

Ocean Depths: The Mesopelagic and Implications for Global Warming

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The mesopelagic or ‘twilight zone’ of the oceans occurs too deep for photosynthesis, but is a major part of the world’s carbon cycle. Depth boundaries for the mesopelagic have now been shown on a global scale using the distribution of pelagic animals detected by compiling echo-soundings from ships around the world, and been used to predict the effect of global warming on regional fish production.

Depth Zonation

The classical concepts for depth zonation [1] in the ocean begin at the seashore (Table 1). Distinct communities are visible on the rocky seashore, and reflect the adaptations of their animals and plants to exposure to air and wave action, as well as the effects of grazing and predation [2]. Below the low-tide mark, plants characterize both the ‘infralittoral’ seabed and the open-water ‘epipelagic’ zones (Table 1). In these sunlit (photic) zones, photosynthesis uses nitrate and produces oxygen, so these indicators of biological activity are lowest and highest, respectively, in the epipelagic (Figure 1). Light penetration depends on the density of sediment and plankton in the water, so the actual depth of the photic zone will extend deeper further from land [3]. Deeper still, light in the twilight — or mesopelagic — zone is insufficient for photosynthesis, but animals can use this zone for feeding, avoiding predators, and other interactions. Thus, respiration dominates, resulting in low oxygen, and such mid-water ‘oxygen-minimum zones’ (Figure 1) harbor distinct fauna [4]. Below the mesopelagic there is no light and less food than in surface waters, so biological activity is low, and oxygen less depleted (Figure 1). However, while conceptually defined, the actual depth boundaries of these zones have not been defined by unsupervised data analysis; new work published by Proud *et al.* [5] in this issue of *Current Biology* now provides such data. The study represented over half of the world ocean. However, it lacked data from major regions, including the mid to south Atlantic, the south-east and north Pacific, and northern Indian Ocean.

Analyses were at 5 m depth intervals to 1,000 m deep, and a spatial resolution of 300 km².

The environment changes less as we go deeper (Figure 1), so we expect the vertical extent of ecological zones to increase with depth. While the rocky seashore may have distinct habitats only tens of centimetres deep, the epipelagic and infralittoral are tens of metres and the mesopelagic hundreds of metres deep. Below 1,000 m there is minimal variation in environmental parameters: it is dark, with the temperature at about $2 \pm 1^\circ\text{C}$ (as in polar seas), nitrate $32 \pm 1 \mu\text{mol l}^{-1}$ and oxygen 4 mg l^{-1} (Figure 1). Thus, there may be just one ecological depth zone below the mesopelagic, a true ‘deep-sea’ zone combining what are sometimes called bathyal, abyssal, and hadal zones. Alternatively, there may be an abyssal zone below 2,000 m where there is even less environmental variation (Figure 1).

However, it remains to be clearly shown whether the abyssal zone is ecologically distinct from the bathyal.

The data shown in Figure 1 are global averages, and local exceptions will occur, particularly in more enclosed waters such as the Mediterranean and Black Seas [6]. The seabed-resident fauna (benthos) will be influenced by these variables but additionally by the seabed substratum and currents. Topographic variation includes about 70,000 seamounts — subsurface mountains over 1,000 m high from seabed, some of which include chemosynthetic hydrothermal vents — on an otherwise almost flat (<2% slope) sediment-cloaked seabed [7]. It is thus possible that the benthos may occupy distinct areas within the pelagic zones.

Deep Scattering Layers

Marine mapping uses the echoes of acoustic signals to detect not only seabed

Table 1. Features of the concepts of ecological depth zones in the oceans.

Depth	Environment	Pelagos	Benthos	Ecosystem function
Above low tide	Tidal air exposure	Epipelagic		Photosynthesis
<200 m	Photic zone	(phytoplankton)	Infralittoral (seaweeds)	
<1,000 m	Twilight zone <1% light	Mesopelagic	Circalittoral	Respiration high High nutrients Lower oxygen
? <2,000 m	Aphotic zone	Bathypelagic	Deep-sea	Respiration low High nutrients
?	<4 °C	Abyssopelagic		
Deepest		Hadopelagic		

The changes in the air and light exposure of the environment with depth are reflected in changes in dominance of plants in both the pelagos (the water-column biota, including phytoplankton) and benthos (the seabed biota including seaweeds and seagrass). These biota then determine the ecosystem function, including concentrations of oxygen, carbon dioxide and available nutrients. The sublittoral is the infra- and circalittoral combined.

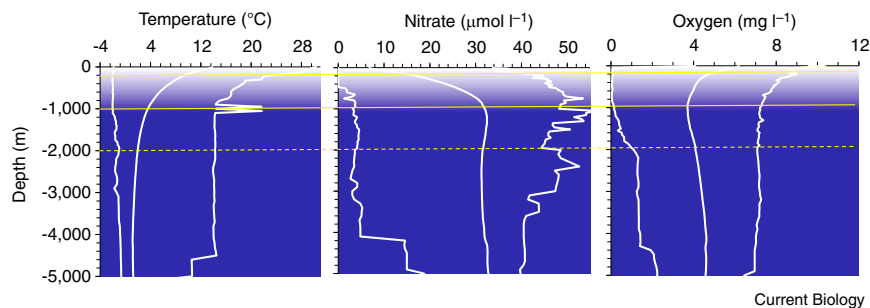


Figure 1. Environmental changes in relation to ocean depth.

