

# **Life at Extreme Depths: Physiological Adaptations of Deep-sea Pelagic Fishes**

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## **Abstract**

The deep pelagic ocean is the largest and least explored ecosystem on Earth. Fishes inhabiting this biome have, through the processes of adaptive evolution, overcome unparalleled biotic and abiotic conditions that include high pressure, no or only very light light, and low biomass. Despite these challenges, fishes have repeatedly invaded this ecosystem, relying on the evolution of complex morphological and physiological systems that permit diversification in this exceedingly harsh realm. This review surveys these systems from an ecophysiological and ecomorphological perspective, focusing on how the diversity of form and physiology relate to functions that increase fitness within an ecosystem that is dimly lit, food poor, and hyperbaric.

## Introduction

Perhaps the most outstanding characteristic of the deep sea is its enormity. With some 71% of the planet's surface covered with seawater, marine habitats represent the largest collection of habitable spaces on Earth. The most familiar and studied of these ecosystems are the shallow waters over the continental shelves at depths between 0–200 m. Beyond the continental margins below 200 m, there exist the most expansive biome on our planet: the deep-sea. Of the estimated 1.37 billion cubic kilometers of Earth's marine volume—nearly 200 times the volume of terrestrial ecosystems (Cohen, 1994)—oceanic waters below 200 m account for 90% of this space. Because of its vastness, the deep-sea and the deep pelagic ocean, remains the least explored environment on our planet. Despite this, researchers are rapidly accumulating knowledge concerning the biotic and physical parameters that have shaped the morphology, physiology, and diversity of fishes that inhabit the deep pelagic realm. Since the beginning of deep-sea biology ushered in by the H.M.S *Challenger* (1872–1876), the field of deep-sea biology, in general, and the study of deep-sea fishes, in particular, have transformed from purely descriptive endeavors to theory-driven and experimentally based disciplines that leverage the most current methods in organismal and evolutionary biology and ecology.

Through the process of adaptive evolution, fishes inhabiting the deep pelagic ocean have overcome some of the most extreme biotic and abiotic properties of any ecosystem on Earth. The primary challenges to biological success in the deep sea include high hydrostatic pressure, little or no light, and low biomass. Despite these challenges, fishes have repeatedly invaded this extraordinary environment and, in so doing, evolved complex, adaptive morphological and physiological systems that permit the proliferation of diversity under these harsh conditions. This chapter explores these systems from an ecophysiological and ecomorphological perspective, taking into account how the diversity of form and physiology relate to functions that increase fitness within an ecosystem that is dimly lit, food poor, and hyperbaric.

## Adaptations to light in the deep sea

There are two sources of light in the deep sea: (1) visible electromagnetic radiation from the sun, moon, and stars and (2) light emitted by organisms inhabiting this ecosystem. The importance and relative magnitudes of these sources change with depth due to the optical properties of water. Organisms living

at the ocean's surface enjoy a rich, polychromatic visual environment; however, with each meter of depth, the visual environment becomes increasingly dark and monochromatic so that by about 200 m even in the ocean's clearest waters, the orange-red ( $>550$  nm) and ultraviolet ( $<400$  nm) parts of the visible spectrum are completely removed (Tedetti and Sempr, 2006; Tyler *et al.*, 1972). In addition to altering the spectral character of light, water effectively absorbs light. At the surface, the radiance of blue 475-nm daylight is approximately  $2.5 \times 10^{19}$  photons  $\text{m}^{-2}\text{s}^{-1}\text{sr}^{-1}$  (Warrant and Locket, 2004). Modeling an eye with a lens acting as a long-pass filter that blocks UV with a 50% cut off at 400 nm and a possessing a rhodopsin sensitive to the same 475-nm light, Warrant and Locket (2004) calculated that, at the surface,  $2.7 \times 10^{21}$  photons  $\text{m}^{-2}\text{s}^{-1}\text{sr}^{-1}$  would be available to the photoreceptor. At a depth of 100 m in clear ocean water, this same eye would struggle for light against a three-orders of magnitude drop in intensity to  $6.8 \times 10^{18}$  photons  $\text{m}^{-2}\text{s}^{-1}\text{sr}^{-1}$ . Because of a precipitous drop in phytoplankton and dissolved organic matter below 100 m, light intensity declines much less rapidly at 1.5 orders of magnitude per 100 m. At 600–700 m, light intensity during the day drops to that of a star-lit night at the surface and below depths of 1000 m there is no usable downwelling light (Warrant and Locket, 2004). Due to this drop in intensity with increasing depth, the visual environment of the deep sea becomes increasingly influence by point-source bioluminescence produced by deep-sea organisms themselves (Herring, 2002; Haddock *et al.*, 2010). Thus, in the dysphotic mesopelagic zone below 200 m to approximately 1000 m, the visual environment is influenced by both downwelling light from above and point-source bioluminescence. Below 1000 m, in the aphotic bathypelagic zone, point-source bioluminescence is the only source of visible light. This transition from an extended and broad-field light above to point-source light below is undoubtedly the most important selective force behind patterns of vision and bioluminescence in the deep sea.

Because the mesopelagic zone represents the transition from surface intensities to near total darkness, the fishes inhabiting this space encounter a wide range of visual environments from extended fields to point-source bioluminescence. Therefore, it is not surprising that it is in this realm that fishes exhibit the most diverse suite of visual adaptations among marine vertebrates. These adaptations can be placed broadly in to three categories: (1) those associated with the eye to form a visual stimulus despite challenging and varied light conditions; (2) those that permit crypsis and the ability to remain hidden in their environment, and (3) those that permit communication—in either conspecific or intraspecific contexts—to find mates, food and increase fitness. Adaptations for forming a visual

stimulus and remaining hidden are treated directly below and adaptations relevant to communication in feeding and reproduction are treated in the subsequent section.

## Eyes of deep-sea fishes

The paramount visual challenges to mesopelagic fishes are to increase sensitivity in this dimly lit environment and to form images of food or predators that could be lurking in any direction in structureless midwaters. The adaptations to increase sensitivity and the scope of the visual field in fishes of the mesopelagic zone are numerous and have been the subject of many studies. These evolutionary innovations, both morphological and physiological, have been ably reviewed by Marshall (1954, 1979), Locket (1977), Munk (1966), Collin *et al.* (1997), Douglas *et al.* (1998b), and Warrant and Locket (2004).

## Optical adaptations

Perhaps the most conspicuous characteristic of the eyes of mesopelagic fishes is their large relative size. A larger eye permits a larger pupil which, in turn, permits the capture of more light and greater visual sensitivity. Although very few empirical data exist, there is a general pattern in which eye size of fishes increases with depth within the mesopelagic zone (Marshall, 1954; Warrant and Locket, 2004). The most thorough demonstration of this pattern was presented by Lisney and Collin (2007) in their study of elasmobranchs. Within the bathypelagic zone, where light is almost nonexistent, the trend of larger eye size as a function of depth reverses (Marshall, 1954; Warrant and Locket, 2004), betraying the reliance on other sensory modalities at these great depths. In their study of eye size in myctophids, however, Busserolles *et al.* (2013) found that variability in eye size was not explained by depth distribution but driven by phylogenetic relationships alone.

Although the design of the eyes of many mesopelagic fishes are identical to that of their shallow-water relatives (e.g., daliid and etmopterid sharks, and some myctophids, sternopychids, and stomiids), many others have altered this conservative architecture. In the open mesopelagic zone, there is no structure within which to hide, and therefore, the ability to scan an expansive three-dimensional space for food and predators is of paramount importance. Consequently, midwater fishes have evolved several morphological features associated with the eye—some simple and some extremely complex—that permit a broadened visual field.

Among the more subtle morphological adaptations for expanding the visual field is the aphakic (i.e., lensless) space in the pupil of species of several families of fishes (e.g., Bathylagidae, Alepocephalidae, Platyptidae, Myctophidae, and Notosudidae). In some of these taxa, the aphakic space is merely a broadened opening to the pupil which permits increase illumination of the lens in all direction. In those fishes with a "rostral" aphakic space, the internal margin of the pupil does not conform to the round shape of the lens, leaving a small gap anteriorly that permits more light to pass through the lens (Munk & Frederiksen, 1974). This, along with slightly anteriorly directed skeletal support for the eyes, a narrow snout, grooves in the snout, or any combination of these structural features, permits binocular visual in the important anterior field where food can be captured and processed. As part of this innovation, posterior (i.e., temporal) areas of the retinae illuminated by the rostral aphakic space are often densely packed with ganglion cells arranged in a fovea. In both cases, unfocussed light from the lateral field may enter through the pupil, bypass the lens, and directly illuminate the retina, thereby corrupting any image signal with noise. Warrant and Locket (2004) pointed out that this may represent an important tradeoff off between acuity and the ability to detect the weak stimulus of predators or prey.

