecundity, at the expense of potential conspecific competitors (males).

BENTHOPELAGIC BOUNDARY LAYER

Numerous studies have found evidence of enhanced abundance and diversity of deep-pelagic fishes associated with the BBL at mesopelagic (continental and island slopes and seamounts), bathyal and abyssal depths (Marshall & Merrett, 1977; Reid *et al.*, 1991; Boehlert *et al.*, 1994). These findings further those of Wishner (1980) and Angel (1990), who found increased abundance and diversity of zooplankton within the BBL. In most cases, this enhanced abundance and biomass within the BBL is thought to result primarily from compression of vertical distribution [*i.e.* compaction from three-dimensional (3-D) into 2-D at an interface] rather than horizontal impingement (Mauchline & Gordon, 1991), although Boehlert *et al.* (1994) provide evidence for active station-keeping over a seamount by the associated micronekton. In most cases, the ichthyofaunal composition of deep-pelagic fish assemblages within the BBL reflects that of the surrounding water column, although there are pelagic fish families with pseudo-oceanic or neritopelagic species that occur in the BBL near abrupt topography, but are absent or less abundant in oceanic waters (Hulley & Lutjeharms, 1989; Parin *et al.*, 1997). Large adults of many families of deep-pelagic fishes apparently adopt a benthopelagic lifestyle (Porteiro & Sutton, 2007), perhaps benefiting from enhanced food supply and concentrating on individuals for reproduction. BBL assemblages probably represent a vital trophic linkage between the pelagic and demersal faunas of deep-sea ecosystems (Mauchline & Gordon, 1991), besides linking neritic and oceanic realms of oceanic islands and continental shelves (Hulley & Lutjeharms, 1989; Reid *et al.*, 1991).

RECENT FINDINGS AND NEW PERSPECTIVES IN DEEP-PELAGIC FISH VERTICAL ECOLOGY

More and more data show that the deep ocean is not a static, unvarying, aseasonal environment. Expanding time-series studies, especially regarding deep-demersal fishes, demonstrate the dynamic and variable nature of deep-sea fish communities (Bailey *et al.*, 2006; Drazen *et al.*, 2012). These findings almost certainly apply to the deep pelagial as well. This change in perspective is one of many that have come about from insights gained since the 1996 FSBI *Deep-Water Fishes Symposium*. In the following section, several, but certainly not all, of the significant advances in deep-pelagic fish vertical ecology will be discussed.

THE GLOBAL IMPORTANCE OF MESO AND BATHYPELAGIC FISHES

Perhaps, the most significant recent finding regarding deep-pelagic fishes is that their global abundance and biomass may have been greatly underestimated, perhaps by an order of magnitude. The current global estimate of mesopelagic biomass (there is not one for bathypelagic fish biomass), based primarily on net catches, is $c. 1 \times 10^9$ t wet mass (Gjørseter & Kawaguchi, 1980), although the authors stated that this was probably an underestimate. All nets are selective in what and how much they catch, with avoidance and extrusion through meshes being the primary factors. Recent intercomparison studies aimed at quantifying gear selectivity have quantitatively demonstrated that catchability of different pelagic trawls is both size and taxon-specific (Pakhomov & Yamamura, 2010; Heino *et al.*, 2011). Recent acoustical studies have generated consistently higher abundance estimates of mesopelagic fishes relative to trawl volume swept-based estimates (Koslow *et al.*, 1997), ranging from seven times higher (Koslow, 2009) to at least an order of magnitude (Kaartvedt *et al.*, 2012). The latter study not only demonstrated efficient trawl avoidance by the lanternfish *Benthoosema glaciale* (Reinhardt 1837), but also presented graphical evidence of a persistent acoustical void left in the wake of an open (non-fishing) trawl, in some cases lasting several hours. This is of course not to say that net-based sampling is not necessary and valuable; acoustics do not provide taxonomic resolution of the composition of scattering layers and do not provide materials for organismal research. The realization of the scale of chronic underestimation of deep-pelagic fish abundance and biomass (and *ergo* macrocrustaceans and cephalopods), however, is striking; acoustically determined mesopelagic fish biomass indicates that 1×10^{10} t, two orders of magnitude larger than the global fisheries landings, is a more realistic global figure. The addition of bathypelagic fish biomass could push that figure to three orders of magnitude, given the immense size of the bathypelagial population.