Depth profiles of sea temperature, nitrate and oxygen based on data from the World Ocean Atlas, which can now be explored as Ecological Marine Units [6]. White vertical lines (left to right) are the minimum, mean, and maximum values for 100 m depth intervals across the world ocean. Yellow horizontal lines indicate boundaries between epipelagic and mesopelagic. The dashed line suggests a potential abyssopelagic boundary.

topography, but also the presence of fish, crustaceans and other materials in mid-water [8]. In the ocean, these acoustic signals detect a ‘deep scattering layer’ (DSL) comprised of animals that migrate vertically in the water column. During the night they rise to feed in shallower waters and by day they shelter from predators in deeper waters [4]. Proud *et al.* [5] provide the first global synthesis of DSL data from around the world. They found the DSL to range from ten to hundreds of metres deep, and to extend horizontally for tens to thousands of kilometres. The DSL was generally centered around 525 ± 100 m below the surface during the day with a secondary DSL around 800 m. Due to vertical migration, both of these DSL would become shallower at night. Thus the acoustic data define the epipelagic to be above 200 m, and mesopelagic between 200–1,000 m, confirming previous site-specific observations [4]. Much higher-density sound-scattering

layers (SSL) occurred within the top 100 m than in the mesopelagic, and lower SSL between 200–400 m; a region the authors called the ‘migrant zone’. These SSL and DSL provide the first global-scale remote sensing of biological data to distinguish the epipelagic and mesopelagic zones.

Significance for Climate Change and Fisheries

Although defining the mesopelagic may largely confirm previous studies, Proud *et al.* [5] took their findings a step further by considering the effect of climate warming on mesopelagic fauna. They predicted remote sensing of higher biomass accumulation because of increases in temperature-driven metabolism, growth, and trophic efficiency through the food-web, assuming sufficient nutrients and food for fish. There is empirical support for such predictions. Field data from off the south-east coast of Australia showed increased growth of fish with modal depth ranges of 20–200 m in response to climate warming [9]. However, the growth of fish with modal depth ranges of 1,100 m and 1,300 m decreased and correlated with cooling of deep waters. Thus ocean warming may benefit fisheries production in the mesopelagic but not in deeper waters.

In the Proud *et al.* study, the depth differentiation between the epipelagic and mesopelagic was important because global warming was predicted to shallow the DSL in some geographic regions; both the depth and densities of the DSL were predicted to change in the future [5].

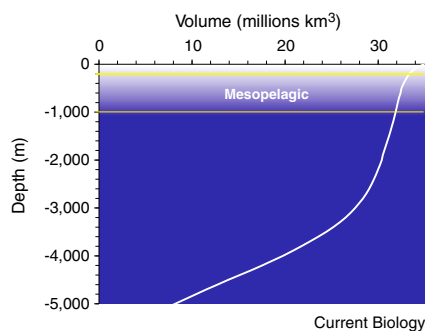


Figure 2. Ocean volume in relation to depth. Change in ocean volume (white line) with depth showing the significant volume occupied by the mesopelagic zone.

Changes in ocean temperature vary geographically, so the authors predicted that fish production will decrease in some areas, including the Atlantic, while increasing in others.

Species-distribution models predict that ocean warming will result in most species increasing their geographic ranges by moving away from the equator, thereby increasing species richness at higher latitudes (see for example [10,11]). Proud *et al.* [5] further predict increased productivity. Together, we can expect climate warming to result in increased biodiversity in terms of species richness and biomass in the epipelagic and mesopelagic zones away from the equator. In contrast, species may suffer temperature stress in shallow equatorial waters. Recent coral bleaching may be a signal of this stress. Indeed, a dip in species richness has been noticed across a wide range of benthic and pelagic, vertebrate and invertebrate, taxa between 0° and -15° latitude [12].

The mesopelagic is a significant zone in terms of ocean volume (Figure 2). As it lacks plants, it is a net consumer of oxygen and producer of carbon dioxide. Whereas carbon dioxide is absorbed from the atmosphere at the ocean surface, and is then assimilated by plant growth, the mesopelagic fauna intercepts about 90% of organic carbon before it can sink to deep-sea sediments, and then releases carbon dioxide back into the water [4]. Indeed, the mesopelagic may contribute as much as 30% of ocean carbon dioxide production [4]. However, faecal pellets from mesopelagic fauna may increase carbon sedimentation rates. Understanding the biology of the mesopelagic is therefore essential for predicting global carbon dynamics and the effects of climate change.