A more complex adaptation for the expansion of the visual field is represented by evolution of the tubular eye, a hallmark design of the teleost families Opisthoproctidae, Giganturidae, Scopelarchidae, Evermannellidae, Stylephoridae, and some species of the families Sternopychidae, Phosichthyidae, and Paralepididae (Marshall, 1979; Herring, 2002; Warrant and Locket, 2004). As the name implies, the lens is large, spherical, and protuding at the end of a tube (Figure 1a). Tubular eyes are immobile and typically directed either dorsally or anteriorly. This modified visual system improves sensitivity, increases contrast, and permits accurate depth perception due to a broad binocular overlap (Figure 1b; Munk, 1966; Herring, 2002; Warrant *et al.*, 2003). Because of the tubular shape, the main field of view associated with the primary retinal surface is significantly reduced when compared with normal spherical eyes. To mitigate this drawback, the tubular eye of some fishes, including some sternopychids, phosichthyids, and ophisthoproctids, have an accessory retina in addition to the main retinal surface (Figure 1a). The thick main retina is illuminated by the anterior of the dorsal binocular field of the extended lens apparatus while the thin accessory retina is illuminated by the lateral monocular field. Despite being sensitive to changes in light intensity, the accessory retina resides too close to the lens for proper accommodation and image formation (Munk, 1966).

In addition to accessory retinae, three other innovations—retinal diverticula, lens pads, and lens folds—have evolved in mesopelagic fishes to expand the visual field. The retinal diverticulum in species of the family Ophisthoproctidae is an ovoid, pouch-like bulge positioned on the lateral surface of the eye, the inner surface of which is lined with a thin layer of rod photoreceptor cells (Figure 1c,d) . The medial surface of the tubular eye is lined with reflective guanine crystals and thus directs lateral sources of light through a clear epidermal window and onto the retinal surface of the diverticulum (Figure 1d). The shape and relative position of the reflective surface and diverticulum permit light detection up to 60°below the eye. It has been proposed that, like the accessory retinae of these and other fishes inhabiting the mesopelagic zone, a retinal diverticulum is incapable of forming an image and its utility is in detecting changes in light intensity brought on by food, predators, or conspecifics in the periphery (Munk, 1966; Frederiksen, 1973). In at least two species opisthoproctid fishes, however, the diverticulum has been modified to permit image formation. The diverticulum of *Bathylychnops exilis* is ventrally directed and possess its own lens which focusses light onto the diverticulum’s retinal surface (Pearcy *et al.*, 1965; Munk, 1966). In a rather astonishing discovery, Wagner *et al.* (2009) reported that the ophistoproctid *Dolichopteryx longipes* possess many small guanine-based mirrors within the diverticulum that reflect concentrated light on the retina of the diverticulum and that this results in a well-focused image (Figure 1d,e). It is reasonable to speculate that other members of the genus *Dolichopteryx*, or indeed the family, possess the ability to produce an image with reflective as well as refractive optics, a unique capability among vertebrates.

Instead of a diverticulum, fishes of the alepisauroid families Scopelarchidae and Evermannellidae have each evolved distinct optical structures that broaden sensitivity and extend their field of vision (Locket, 1977). Located laterally within the eye between the lens and the opening of the pupil, the scopelarchid lens pad illuminates the dorsal section of the retina with light from the ventral direction (Figure 1b). Evermannellids possess optical folds that cover the ventrolateral surface of the exposed tubular eye which direct light through the lens of the tubular eye. Although these groups of fishes represent closely related lineages (Baldwin and Johnson, 1996; Davis and Fielitz, 2010), the different topological position and development of these structures indicate separate evolutionary origins.

The preceding optical innovations concern the expansion of the visual field through greater retinal illumination. In addition to this, many mesopelagic fishes optimize the absorbance of light by the retina with a tapetum, a reflective surface composed of guanine positioned behind the photoreceptors.

In teleost fishes, this reflective layer is typically embedded in the retinal pigment epithelium (Douglas *et al.*, 1998b), while in deep-water chondrichthyans, the tapetum is typically located in the choroid layer (Denton and Nicol, 1964). The function of the tapeta is to illuminate photoreceptor cells with reflected light that has passed through them. It has been proposed that this effectively elongates the outer segment of the photoreceptor where the opsin pigments reside (Warrant and Locket, 2004), however, others have proposed that the tapetum enhances sensitivity by increasing the signal to noise ratio (Denton and Nicol, 1964; Muntz, 1990). Perhaps the most notable and intriguing example of this relationship is found in the stoplight loosejaw, *Malacosteus niger*. The tapetum of *M. niger* is composed of the carotenoid pigment astaxanthin and reflects light most effectively at 700 nm, a match to both its rod photoreceptor sensitivity and own bioluminescence (Douglas *et al.*, 1998b). As is demonstrated later in this chapter, this is but one of several adaptations permitting private and stealthy vision by some species of the family Stomiidae.

### **Neural adaptations**

Unlike the optical innovations considered above, the underlying neurophysiological mechanisms of vision in deep-sea fishes are identical to all other vertebrates. After being altered in direction or quality by the optical media of the eye, light illuminates the outer segments of the retinal photoreceptor cell, which contain the visual pigment, a G-coupled-protein receptors that, when exposed to light, bleaches and initiates a signal cascade. For the most part, neural adaptations for effective vision in the deep sea represent relatively subtle modifications of this physiology and include changes to the cellular composition of the retina and minor shifts in the molecular composition of photoreceptor pigments. As subtle as these changes may be, they have resulted in extraordinary adaptive shifts in phenotype that permit vision in the most challenging photic environment on Earth.

In terms of cellular composition, the retinae of deep-sea fishes are nearly uniform in that they possess only rod photoreceptors and lack cone photoreceptors altogether. Thus, deep-sea fishes make use of dark-suited photoreceptors that shallow-water and terrestrial vertebrates use in nocturnal vision. Rhodopsin, the visual pigment typically associated with rod cells, is composed of retinal—a vitamin A<sub>1</sub>-based chromophore—bound to an opsin protein. The rod cells of a few deep-sea fishes and terrestrial vertebrates contain porphyropsin, a pigment that utilizes A<sub>2</sub>-based 3,4-dehydroretinal, rather than retinal, as the chromophore. During bleaching, the chromophore of the rod visual pigment absorbs

light and the amino-acid sequence of the opsin protein constrains the spectral absorbance of the chromophore. The interaction of specific amino acids of the rod opsin protein with the pigment's chromophore constrains the absorbance peak  $\lambda_{max}$  and thus the spectral sensitivity of the pigment and the phenotype of the fish (Yokoyama and Yokoyama, 1996; Menon *et al.*, 2001). The  $\lambda_{max}$  values of retinal-based rhodopsin pigments are of much shorter wavelengths than porphyropsin-based pigments utilizing the same opsin (Douglas *et al.*, 1998b; Bowmaker *et al.*, 1988). Therefore, in the course of adaptation to the visual environment of the deep sea, fishes had at their disposal two molecular pathways: alternative chromophore utilization and tuning of the pigment through amino-acid evolution.

With only a very few striking exceptions, the visual pigments of deep-sea fishes are sensitive to a narrow spectrum of visible light, about 468–494 nm (Douglas *et al.*, 1998b; Douglas and Partridge, 1997). This spectral sensitivity is conveniently similar to the wavelength of available downwelling light in the mesopelagic, about 475 nm. A broad match between  $\lambda_{max}$  of deep-sea fishes and the background illumination from downwelling light is congruent with the sensitivity hypothesis which explains this relationship on the basis that, in the course of adaptation to a new photic environment, animals will match the  $\lambda_{max}$  of a photopigment to background wavelengths in order to increase sensitivity. However, it has been demonstrated that invoking the sensitivity hypothesis to explain the distribution of  $\lambda_{max}$  is perhaps too simplistic. Douglas *et al.* (1998b) calculated the most sensitive photoreceptor pigments at various depths given spectral irradiance and attenuation coefficients. Their calculations predict that, for most of the world's deep-sea environment, the photoreceptor pigments of most fishes should have a  $\lambda_{max}$  of 474 nm or less. Therefore, considering the broader range of the  $\lambda_{max}$  of deep-sea fishes, this is a rather poor match. Furthermore, fishes caught from the same depth in the same trawl and presumably in the same photic environment may have  $\lambda_{max}$  values that differ by more than 20 nm. In addition, the sensitivity hypothesis predicts that  $\lambda_{max}$  values should decrease (i.e., shift to the blue) with increased depth. Partridge *et al.* (1989) found this prediction to be false and that there is no substantial positive correlation of sensitivity with depth. Thus, the sensitivity of the visual pigments of deep-sea taxa appear to be tuned to the other source of light in this environment: bioluminescence.