Quantitative sampling caveats notwithstanding, recent net-based surveys have also provided new perspectives on the ecological importance of deep-pelagic fishes. For example, the classical krill-dominated food web paradigm of the Southern Ocean is being challenged by the finding that mesopelagic fishes are also major energy transmitters. Flores *et al.* (2008) found that the energy density of a single species of lanternfish, *Electrona antarctica* (Günther 1878), is at least 36% of the energy stored in krill *Euphausia superba* stocks in the Lazarev Sea. In the Atlantic and Pacific Oceans, the use of larger nets has greatly increased the biomass estimates of deep-pelagic fishes (Merrett *et al.*, 1986; Brodeur & Yamamura, 2005; Sutton *et al.*, 2008; Fock & Ehrich, 2010; Cook *et al.*, 2013). Taken in concert, the increased abundance and biomass estimates of deep-pelagic fishes derived from both nets and acoustics suggest that their role as tertiary and higher trophic-level consumers, their importance as prey for apex predators and their role in global biogeochemical cycles should be reconsidered. Through their intensive vertical migrations, feeding in the epipelagial, and their respiration and excretion in the meso- and bathypelagial, deep-pelagic fishes represent a significant component of the biological pump of organic carbon to deeper waters (Angel, 1989a; Longhurst *et al.*, 1990; Angel & Pugh, 2000). Apart from trophic significance, recent estimates suggest that up to 15% of oceanic carbonate is contributed by marine fishes through their intestinal production (Wilson *et al.*, 2009). Because fish carbonates are more soluble than other sources, this phenomenon may explain up to one-fourth of the alkalinity within the top 1000 m

of the ocean. This phenomenon has puzzled oceanographers for decades. Considering that deep-pelagic fishes likely represent the majority of Earth's fish biomass, and that the oceans are becoming more acidic, the ramifications of the abundance and biomass estimation of deep-pelagic fishes will probably increase in importance.

The use of larger, commercial-sized, opening and closing trawls for midwater sampling has not only increased the absolute biomass estimates of deep-pelagic fishes in some ecosystems, but has also changed perceptions of the vertical distribution of that biomass. As mentioned previously, there is a well-documented trend for the abundance and biomass of both deep-pelagic and deep-demersal fishes to decline logarithmically with depth (Angel & Baker, 1982; Haedrich, 1996; Sutton *et al.*, 2010a). The Census of Marine Life MAR-ECO study (Vecchione *et al.*, 2010) over the northern Mid-Atlantic Ridge (MAR), using commercial-sized, discrete-depth trawls, however, found a maximum water column fish biomass between 1500 and 2300 m (Sutton *et al.*, 2008), a finding later confirmed in separate studies (Fock & Ehrich, 2010; Cook *et al.*, 2013). The concept of Heincke's law, that larger fishes live at deeper strata, has been questioned as being an artefact resulting from net avoidance of larger fishes at shallow depths. The same may hold true for the bathypelagic. Rectangular midwater trawls, the primary tool upon which most of the views on vertical ecology are based, are probably avoided by larger bathypelagic fishes (*e.g.* large pelagic eels, platytroutids and melamphaidae) that make significant individual contributions to total biomass.

TOPOGRAPHIC ASSOCIATIONS AND THE IMPORTANCE OF GELATINOUS ZOOPLANKTON IN DEEP-PELAGIC FISH ECOLOGY

Regarding the MAR finding of higher than expected bathypelagic fish biomass by Sutton *et al.* (2008), topographic association was cited as a possible explanation, as much of the ridge summit extends into the 1500–2300 m depth layer. Integrating results of various studies, there appears to be adequate evidence to suggest that mid-ocean ridges may cause changes in the ecological structure of deep-pelagic fish assemblages relative to abyssal ecosystems. When the enormity of the mid-ocean ridge systems (*e.g.* 45.7% of the seafloor area of the North Atlantic Ocean between 800 and 3500 m depths; Priede *et al.*, 2013) is considered, findings such as these acquire global significance.

Conspicuous ichthyofaunal components of the bathypelagic fish assemblage comprising the bathypelagic biomass maximum observed over the MAR were *Bathylagus euryops* Goode & Bean 1896 (Bathylagidae) and *Scopelogadus beanii* (Günther 1887) (Melamphaidae), the first and fifth-ranked species in terms of overall abundance (Sutton *et al.*, 2008). Both of these species are also known to feed on gelatinous zooplankton (Mauchline & Gordon, 1983; Gartner & Musick, 1989). Thus, an alternative trophic pathway (fishes and gelata; Haddock, 2004) may be responsible for this unexpected ecosystem structure. Research in the 2000s has continued to increase appreciation of the role of gelatinous zooplankton in deep-pelagic ecology in general (Robison, 2004), and in the bathypelagic biome in particular. The reduced shear forces at depths below the mixed layer are probably responsible for the proliferation of large gelatinous organisms with expansive but fragile feeding appendages (Hamner & Robison, 1992). There appears to be increasing evidence for an

underappreciated trophic linkage in the bathypelagic biome: gelata and higher trophic levels.