REFERENCES

1. Costello, M.J. (2009). Distinguishing marine habitat classification concepts for ecological data management. *Mar. Ecol. Progr. Ser.* 397, 253–268.
2. Costello, M.J., and Emblow, C. (2005). A classification of inshore marine biotopes. In *The Intertidal Ecosystem: the Value of Ireland’s Shores*, J.G. Wilson, ed. (Dublin: Royal Irish Academy), pp. 25–35.
3. Stal, L.J. (2016). Chapter 7. The euphotic realm. In *The Marine Microbiome*, L.J. Stal, and M.S. Cretoiu, eds. (Switzerland: Springer International Publishing), pp. 209–225.

4. Robinson, C., Steinberg, D.K., Anderson, T.R., Arístegui, J., Carlson, C.A., Frost, J.R., Ghiglione, J.-F., Hernández-León, S., Jackson, G.A., Koppelman, R., *et al.* (2010). Mesopelagic zone ecology and biogeochemistry – a synthesis. *Deep Sea Res. II* 57, 1504–1518.
5. Proud, R., Cox, M.J., and Brierley, A.S. (2017). Biogeography of the global ocean's mesopelagic zone. *Curr. Biol.* 27, 113–119.
6. ESRI. (2016). Ecological Marine Units. Accessed at <http://www.esri.com/ecological-marine-units> on 15th November 2016.
7. Costello, M.J., Cheung, A., and De Hauwere, N. (2010). Topography statistics for the surface and seabed area, volume, depth and slope, of the world's seas, oceans and countries. *Environ. Sci. Technol.* 44, 8821–8828.
8. Andréfouët, S., Costello, M.J., Rast, M., and Sathyendranath, S. (2008). Earth observations for marine and coastal biodiversity. *Remote Sens. Environ.* 112, 3297–3299.
9. Thresher, R.E., Koslow, J.A., Morison, A.K., and Smith, D.C. (2007). Depth-mediated reversal of the effects of climate change on long-term growth rates of exploited marine fish. *Proc. Natl. Acad. Sci. USA* 104, 7461–7465.
10. Basher, Z., and Costello, M.J. (2016). The past, present and future distribution of a deep-sea shrimp in the Southern Ocean. *PeerJ.* 4, e1713.
11. Saeedi, H., Basher, Z., and Costello, M.J. (2016). Modelling present and future global distributions of razor clams (Bivalvia: Solenidae). *Helgoland Mar. Res.*, in press. DOI 10.1186/s10152-016-0477-4.
12. Chaudhary, C., Saeedi, H., and Costello, M.J. (2016). Bimodality of latitudinal gradients in marine species richness. *Trends Ecol. Evol.* 31, 670–676.

Functional Connectomics: How Maggots Make Up Their Minds

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How *Drosophila* larvae select one behavior or a sequence of behaviors, and then persist in the final one, has been addressed by a powerful combination of electron-microscopy reconstruction of neuronal connections, genetic manipulations, electrophysiology, and neuronal modeling. Surprisingly, reciprocal inhibitory synaptic connections are major players in choosing, sequencing and maintaining behaviors.

The future is here! For the past decade, I have been telling classes of graduate students that their careers will see huge advances in how circuits of neurons produce behaviors, largely because new technologies are providing approaches for working out these circuits that previous generations of neuroscientists could only dream about. These new technologies include molecular genetics, virology, dyes for recording, activating, and silencing neurons [1], electron microscopy reconstruction to produce cellular-level 'connectomes' [2], and computational approaches for both data analysis and modeling [3]. A new paper by Jovanic *et al.* [4] is an excellent example of how these new techniques can be used in a powerful way to figure out how neurons communicate with one another to produce and coordinate behaviors.

This study uses larval *Drosophila* (aka maggots) which, at the developmental stage used, is a segmented worm composed of a head, a telson (tail), and

eleven intermediate segments — three thoracic and eight abdominal — each with a ganglion composed of fewer than 1000 neurons that connects to adjacent ganglia via connectives. Segments move mainly by longitudinal muscle contractions, with subsequent elongations produced by a high internal pressure. Each intermediate segment can bend, by contracting the longitudinal muscles on one side, or shorten, by contracting all the longitudinal muscles at once. In addition, the larva can crawl by producing a sequence of ventral shortenings that move along the body, pushing the animal forward. Under the experimental conditions used by Jovanic *et al.* [4], unperturbed larvae crawl continuously; in response to a mild mechanical stimulus, provided by air current directed at them, the larva stops crawling and either bends (randomly left or right) or shortens (called 'hunching' in this paper). If the stimulus is maintained, the larva returns to crawling after several seconds, but the authors focused on the

initial response, either bending or hunching.

A previous study [5] had shown that a particular type of mechanosensory ending, known as the chordotonal organ, was responsible for producing both bending and hunching. Which of the two behaviors was elicited was probabilistic, even when the same set of chordotonal organ neurons were repeatedly activated optogenetically by expressing the dye CsChrimson [6] in a subset of chordotonal organ neurons. To work out the circuitry of the neurons involved in choosing between bending and hunching, the authors tested the contributions of a set of interneurons called 'Basin Projection Neurons' — named for the shape of their dendritic trees and the fact that they had axons that projected out of the ganglion containing the cell body — henceforth called B neurons. These neurons had been previously shown to receive strong chordotonal organ input [7]. They were originally identified by behaviorally