The vast majority of deep-sea organisms are bioluminescent (Herring, 2002, 1978). Therefore, a hypothesis that explains sensitivity in terms of detecting the light emissions of prey, predators, and conspecifics is perhaps more attractive than one based on the sensitivity to downwelling irradiance.

Unfortunately, the spectral properties of bioluminescence of regrettably few taxa have been studied and, thus, an evaluation of the correspondence between patterns of photoreceptor sensitivity and light produced by deep-sea organisms has been difficult. Despite this, Partridge *et al.* (1989) integrated limited data concerning typical fish bioluminescence, eye size, outer-segment lengths of fish photoreceptors, visualization range, and water type to produce models of the most sensitive visual pigments given values for these parameters. The calculated values of  $\lambda_{max}$  sensitized to point-source bioluminescence are indeed different than those calculated for sensitivity to downwelling light and offer a much better match to experimentally derived  $\lambda_{max}$  data (??). In further corroboration of adaptation to point sources, Turner *et al.* (2009) reported that myctophid  $\lambda_{max}$  values correspond well to limited emissions data for myctophid bioluminescence, about 469–474 nm (Nicol, 2009; Herring, 1983; Widder *et al.*, 1983; Denton *et al.*, 1985). In total, these data suggest that bioluminescence is the selective force behind tuning of visual pigments in fishes.

Perhaps no other group of deep-sea fishes exemplifies adaption to the visual constraints of the deep sea more than species of three genera in the dragonfish family Stomiidae. Sensitized to their own photophores that produce red emissions greater than 700 nm, species of *Aristostomias*, *Malacosteus*, and *Pachystomias* evolved extremely specialized visual pigments, some with peak absorption wavelengths greater than 650 nm (Douglas *et al.*, 1998b). *Aristostomias* and *Pachystomias* achieve far-red sensitivity by possessing three and possibly four long-shifted rhodopsin (Partridge and Douglas, 1995; Douglas *et al.*, 1998b). In addition to rhodopsins sensitive to emissions of approximately 520 nm, these taxa utilize an additional porphyropsin pigment composed of the same opsin bound to 3,4-dehydroretinal (as opposed to retinal) that permits a  $\lambda_{max} \approx 550$  (Bowmaker *et al.*, 1988; Partridge *et al.*, 1989; Partridge and Douglas, 1995; Douglas *et al.*, 1998b). In an astonishing discovery, Douglas *et al.* (1998a) found that *Malacosteus niger* has both a red-shifted rhodopsin-porphyropsin pair based on the same opsin protein and a photosensitizer composed of defarnesylated and demetalated derivatives of bacteriochlorophylls c and d that permits sensitivities to wavelengths greater than 630 nm. The functional significance of these phenotypes, although untested, is apparent. Because nearly all other deep-sea taxa possess rhodopsins sensitive to only blue-shifted wavelengths, species with the capability to both produce and perceive far-red emissions are afforded a private bandwidth to communicate with conspecifics and illuminate unknowing prey (??). In addition, this active yet private sensory modality may extend far beyond the spatial limits of passive mechanoreception. A

visual system based on long-wave emissions and sensitivity would be able to illuminate and visualize prey at a range of about 1.3 m, approximately 10 times the effective range of the lateral-line system (Partridge and Douglas, 1995).

The molecular basis of loosejaw far-red sensitivity has been the subject of several studies and, as a result, the specific tuning events—down to the amino-acid level—responsible for longwave vision have been uncovered (Hunt *et al.*, 2001; Yokoyama *et al.*, 2008; Kenaley *et al.*, 2014). The loosejaw system serves as informative model in the elucidation of visual adaptation in the deep-sea. The body of this work suggests that only a relatively few opsin amino acids substitutions at sites which bind to the chromophore (i.e., tuning sites) are responsible for dramatic shifts in phenotype (Hunt *et al.*, 2001; Kenaley *et al.*, 2014). The pace of this change can be relatively quick, as well. Kenaley *et al.* (2014) inferred that shifts between red- and -blue based visual systems have occurred rapidly over short geological time scales and that these shifts were in response to strong positive selection. The underlying selective force is likely the unique red bioluminescent capabilities of the loosejaws, an inference that supports the point-source hypothesis of spectral tuning in deep-sea fishes.

This narrative of rapid evolution of visual systems in concert with far-red, point-source bioluminescence does not stop at the taxonomic boundaries of the dragonfishes. In fact, the visual sensitivity of at least two species of myctophids, the preferred prey of dragonfishes (Sutton and Hopkins, 1996b), are red shifted. Douglas *et al.* (2002) uncovered that the retina of *Bolinichthys longipes* contains a chlorophyll-based, photostable pigment that absorbs maximally at around 670nm. Thus, as in *M. niger*, such a pigment may confer longwave photosensitivity. Hasegawa *et al.* (2008) later reported that the rhodopsin of *Myctophum nitidulum* had a  $\lambda_{max}$  of 522 nm, a dramatic red shift relative to all myctophid taxa other than *B. longipes*. The red-shifted visual capabilities of these two species may confer a distinct advantage in that they can detect the otherwise private wavelength of their predominant predators at ranges of 1 m in the case of *M. nitidulum* and up to 7 m in *B. longipes* and thus evade being eaten (Turner *et al.*, 2009) . These studies suggest that a deep-sea arms race is being waged whereby predators arrive at an adaptive peak of private wavelengths which in turn drives an adaptive countermeasure in their prey.

## **Remaining Hidden**

Just as the preceding sections emphasize the importance of maximizing visual sensitivity and detecting objects in a challenging photic environment, there is an equally bewildering array of mechanisms employed by deep-sea fishes to defy detection. Although the primary task of staying hidden is simple, even in this light-limited space, remaining so is incredibly complex. The morphological and physiological mechanisms permitting deep-sea organisms to remain hidden have received relatively little scientific scrutiny, especially as they relate to fishes. This is no doubt due to the logistical hurdles associated with *in-situ* and onboard sampling and experimentation in the offshore oceanic setting. Despite this lack of knowledge, there exist several excellent reviews of camouflage and crypsis in the deep sea, namely MCFALL-NGAI (1990), Herring (2002), and Johnsen (2014). Readers who may be especially interested in the biophysical aspects of camouflage in the deep sea should review Johnsen (2014).

Unlike nearshore and terrestrial ecosystems, the deep open ocean is featureless and thus there is nothing to hide behind or within. Because of this, the animals inhabiting the mesopelagic zone are bathed in downwelling irradiance. Therefore, midwater fishes must overcome being either too bright or too dark relative to a dim background. To mitigate the contrast imposed by their bodies, mesopelagic fishes depend on four strategies: transparency, reflectivity, coloration, and countershading. Each of these strategies is discussed in turn below.

### **Transparency**

As pointed out by Johnsen (2014), transparency is perhaps the most simple and effective strategy to remain hidden in the pelagic realm; however achieving transparency is incredibly complex and perhaps the least understood of all the proposed mechanisms. To achieve complete transparency requires that the body of a fish have the same refractive properties of water. Thus, the easiest path to transparency would be a body composed of water, an impossibility given that, for fishes in particular, organisms must maintain opaque tissue for normal organismal function (e.g., epidermis, gut and brain tissues, bone, muscle, etc.). This requirement seems to have limited the occurrence of transparency to the relatively short period of larval development in fishes, including those that inhabit the deep sea. Many fishes are extremely laterally compressed, a property that reduces the scatter of light, and thus increase transparency, by reducing the optical path length (Johnsen, 2014). The leptocephali of elopomorph fishes (eels and allies) represent the most extreme examples of this with

paper-thin bodies (Miller, 2009). Aside from shape, transparent larval fishes may utilize at least three cellular adaptations to reduce the scatter of light (Johnsen, 2014). These include (1) adjusting the size, shape, and arrangement of organelles and intracellular components, (2) the present of clearing agents of high refractive index that match that of the tissues they surrounds, and (3) no special modification, but rather reduced complexity of tissues. The distribution of these three strategies among marine fishes is largely unknown, however, elopomorph leptocephali apparently utilize at least the third mechanism in that much of their mass is clear gelatinous extracellular tissue, although this may also be an adaptation for increased buoyancy (Miller, 2009). In regards to adult deep-sea fishes, the degree to which adult fishes inhabiting the deep-sea rely on any of these cellular strategies is unclear. While not completely transparent, some deep-sea taxa (e.g., stomiiforms of the genera *Argyropelecus*, *Valencienellus*, and *Vinciguerria*), maintain body parts composed of transparent tissues. These and other partially transparent deep-sea fishes may reduce light scatter in some parts through transparency and in other parts of their bodies rely on additional strategies including, reflectivity, coloration, or counterillumination (Figure 2).