In the past two decades, observations from acoustics, submersibles and from camera systems and nets towed close to the bottom have provided increasing evidence of enhanced abundance associated with abrupt topography such as seamounts, island slopes, mid-ocean ridges and submarine canyons (Sigurðsson *et al.*, 2002; Fock *et al.*, 2004; Genin, 2004; Pusch *et al.*, 2004a; Gartner *et al.*, 2007; Sutton *et al.*, 2008, 2010b). This enhanced abundance and biomass are thought to result from both vertical and horizontal compression of otherwise broad distributions and active association (Porteiro & Sutton, 2007), and there is some evidence for horizontal migrations of oceanic fishes into shallower waters (*e.g.* Hawaiian mesopelagic boundary community; Benoit-Bird *et al.*, 2001). The reduced mesopelagic fish abundance seen directly over some shallow-summit seamounts (*e.g.* Atlantis, Great Meteor and Cross Seamounts) may be due to enhanced predation by demersal and benthic fauna, or more likely due to active horizontal avoidance by the mesopelagic fish fauna whose daytime vertical distributions are deeper than the summit depth (Pusch *et al.*, 2004b; De Forest & Drazen, 2009). Sutton *et al.* (2008) reported large catches of terminal-sized, often gravid, deep-pelagic fishes caught in pelagic nets towed within the BBL of the northern MAR, and suggested that this topographic association may have basin-wide ramifications for genetic structure of pelagic fish if the largest, 'fittest' individuals assembled there for spawning.

INTERCONNECTIVITY OF THE PELAGIC OCEAN VERTICAL BIOMES

In addition to the changing perception of the importance of deep-pelagic fishes in the overall ecology and biogeochemistry of the sea, increased sampling resolution and observing technologies have changed perceptions of the interconnectivity of previously presumed discrete vertical depth zones. Although certain taxa of fishes are characteristic of certain depth zones, as described above, active flux of fishes between the various depth strata has been recently demonstrated from surface waters to the deepest depths. This finding parallels the statement of Haedrich (1997), when referring to demersal fish depth distributions, '*This well-established view of clearly defined communities by depth appears to be too simplistic and somewhat out of date*'.

On the largest spatial scale, ontogenetic migrations, which are well-documented for deep-pelagic fishes (Loeb, 1986), tend to break down easy characterization of deep-pelagic fishes as belonging uniquely to any specific vertical zone. Larvae and juveniles generally reside in the epipelagial, where planktonic food occurs at concentrations acceptable for fast-growing fishes with low locomotory capability. With increasing age, size and ostensibly detection probability by epipelagic predators, individuals descend to meso and bathypelagic depths, even to the seafloor in the case of deep-demersal and bathybenthic species. When coupled with ontogenetic shifts in diet, and variable forms of active vertical migration, the various life stages of pelagic fish species present complex panoplies of ecotaxonomic units that structure the vertical ecology of the pelagic ocean (Hopkins *et al.*, 1996).

Ontogenetic depth variation notwithstanding, recent data suggest that occupation of multiple depth zones by pelagic fishes is a much more widespread phenomenon than previously thought. Some wide vertical distributions result from active vertical

movements away from a centre of distribution, either upwards or downwards, while others appear to simply result from tolerance of a wide range of environmental conditions.

As more data accrue, the more interconnected the epipelagial and deeper strata appear. Tagging studies of large putative holoepipelagic fishes have revealed that deep diving into meso and even bathypelagic depths is common. For example, the whale shark *Rhincodon typus* Smith 1828 routinely dives to between 200 and 500 m, and has been recorded to 1286 m (Brunnschweiler *et al.*, 2009), only 22 m deeper than the recorded dives of the basking shark *Cetorhinus maximus* (Gunnerus 1765) (Gore *et al.*, 2008). Likewise, the white shark *Carcharodon carcharias* (L. 1758) routinely dives to 300 m and at times reaches 1000 m (Bonfil *et al.*, 2005). The perception of this species in particular is changing; once considered a coastal predator, *C. carcharias* now appears to be an oceanic shark that migrates inshore to feed. Among large teleosts, bluefin tuna *Thunnus thynnus* (L. 1758) are known to dive to >1000 m (Wilson & Block, 2009; Lawson *et al.*, 2010). If the centre of distribution of these fishes is considered to be primarily epipelagic, then these examples represent active downward fluxes. Likewise, if the centre of distribution of primarily mesopelagic fishes is considered to be between 200 and 1000 m, *i.e.* all or nearly all individuals occur between these depths during daylight, then their nocturnal migration would be considered an upward active flux into the epipelagial. Ostensibly, both of these active fluxes are for feeding, suggesting that the deep pelagial is a fundamental element of the ecology of many large epipelagic fishes, and the epipelagial is certainly integral to the ecology of nearly all mesopelagic fishes.