## Reflectivity

Many mesopelagic fishes have silvery bodies and the broad phylogenetic occurrence of this character among mesopelagic teleosts suggests multiple evolutionary origins and belies its adaptive significance. Silvering is a conspicuous feature of species in the families Sternopychidae, Gonostomatidae, Myctophidae, Bathylagidae, and Steindechnaridae. The developmental origins of silvering are the same across all these groups in that in every case it is derived from the deposition of anhydrous guanine (Denton and Land, 1971; Denton and Nicol, 2009; Levy-Lior *et al.*, 2008). The function of silvering is to reflect light and, because light in the open ocean is symmetrical relative to the vertical, any light reflected from a mirror-like body will render the body invisible. A reflective system such as this works only if the face of the mirrors of the body are vertically arranged. In perhaps the best example of silvering in the deep sea, the hatchetfishes of the family Sternopychidae are extremely laterally flattened, a body plan the permits a near vertical surface (Figure 2a,b). In addition, during migrations to the surface and back, hatchet fishes maintain a vertical body posture (Janssen *et al.*, 1986). Furthermore, the guanine crystals of these and other fishes are precisely arranged in stacks so that they maintain vertical orientation (Figure 2a). These morphological, behavioral, and biophysical innovations create

surfaces that reflect nearly 100% of the incident light and thus permit near total invisibility (Denton and Land, 1971). During night, when downwelling irradiance decreases by several orders of magnitude, this highly reflective surface is likely a liability in that any flash of bioluminescence from a predator could indicate the prey's position. To mitigate this risk, hatchetfishes disperse chromophores over their stacks of guanine at night, thereby reducing their reflectivity (Figure 2b; Herring, 2002).

### Coloration

Beyond silvering, the color of fishes inhabiting the deep sea are well suited to remaining hidden in this unique photic environment. Rather than reflecting light like many mesopelagic fishes (Figures 2a), deep-sea fishes rely on black or, in limited cases, red pigmentation to remain hidden (Figure 2c,d). Both of these colors would appear invisible in the short-wave background irradiance of the mesopelagic ocean or if exposed to point-source blue bioluminescence (Johnsen, 2005). The use of red as an absorbing pigment is rare in deep-sea fishes (Johnsen, 2014), although this is a hallmark feature of many whalefishes of the order Cetomimiformes and a few distantly related taxa in the families Scorpaenidae, Peristediidae, and Chiasmodontidae. The dearth of red pigmentation is no doubt due to the fact that vertebrates are incapable of producing carotenoids (Leclercq *et al.*, 2009) and must rely on ingestion of invertebrates that accumulate these compounds for the purpose of remaining hidden themselves (Herring, 1973; Johnsen, 2005). On the other hand, the pigment responsible for black coloration in vertebrates, melanin, is synthesized in high quantities in teleost integument (Leclercq *et al.*, 2009). Thus, the evolutionary choice of a melanin-based system for light absorption does not restrict the diet of a fish to prey that is relatively poor in quality.

Within any one species of fish, especially those that inhabit the mesopelagic, color may not be uniform across the body. A completely silvered fish viewed from above would reflect downwelling irradiance and therefore betray its position to predator or prey. As a countermeasure, midwater fishes rely on countershading in which the dorsal aspect is darkly pigmented and equipped to absorb the weak blue background light (Figure 2a,b). Because many mesopelagic fishes engage in diel vertical migrations or otherwise do not maintain a position within an isolume (i.e., depths of similar light intensity). (Pearre, 2003), the intensity of downwelling light is not constant. Therefore, the success of dorsal countershading through pigmentation is not straightforward and requires that a fish possess the ability to mediate the amount of pigment in the integument and thus the amount of light absorbed.

The ability to modulate pigment patterns is a pervasive quality of fish melanophores (Leclercq *et al.*, 2009) and a strategy used by at least a few groups of midwater fishes (Herring, 2002).

### **Counterillumination**

Even in the dimly lit midwaters, a fish will cast a conspicuous silhouette and be detectable from below. As a solution to this, many mesopelagic fishes have evolved ventral counterillumination in the form of an array of bioluminescence photophores. The production of light from ventral photophores at the same frequency, intensity, and angular distribution as background irradiance renders the fish invisible against the downwelling light. The few experimental studies of ventral counterillumination in mesopelagic teleost fishes have demonstrated that these taxa have rather precise control of these parameters and thus the ability modify light production to match light from above (Denton *et al.*, 1972, 1985; Case *et al.*, 1977; Mensinger and Case, 1990). There exist notable exceptions to this. For instance, rather than adjust the intensity of photophore emittance to match downwelling light, lanternsharks of the family Etmopteridae maintain precise positions within an isolume.

### **Adaptations to low biomass**

In the deep open ocean, zooplankton and micronekton biomass decreases exponentially with depth up to within about 100 m of the bottom (Angel and Boxshall, 1990; Angel and Baker, 1982). Therefore, obtaining energy in the deep sea is an altogether different task than feeding in shallow and nearshore systems. Fishes that live in the sparsely inhabited meso- and bathypelagic zones overcome this lack of biomass by relying on strategies that reduce their need for food (i.e., increasing efficiency), effectively and regularly find food, or escaping to a more food-rich environment to feed. This first strategy, being energy efficient, is perhaps the primary key to survival in this energy-poor environment. As pointed out by Herring (2002), being efficient is largely accomplished through maximizing energy input and remaining metabolically efficient between periods of energy acquisition.

## **Maximizing efficiency**

### **Maximizing energy input**

Maximizing the amount of energy ingested during a feeding event is perhaps the most conspicuous aspect of the biology of deep-sea fishes, especially bathypelagic species. Although essentially no data exist concerning the feeding behavior of deep-sea fishes, much has been inferred from the relationship between morphology and prey choice. The central theme of this behavior is the ingestion of either large prey items or at least a large number of small prey items. In addition to more subtle morphological innovations, deep-sea fishes possess large mouths often laden with enormous fangs to effectively capture large prey items. For instance, the dragonfishes of the family Stomiidae—the top mesopelagic and upper bathypelagic predators—consume prey that is often greater than 50% of their body length and sometimes much larger (Clarke, 1982; Sutton and Hopkins, 1996b). To accommodate these large prey items, stomiids possess jaws that are in excess of 30% body length or several times the length of the neurocranium and open to gape angles greater than 100° (Tchernavin, 1953; Günther and Deckert, 1959; Kenaley, 2012). Furthermore, this massive gape is directed anteriorly by a hinge at the posterior of the neurocranium, the so-called occipito-vertral gap (Schnell and Johnson, 2012). It remains unknown in what manner (i.e., kinematics, timing, etc) dragonfishes use these morphological features in their feeding behavior; however a few authors have invoked a rat-trapping model whereby the dragonfish opens its jaws to this large gape angle, lures a prey item within or near the gape, and then shuts the jaws rapidly on the prey (Gartner *et al.*, 1997). This exemplifies the lie-and-wait ambush strategy that many deep-sea fishes engage in. Although this strategy prolongs foraging time relative to more active modes of feeding and, thus, increases energy demand between feedings, the passive nature of the strategy and potential for a huge meal may offset the energy loss. In the case of the loosejaw dragonfishes, the very act of closing the jaw involves an innovation that improves efficiency. With no skin between the bones of the mandibles (Figure 3), the jaw encounters significantly lower magnitudes of drag compared to other dragonfishes and, because no water is compressed, intra-oral pressure is not increased. Due to a reduction of resistive forces, the adductor muscles that power closing are smaller in loosejaws; this, in turn, reduces metabolically active tissues (Kenaley, 2012). Furthermore, because resistive forces are decreased along the length of the jaw, the loosejaw condition may have permitted the evolution of longer jaws with lower mechanical advantages that close just as quickly as

other dragonfishes but through a more expansive gape. Thus, the absence of skin between the lower jaw may be seen an innovation that reduces the metabolic cost of closing an extremely elongate lower jaw, while at the same time maintaining performance (Kenaley, 2012).

Other groups of deep-sea fishes that specialize in ambush predation of large prey amount to little more than a head and stomach. This is a body plan that defines females of the deep-sea anglerfishes and black swallows of the family Chiasmodontidae. With enormous jaws and fang-like teeth, these taxa are capable of ingesting inordinately large prey and it would appear that at least some of them are not gape limited, a factor that determines maximum prey size in many other groups of predatory fishes (Wilson, 1975; Scharf *et al.*, 2000). Rather, the expansive capacity of the short esophagus or stomach are what limit prey size and thus maximum energy consumption. Several published accounts document dead ceratioids floating on the ocean surface with enormous prey lodged within the gut cavity, apparently killed by their prey (see Pietsch, 2009; Figure 4a). Chiasmodontids appear limited by their gut capacity as well. The chiasmodontids demonstrate perhaps the most extreme preference for large prey and are capable of consuming other predatory fishes several times their body length (Figure 4b). Species of both groups possess large hinged teeth that rotate posteriorly about their sockets (Melo, 2009; Pietsch, 2009). Thus, it is unlikely that any captured prey within the oral cavity is able to struggle its way anteriorly, out of the esophagus and jaws, whether the predator would like to relinquish the prey or not.

Fishes that inhabit the upper mesopelagic—where food resources are slightly more plentiful and from where migrations to the food-rich epipelagic are more common—are equipped with more modest feeding morphologies. The most abundant groups in this realm, the myctophids and basal stomiiforms (i.e., families Gonostomatidae, Sternopychidae, and the polyphyletic Phosichthyidae), specialize in the consumption of zooplankton, typically calanoid copepods (see Gartner *et al.*, 1997, and references therein). These species lack enormous fangs, have more modest gapes and many fine oral teeth, and have a branchial morphology that is best suiting for sieving smaller prey items from ingested water (i.e., numerous, long gill rakers). Members of this zooplantivorous feeding guild that feed on other crustaceans (e.g., penaeidean and caridean shrimp) include members of the families Bregmacerotidae, some species of Melamphaidae, and the eel families Nemichthyidae and Dericthyidae. These anguilliform representatives rely on sniping larger crustacean prey rather than sieving smaller prey.

Yet others specialize in the consumption of gelatinous zooplankton, a relatively low quality food

(Larson, 1986; Clarke *et al.*, 1992; Doyle *et al.*, 2007). This trophic guild is represented by members of the family Melamphaidae, Opisthoproctidae, and Bathylagidae. The feeding morphology of these fishes is defined by a small gape, many small, sharp, shearing teeth, no or minute gill rakers, and an extended, coiled intestines (Gartner *et al.*, 1997). This low-energy food requires that these fishes be active foragers, finding dense concentrations of gelatinous prey and feeding for long periods once this resource is found. There is evidence that fishes of these groups seek out aggregations, especially gelatinous zooplankton communities that form extremely dense swarms over continental slopes (Wiebe *et al.*, 1979; Madin *et al.*, 2006; Graham *et al.*, 2001). Gartner and Musick (1989) reported that the meleophaid *Scopelogadus beanii* feeds acyclically on salps over diel time scales. Furthermore, Kenaley *et al.* (2014) found that this species is capable of drag-based labriform locomotion, a swimming strategy that conveys high maneuverability at low speeds and permits effective utilization of abundant, three-dimensionally distributed prey (Walker and Westneat, 2002a,b). Thus, like deep-sea piscivores and crustacean planktivores, gelatinous zooplanktivores appear to conform to long-standing models of the relationship between prey distribution, motility, and feeding locomotor behavior (Webb, 1984).

### Minimizing energy output

Once food is captured and assimilated, mesopelagic fishes face the challenges of reducing the rate at which energy is lost, a factor that, if too rapid, requires more frequent searches for food (e.g., a diel vertical migration) or results in decreased somatic growth and reproductive output. Primary among the physiological challenges associated with energy loss is the maintenance of buoyancy. Because deep-sea pelagic fishes must regulate their position in the water column—to remain stationary, ascend, or descend—efficiencies gained in the physiology of buoyancy permit greater allocation of limited energy resources to growth and reproduction. Gas bladders play a role in the buoyancy of midwater teleost fishes like they do in nearly all other members of the group, however, because these species live at such extreme depths, the gas bladders of deep-sea fishes must be equipped to accommodate extreme pressures. For those species that engage in diel vertical migrations, this problem is compounded because not only must they secrete gas against very high hydrostatic pressures at depth, they must also modulate this secretion out of or into the bladder during ascents or descents. As a consequence, many deep-sea pelagic fishes have modified gas bladders systems and other compensating physiological systems that reduce the requirements for such an expensive system. For example, gas bladders of many

midwater fishes have an extended rete system of greater length that increase the potential for counter-current exchange and, thus, the ability to exchange gasses against high gradients (Pelster, 1997).

The simplest strategy to reduce the cost of buoyancy and mitigate sinking force is for a fish to take on a density most similar to sea water, approximately  $1026 \text{ kg m}^{-3}$  at  $20^\circ\text{C}$ . The basic contributors to increased density relative to sea water include protein ( $1030 \text{ kg m}^{-3}$ ), muscle ( $1050$ – $1060 \text{ kg m}^{-3}$ ), and especially bone ( $2040 \text{ kg m}^{-3}$ ). Deep-sea fishes reduce both volume and density of these tissues, particularly bone and muscle (Denton, 1963; Denton and Marshall, 1958), but also protein (Yancey *et al.*, 1992). As a result, deep-sea fishes tend to be much softer, more watery, and more flexible than near-shore or surface fishes (Herring, 2002; Pelster, 1997).

Alternatively, a fish may increase the proportion of body materials that are less dense than water and lipids in particular. The most common types of lipids used for buoyancy in deep-sea fishes include squalene, wax esters, alkyldiacylglycerols, and triacylglycerols (Pelster, 1997). Wax esters are particularly important in generating positive buoyancy in deep-sea fishes because they are metabolized at lower rates and provide the most positive lift among these lipid classes (Patton *et al.*, 1975; Pelster, 1997). Many midwater fishes secrete wax esters extracellularly in great quantities and often within a regressed gas bladder (Reinhardt and Vleet, 1986; Nevenzel and Menon, 1980; Childress and Nygaard, 1973). Those species that fill a gas bladder with lipids forgo the metabolically expensive process of controlling gas volume for a system that provides statics levels of lift regardless of depth. For some other species, especially those that live in the bathypelagic, the cost of secreting gasses against enormous pressures has been lost with the gas bladder altogether and replaced by the positive lift of lipids (Pelster, 1997).

If deep-pelagic fishes reduce metabolically active tissues as part of buoyancy regulation, the question arises as to whether there is a convenient consequence of reducing metabolic rates. Limited data on the metabolic rates of deep-sea taxa suggest that this is indeed the case. Both Torres *et al.* (1979) and Torres and Somero (1988a,b) reported very strong relationships between lower oxygen consumption with deeper vertical distributions in mesopelagic fishes from off California and in the Antarctic Ocean, respectively, even after the effect of lower temperatures on metabolic rate was accounted for. This is now well established, having been demonstrated for midwater fishes captured from other localities (Figure 5; Childress, 1995). The proximate causes of reduced metabolic rates in deep midwater fishes appear related to reduced locomotor capacity. Midwater fishes show a marked decline in protein

content and in glycolytic and Krebs-cycle enzymatic activity within axial musculature, but not the heart or brain (Yancey *et al.*, 1992; Childress and Somero, 1979; Cowles and Childress, 1995). The decline in factors contributing to locomotor activity has, in turn, been attributed to a reduction in visual detection of prey and predators. Compared to epipelagic fishes, meso- and bathypelagic fishes do not engage as often in visually stimulated escape responses from predators or strike responses toward prey due to the limited levels of light in the deep sea (Childress, 1995).

## Finding prey

Given the sparse nature of food resources in the deep sea, finding prey is an extremely difficult task. The first principle of consuming prey is detecting that it is near. To detect prey, deep-sea fishes rely on at least two specialized systems: lateral-line sense and illuminating prey. In many species still, finding prey is as simple as having the prey find them through complex luring systems.