Connectivity between the meso and bathypelagial has been much more difficult to determine, namely because of the lack of bathypelagic sampling in general (Webb *et al.*, 2010), and particularly in discrete-depth fashion (Wiebe *et al.*, 2010). Progress is being made, again largely from sampling programmes just prior to, and during, the Census of Marine Life. In an analysis of 1938 and 185 discrete-depth meso and bathypelagic samples, respectively, spanning 30 years and much of the Atlantic Ocean (Gulf of Mexico, Sargasso Sea, northern mid-Atlantic and eastern South Atlantic) (T. T. Sutton, unpubl. data), it was found that of the 234 fish species collected below 1000 m, between 66 and 74% (depending on location) were also collected above 1000 m. These species represented between 62 and 92% of all individuals and >68% of all biomass of fishes collected below 1000 m. This high degree of overlap was reflected in discrete-depth data from the Sargasso Sea, a highly stratified, oligotrophic oceanic regime: 21 fish species were collected only above 1000 m, 20 species only below 1000 m and 40 species were common to both strata (Sutton *et al.*, 2010a). Further, the numerically dominant fish of the Sargasso Sea, the bristlemouth *Cyclothone braueri* Jespersen & Tåning 1926, comprised 47% of all individuals collected above 1000 m and 41% of all individuals collected below 1000 m. Likewise, in the far North Atlantic Ocean, the top four species comprising the maximum fish biomass between 1500 and 2300 m [*Cyclothone microdon* (Günther 1878), *B. euryops*, *Serrivomer beanii* Gill & Ryder 1883 and *Scopelogauds beanii*; 61% of total biomass] were all also routinely taken above 750 m (Sutton *et al.*, 2008). Many of the species common to the epi and mesopelagial and the bathypelagial appear to be widely distributed 'spanners', with apparently limited diel vertical migration (Marshall, 1971; Kobayashi, 1974). There is evidence, however, of active vertical migration of some bathypelagic taxa. Angel (1989b) reported migration of

the lanternfish *Ceratoscopelus warmingii* (Lütken 1892) from 1600 to 1700 m in the Azores region, while Domanski (1986) reported migration of decapods from 1200 m in central oligotrophic gyres. More recently, Cook *et al.* (2013) definitively showed that the frequent captures of bathypelagic organisms (fishes, decapods and cephalopods) in the epipelagic zone over the Charlie-Gibbs Fracture Zone of the MAR was not due to sampling bias or contamination, as these organisms were sampled over a seamount with a maximum depth of 600 m. Further, these authors also showed a large-scale diel vertical migration of bathypelagic biomass from below 1000 m to above 750 m at night-time.

There appears to be an increasing body of evidence that shows that while specific faunal elements appear to be characteristic of specific vertical depth zones of the pelagic ocean, there is considerable connectivity between the faunas in both an active (migration) and inactive (ontogenetic descent, spanning) sense. Given the elevated global abundance and biomass estimates of deep-pelagic fishes, their role in biogeochemical cycling, and their potential conversion of alternate food sources into higher trophic level biomass, it would appear that a large gap in the understanding of pelagic ecosystems is the bottom of the box, in other words, the strata below 200 m and even 1000 m. This change in understanding suggests the need for studying whole-water column processes rather than pre-defined zones of importance if the deep ocean and its services are to be managed and conserved in an ecosystem-based context.

DISCUSSION

Knowledge of the deep-pelagic ocean certainly lags behind that of nearly every other ecosystem on Earth, despite it being the largest. In the Earth's largest living space, the bathypelagic biome, there is not even a complete inventory of the fauna (Webb *et al.*, 2010), much less a quantitative understanding. That said, great progress has been made on many fronts in the last two decades. Many of the major patterns of distribution have been quantified, at least in the upper 1000 m, and in some cases striking exceptions to the rule have been found. In an environment as massive and logistically difficult to study as the deep ocean, where experimental manipulation is generally out of the question, these exceptions represent natural experiments that allow better understanding of underlying ecological processes. When new methods and technologies are applied, especially when used in concert, new perspectives on the composition, abundance, distribution and ecology of the deep-pelagic fauna are gained. The near future will probably see rapid expansion of emerging technologies such as optical and acoustic imaging, autonomous vehicles and observing networks, to name a few, thus allowing unprecedented access to the deep-pelagic. Widespread application of advanced genetic analyses will probably change the concept of what constitutes an oceanic species. Likewise, advances in biochemical methodology will undoubtedly reveal pathways of elemental and molecular exchange that refine and redefine views of material fluxes. As humans expand resource extraction and habitat impact in the deep ocean, so too must understanding of the ecosystems, their processes, and their services be expanded if sustainability is to be achieved.

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