### Passive detection of prey

This first modality, the passive lateral-line sense, is a mechanosensory system that detects shear forces, that is, movement of water surrounding the body to a range of about 1–2 body lengths (Coombs *et al.*, 1988). Specializations include several that are typical of fishes living in still environments and include a proliferation of superficial neuromasts, widening of the head canals, and enlargement of canal organs (Denton and Gray, 1988; Montgomery *et al.*, 1995; Coombs *et al.*, 1988). Because superficial neuromasts are most sensitive to low frequencies, generally 10–50 Hz (Coombs *et al.*, 1988; Montgomery *et al.*, 1995), they are best suited to detecting the stimulus from slowly swimming organisms Bleckmann *et al.* (1991). That deep see fishes have dense arrays of superficial neuromasts, some of them mounted on stalk- or hair-like papillae and lining fin ray (Figure 6a), suggests that they are well tuned to detecting prey as it enters a near field. Although canal organs typically supply sensitivity to disturbances of higher frequencies of about 50–200 Hz (Coombs *et al.*, 1988), the specialized canal morphology of dee-sea fishes conveys additional sensitivity to stimuli more in line with free neuromasts (Denton and Gray, 1988; Marshall, 1996). Fishes that have either or both of these specializations often lack any of the ocular specializations discussed above that would permit increased visual sensitivity to the presence of prey. Therefore, it appears that in their adaptation to the deep pelagic environment, some lineages have opted for increased mechanosensory capabilities over visual sensitivity. For instance, the

eyes of species of the malemaphaid genus *Poromitra* are minute, typically around 10% of head length (Figure 6b; Ebeling, 1975), yet the lateral-line sense is approximately 100 times more sensitive to stimuli of 5–15 Hz than shallow-water taxa (Denton and Gray, 1988).

Perhaps the most direct method of detecting prey in this dark environment is to cast light upon it. Several groups of deep-sea fishes, including the myctophids and stomiid dragonfishes, are equipped with photophores positioned next to their eyes that are reminiscent of flashlights (Figure 7). Given the size of the pupils of these taxa and what is known about the light that they produce, myctophids and stomiids are probably capable of illuminating and detecting prey many meters away (Herring, 2002; Haddock *et al.*, 2010). Therefore, this method of detecting prey has a much more effective range than does the lateral line; however, this range comes at a cost. Because eyes of nearly all deep-sea animals are sensitive to the blue-wave bioluminescence produced by these species, a light cast from these organs would betray the position of a lie-and-wait predator. Rather than scanning a distant field, deep-sea fishes equipped with illuminating photophore may emit flashes of light once a prey item is detected at some closer distance via other senses (i.e., the lateral line). The far-red producing dragonfishes represent an exceptional case of illumination in deep-sea fishes. As discussed in a previous section, through their ability to produce red light from accessory orbital photophores and to perceive this light with modified rhodopsins, these fishes are afforded a private bandwidth with which to illuminate and visualize unknowing prey. For these fishes, a red flashlight could remain alit without causing detection, thereby permitting the predator to extend its perceptive field well beyond the range of its lateral line.

### **Illuminating prey**

### **Luring prey**

As eluded to above, many pelagic deep-sea fishes rely on a lie-and-wait ambush foraging strategy. Prey densities in the deep sea are likely so meager that without some mechanism to attract prey, an ambush strategy would be ineffective. Thus, many groups of fishes, especially those specializing in acquiring large prey items, have evolved bioluminescent systems that lure prey. Perhaps the most interesting group of luring fishes are the ceratioid anglerfishes. Females of the group possess a modified dorsal-fin spine (the illicium) tipped with a bioluminescent bait (the esca). Light emitted from the esca is mediated by a colony of luminescent bacteria, the species of which may be unique to each

species of ceratioid Pietsch (2009). Illicial luring in ceratioids is achieved through a combination of bioluminescence and movements of the esca and its appendages. The kinematics of luring patterns are probably very complex given the extensive nature of illicial musculature (Pietsch, 2009). In addition to the illicial apparatus, species of left-vent seadevils, genus *Linophryne*, are equipped with a very elaborate chin barbel that produces light from endogenous rather than bacterial sources.

Surpassing the complexity and diversity of the barbels of the linophrynid angler fishes are the hyoid barbels of the stomiid dragonfishes. Species of all but a few of the 28 genera possess these structures, which are often highly dendritic, composed of dozens of bifurcations. The hyper-diverse genus *Eustomias*, containing some 120 of the 290 species within the family, possess the most complex barbels, some resembling fiber-optic filaments. The intricate and subtle variation of the barbel is often the sole discriminating character between species (Gibbs *et al.*, 1983; Johnson and Rosenblatt, 1971). The use of these barbels by a dragonfish has not yet been observed *in situ* and, therefore, the specific utility in feeding must remain speculative. Stomiid barbels may be used in sexual communication as well in conjunction with sexually dimorphic cephalic photophores, however, unlike the latter, size or shape of barbels does not appear to vary between sexes (e.g., Gibbs *et al.*, 1983 and Sutton and Hartel, 2004). It is therefore most likely that these structures are used solely in the attraction of prey.

Especially for taxa with highly complex bioluminescent structures, like the genera *Eustomias*, *Himantolophus*, and *Linophryne*, it is tempting to speculate that these structures mimic the specific bioluminescent signatures of the specific food items of their prey (Herring, 2002). Unfortunately, there have been no experimental evaluations of this hypothesis in any deep-sea predator. Herring (2002) argued that because these structures often undergo considerable change through ontogeny, the luminescent signal they produce must change and thus mimicry of a specific taxon is unlikely. This pattern, however, should not disqualify specific mimicry. Although the taxonomic breadth of the prey of many dragonfishes, for instance, is surprisingly narrow (Sutton and Hopkins, 1996b), it may vary through ontogeny as well, with younger and smaller fish consuming different prey than larger size classes (Clarke, 1982; Butler *et al.*, 2001; Sutton, 2005). Therefore, ontogenetic repatterning of luring devices may reflect concomitant changes in resource preference. Herring (2002) hypothesized that, as an alternative to specific mimicry, barbels and escae may imitate the release of luminescent fecal pellets that indicate the presence of a potential food item.

## Leaving the food-poor environment

The simplest behavioral solution to the problem of low biomass in the deep sea is to leave this barren realm for a more productive area. The great majority of mesopelagic fishes undertake diel vertical migration (DVM) out of the mesopelagic to the rich epipelagic at night and back to depth during the day (Pearre, 2003). The fishes and the food they chase to the epipelagic as the sun sets no doubt constitutes the largest mass movement of animal life on earth. That this movement is driven by hunger in fishes and other micronekton is well established (see Pearre, 2003, and references therein). The most compelling evidence for this concerns the gut contents of fishes at various depths: individuals caught in the mesopelagic during the day have contents in various states of digestion, those captured at intermediate depths while ascending have empty stomachs, and individuals captured near the surface at night and while descending contain fresh, undigested food items. In addition, a hunger-driven model of DVM predicts that fishes consuming larger prey that may sustain an individual over several days (e.g., as is the case for many stomiids) are more likely to engage in asynchronous DVM, migrating only when a deterioration in nutritional state demands movement to the food-rich epipelagic, than fishes eating smaller, lower-quality prey. Indeed, planktivores are typically regular, synchronous diel migrators (e.g., many myctophids, Merrett and Roe, 1974) and asynchronous DVM has been described for many stomiid taxa whereby some presumably satiated components of a population remain at depth (Clarke, 1974; Sutton and Hopkins, 1996a; Kenaley, 2008).

The question then arises as to why mesopelagic fishes undertake energetically expensive DVMs rather than remain in the epipelagic. To address this, it is prudent to first consider the cost of the migration and how midwater fishes mitigate this. Although this has never been studied in detail, the energy output during DVM is certainly greater than the cost of staying at depth, but by how much is uncertain. In addition to the cost of swimming up and down, these fishes must actively regulate gases, travel through high sheer forces associated with currents and, in many regions, face drastic changes in ambient water temperature. The possibility exists that mesopelagic migrants mitigate these costs by swimming at a metabolically efficient speed (i.e., the  $U_{opt}$ , the lowest cost of transport, Videler, 1993) For example, a 10-cm individual of *Photostomias goodevari*, a loosejaw dragonfish, undertaking DVM from between 800–1000 m swims 8000–10000 body lengths (BLs) one way over the course of about 3–4 h (Figure 8). This translates to a sustained swimming speed of approximately 0.56–0.93 BL s<sup>-1</sup>, a slow, but comparable, sustained swimming speed relative to other fishes (Videler and Wardle,

1991). Without *in-vitro* study of the cost of transport (COT) in this or any other mesopelagic fish, whether fishes undertaking DVMs tune swimming speed to reduce the metabolic impact of this behavior will remain an open question. However, other authors have predicted that fishes maximize energetic efficiency by swimming at speeds of close to  $1 \text{ BL s}^{-1}$  (see Videler, 1993, and references therein).

In addition, what may at first appear to be a very costly endeavor may in fact be a relatively modest component of a migrator's energy budget. For mesopelagic copepods, the net energy cost of DVM represents 11.6% of diel energy loss (Svetlichny *et al.*, 2000). What, then, is this cost to a mesopelagic teleost? Hopkins and Baird (1985) reported the only estimated migration cost of a midwater fish, *Lampanyctus alatus* (family myctophidae), based on respiration data from Torres *et al.* (1979) and cost of transport of salmonids. A typical 500-m migration to the surface and back accounts for about 20% of the diel energy loss and less than 20% daily feeding ration or the caloric value of one adult copepod. This is a rather modest cost, especially considering the reward of higher prey densities in the epipelagic. Even for a deep mesopelagic fish, undertaking migrations nearly twice as long, this cost remains low. Consider an overly simplified energetic budget for a 10-cm *P. goodei* weighing 3.9 g (Kenaley, unpublished data) that ignores the effects of temperature on metabolic rate and COT and includes only the cost of the roundtrip migration and the mass-specific resting metabolic rate (see Clarke and Johnston, 1999). Assuming a COT of a rainbow trout (*Onchorhynchus mykiss*) swimming at a comparable speed of  $0.7 \text{ BL s}^{-1}$  ( $2.7 \text{ kJ kg}^{-1} \text{ km}^{-1}$ , Videler, 1993), the cost of a 1600–2000-m roundtrip represents approximately 10–12% of the diel energy loss. If COT of transport is lower, for example, as low as a migrating european eel (*Angilla anguilla*) swimming at  $0.5 \text{ BL s}^{-1}$  ( $0.42 \text{ kJ kg}^{-1} \text{ km}^{-1}$ , Ginneken *et al.*, 2005), the same round trip represents a much reduced 1.6–2.0% of daily energy loss. Therefore, even if important physiological factors are ignored, a simplified energetics model such as this establishes that the cost of migration may be relatively minor, especially if fishes engaging in DVM swim at higher efficiencies in terms of COT and at speeds that approach  $U_{opt}$ . A more thorough analysis of the metabolic profile of mesopelagic fishes that accounts for important factors ignored here (e.g., thermal influence on metabolism) and in Hopkins and Baird (1985) (e.g., variation in individual COT), will no doubt produce more realistic estimated costs for DVM.

Even if the cost is modest, the question remains why midwater fishes simply do not remain in the food-rich epipelagic and forgo the descent altogether. The selective forces behind this strategy are likely complex; however, escaping increased predation risk in the epipelagic is likely very important

among them. The warm surface waters of the open ocean contain many visual predators that exact a heavily toll on epipelagic micronekton (see Baum and Worm, 2009, and references therein). Escaping to the midwaters during the day and arriving back to the epipelagic at night, only when visual predators are less effective, reduces this risk. Most authors agree, however, that other factors probably explain DVM behavior with bioenergetic efficiency chief among them (see Pearre, 2003, and references therein). Moving below the thermoncline to waters that may be 20–30°C colder than near the surface significantly reduces metabolic rate (Clarke and Johnston, 1999). Furthermore, lower temperatures at depth may represent thermal preferenda that match an optimal temperature for physiological activity, the temperature at which maximum growth is sustained (Jobling, 1981). It seems likely that these mesopelagic migrants have adopted a strategy to increase energy assimilation based on DVM behavior that combines optimizing foraging resources in the epipelagic and thermal resources in the mesopelagic.

## **Reproduction in the deep pelagic**

Due to the lack of biomass in the deep sea, populations struggle for resources. This results in intraspecific allocation of limited resources, a driving selective force in the reproductive strategies of deep oceanic species (Herring, 2002). The evolutionary response of species living in the barren environment of the deep pelagic can be broadly categorized as demographic, resulting in skewed sex ratio, or dimorphic, that is, a sex-based difference in body form. While lack of resources drive the evolution of demographic and dimorphic reproductive strategies, this defining challenge of the deep sea also limits the size of populations and reduces the number of available mates. In response to this, fishes living in this environment have evolved a number of mechanisms to locate one another. This primary task of finding a mate is much like finding prey. Thus, the adaptations that make finding a mate in this barren seascape possible are, for the most part, very similar to those that have evolved to locate prey.

### **Allocating resources**

Based on demographic theory, the extremely limited nature of biomass in the deep sea predicts highly biased sex ratios and sexual dimorphism of size. In systems of such limited food resources, the less expensive sex should be over produced (Charnov, 1982). Furthermore, because female fecundity is largely dependent on body mass, females require more food resources and are thus more expensive. This

should result in fewer and larger females (i.e., fecundity selection; see Blanckenhorn, 2000). These predictions are supported by studies of deep-sea demography—females tend to be larger and outnumber males in major taxonomic components of this ecosystem, including the Stomiiformes, Myctophidae, Cetomimiformes, and Ceratioidei (Clarke, 1983; Merrett, 1994; Herring, 2002; Johnson *et al.*, 2009; Pietsch, 2009). The strategy of early reproductive maturity and its resulting smaller body size in males is likely due to high adult male mortality and to low population densities and resource levels that limit male-male competitive. It appears that the strength of these factors has, in some cases, led to the repeated evolution of male dwarfism in the deep pelagic.

Sexual parasitism in the ceratioid anglerfishes is undoubtedly the most well-known case of sexual dimorphism in the deep sea. In this system, a minute male, lacking any functional gut or feeding system, attaches to a relatively gigantic female (see Pietsch, 2009). For example, the females of *Ceratias holboelli* may be more than 60 times longer than males and more than  $5 \times 10^6$  as heavy (Bertelsen, 1951; Pietsch, 2005). Attachment varies between family, with some males attaching temporarily and others embedding permanently within the side of the female, fusing circulatory systems so that he becomes dependent on the female for all basic physiological functions (Figure 9a,b). As pointed out by Shine (1989), this type of association would be expected on theoretical grounds: if a male does not have to feed to increase fitness, the best place to maximize his reproductive success is directly next to the female. For both sexes, the adaptive nature of attachment and fusion is clear: in species with such low population densities and encounter rates, once a mate is found, attachment greatly increases the likelihood that gametes are exchanged and fertilization is successful. For truly parasitic species, a permanent attachment permits repeated copulations, obviating the need to locate a mate again.

Although most extreme, substantial size dimorphism is not unique to the ceratioids. Gonostomatids of the genus *Cyclonthone*, species of the stomiid genus *Idiacanthus* (Figure 9d), and the live-bearing ophidiid genus *Paratbrotula* are among the other notable dimorphic groups (Herring, 2002). In a recent astonishing discovery based on integration of developmental and comparative morphology and molecular sequence data, Johnson *et al.* (2009) showed that fishes previously assigned to three families with remarkably different morphologies—Mirapinnidae (tapetails), Megalomycteridae (bignose fishes), and Cetomimidae (whalefishes)—are larvae, males, and females, respectively, of a single family, Cetomimidae. Mature bignose males (so named due to their enlarged olfactory rosettes) are much less than 50% the length of mature cetomimid females (Figure 9c). What is more, the feeding and gut

apparatus in adult males is nonfunctional just as it is in males of the Ceratioidei. To sustain itself through a search for a female and eventual reproduction, a male must consume an enormous bolus of copepods as a tapetail larva and, during transformation to adult, assimilate the bolus into an enlarged liver. The dimorphism in ecologically important systems like the feeding apparatus in the cetomimids and ceratioids indicates that natural selection, as much or more than sexual selection, is responsible for the evolution of this intriguing reproductive strategy (Shine, 1989).

### Finding a mate

The vast space between individuals with a population of a deep-sea species creates a demographic barrier to reproduction. Low population densities engender the risk of low encounter rates and, in turn, low reproductive rates (Herring, 2000; Baird and Jumper, 1995). For less abundant species to overcome this mate encounter problem (see Baird and Jumper, 1995) and find sparsely distributed conspecifics of the appropriate sex, they must either search a larger area of the surrounding seascapes over a given time or increase the distance over which they can perceive a signal from a potential mate. For the most part, deep-sea fishes are small, typically much smaller than those that inhabit the epipelagic (e.g. scombrids, xiphioids, etc). Thus, if most fishes maximize energetic efficiency during sustained swimming by cruising at speeds of close to  $1 \text{ BL s}^{-1}$  (see Videler, 1993), deep-sea fishes do not scan expansive spaces quickly for mates. It has therefore been argued that these fishes rely on signal optimization to increase encounter rates (see Herring, 2000). The systems implicated most often in sexual communication between deep-sea fishes are bioluminescence and olfactory signals.

Cephalic photophores of several groups of deep-sea species are sexually dimorphic and this indicates their importance in sexual signaling. For the three most abundant deep-sea pelagic lineages, the myctophids, dragonfishes, and ceratioid anglerfishes, dimorphic bioluminescent systems represent hallmark characters that distinguish the sexes. In stomiids, the postorbital photophore is larger in males (Figure 10a,b), male lanternfishes often possess larger cephalic and precaudal photophores on the trunk (females may lack the latter), and female ceratioids possess bacterial-mediated photophores mounted on modified dorsal-fin spines (see Herring, 2007 and references therein). Males of these sexually dimorphic species probably emit a bioluminescent flash that elicits a response from a female to indicate her status as such and her readiness to reproduce. For the dragonfishes, the enlarged postorbital photophore of males may produce a greater photon flux than that of females and thus produce a signal

that is perceptible at a greater distance (Herring, 2000). As pointed out by Herring (2000), females receiving this signal over long ranges can respond with only weaker signals from a smaller postorbital organs. Flashes of smaller fluxes may result in the male not receiving the female response. This would result in a dead zone in which signals are lost and the female must close by swimming closer to the male. There is evidence, however, that males of some species (e.g., species of the genus *Malacosteus*) may compensate for this weaker signal with a larger orbit (Figure 10c)—a larger eye would enable detection of bioluminescence at greater distances. Furthermore, species of *Malacosteus* possess slightly larger far-red emitting accessory photophores, suggesting that longwave bioluminescence of these taxa are also importance in sexual communication (Figure 10c; Kenaley, In Prep.).

The primary question concerning sexually dimorphic bioluminescent systems is whether, given a certain distance, the signal will reach the prospective mate. For most deep-sea species, this would seem unlikely. According to Herring (2000), if a deep-sea fish emits the brightest flashes recorded in the clearest ocean water, a photophore can produce a relatively strong signal of  $8 \times 10^2$  to  $8 \times 10^4$  photons  $\text{cm}^{-2} \text{ s}^{-1}$  at a range of 10 m. Based on trawl data, Herring (2000) also estimated that nearest-neighbor distances within populations of many deep-sea species was within this effective range. These data, however, do not distinguish sexually immature from mature individuals, nor do they account for sex ratios that may be highly skewed in some populations (Marshall, 1979; Mead *et al.*, 1964). In addition, Herring (2000) estimated that populations of majority of bathypelagic species will often have nearest-neighbor distances at or in excess of 50–100 m, well beyond the effective range of a bioluminescent flash. Based on these data, it therefore seems unlikely that sexual communication is mediated by bioluminescent signals alone.

The range limitations of bioluminescent systems implicate the other conspicuously sexually dimorphic sensory system in deep-sea fishes, olfaction, in sexually communication over the long distances required by these populations. The importance of chemoreception in sexual signaling is underscored by the intriguing pattern in bathypelagic fishes in which males may have either large or small eyes, however, they have enlarged olfactory systems in almost all cases. The ceratioid anglerfishes represent perhaps the clearest demonstration of this relationship. Free-living males of the family Linophrynidae probably rely on both visual and chemosensory signals as demonstrated by their enlarged semitubular eyes and enormous nostrils (Figure 11a). In most other ceratioid families (e.g., Gigantactinidae, Melanocetidae, Oneirodidae, Thaumatichthyidae), the eyes of free-living males are reduced, and so

to, presumably, is a reliance on visual signals; however, olfaction is likely important as indicated by the enlarged nostrils of males of these species (Figure 11b). That the nostrils of males of these taxa quickly degenerate once they attach to a female is more strong circumstantial evidence of how important olfaction is in locating a conspecific female. Further evidence of sexual communication mediated by olfaction, especially for fishes with low population densities, can be found amongst the sternoptychid hatchetfishes. Species of with lower population densities (e.g., *Sternopyx diaphana*) have sexually dimorphic olfactory organs while both sexes of those with higher densities (e.g., *Argyropelecus hemigymnus*) are similarly small (Baird and Jumper, 1995; Herring, 2000). The importance of using long-range olfaction in hatchetfishes and other deep-sea taxa in overcoming the encounter problem was underscored further by Baird and Jumper (1995) who estimated encounter probabilities based on density, swimming speed, and perception distance and established an exponential increase in time between encounters with perception distance.

Should finding a mate prove too difficult, some deep-sea fishes can resort to hermaphroditism. Synchronous hermaphroditism is found only in a few groups of mesopelagic fishes, including species of the families Notosudidae and Alepisauridae (Herring, 2000). Among vertebrates, this sex allocation strategy is largely limited to species existing at very low densities (Ghiselin, 1969) or in species which do not engage in promiscuity (Charnov, 1982). Both of these characteristics likely apply to the the notosudids and alepisaurids. Sequential hermaphroditism, protandry in particular, has evolved repeatedly in bathypelagic taxa (see Herring, 2000), thereby suggesting that there is an adaptive advantage to male-to-female sex reallocation in the extreme demographic, physical, and biological, conditions of this ecosystem. The size-advantage model, the most widely recognized theory that seeks to explain the adaptive significance of sequential hermaphroditism in vertebrates, is aptly applied in these cases. It predicts that an organism will change sex when functioning as the opposite sex will increase reproductive fitness over functioning as the current sex (Warner, 1988, 1975; Ghiselin, 1969). In matings systems like those of most deep-sea fishes in which mates pair at random and are not monopolized, the size selection model predicts protandrous hermaphroditism so that individuals may increase fitness through the higher fecundity of larger females. Other factors, including the relatively low mobility of most deep-sea taxa (Warner, 1988, 1975) and the selection potential for decreased male size (see above), are likely to contribute to the preponderance of protandry in bathypelagic fishes. The importance of protandry to the reproductive fitness of bathypelagic taxa is emphasize further by a

pattern of transition from facultative protandry in shallower species to obligate protandry in deeper dwelling species (Herring, 2000). The proximate signals that initiate reallocation of sex in facultative species, whether demographic and biological (e.g., sex ratio, population density, sexual signaling) or environmental (e.g., temperature, seasonality, etc.) remains unknown.

## Adaptations to high pressures

Although how other important dimensions unique to the deep sea, whether biological or physical, have affected the evolutionary trajectory of fishes that inhabit the realm have received more scientific scrutiny, there is no doubt that hydrostatic pressure should be implicated in their physiological adaptation. In terms of quantifying the difficult nature of surviving at depth, the relationship between pressure and depth, increasing 1 atmosphere (atm) or 101.3 kPa every 10 m, is perhaps the most daunting physical parameter. Our understanding of how deep-sea fishes have adapted to high hydrostatic conditions has been informed by studies of fishes adapted to surface pressures and, to some limited extent, comparative studies of deep-sea taxa (Somero, 1992). The overwhelming majority of this comparative work has focused on deep benthic taxa, with the more fragile and difficult experimental subjects of the pelagic largely omitted from study. Nonetheless, pervasive patterns concerning the effects of pressure on physiological systems elucidated in this work no doubt extend to deep-pelagic species as well.

Studies of the effects of hydrostatic pressure reveal three important physiological perturbations that must be addressed by fishes living at great depths: altered protein-protein and enzyme-substrate interactions and cell-membrane functions (Somero, 1992). Due to pressure's disruptive effect on the weak bonds that control the three-dimensional structure and volume of a protein, even modest increases in pressure can induce substantial changes in protein function. The adaptive response of proteins to high pressure has, for the most part, been the evolution of pressure-insensitive orthologs rather than the evolution of paralogous proteins optimized to pressures of various depths (Somero, 2003; Gibbs, 1997). This may permit a deep-sea fish a wider range of depth over which ontogenetic development and important ecological behaviors (e.g., diel vertical migration) can be take place.

Enzyme activity is extremely sensitive to pressure due to its affect on the large number of weak bonds involved in protein-ligand interactions. Thus, a broad array of enzymatic systems show pertur-

bations to normal activity at rather modest depths, including dehydrogenase enzymes and adenylyl cyclases at only 50–100 atm (500–1000 m, Somero, 1992). In the case of muscle-type lactate dehydrogenase (LDH), the enzyme responsible for conversion of NADH to NAD<sup>+</sup> during anaerobic respiration, deep-water species have evolved more invariant reaction rates over broad range of depths whereas the LDH of shallow species are increasingly active at greater depths (Siebenaller and Somero, 1978, 1979).

High hydrostatic pressure also compresses the lipid bilayer of the cell membrane and reduces molecular mobility. This, in turn, reduces membrane fluidity (Somero, 1992). Adaptations to maintain membrane fluidity (i.e., homeoviscous adaptations) have been reported in several groups of deep-sea demersal fishes (Sebert, 2002; Somero, 1992). Alternative lipid composition, incorporation of unsaturated fatty acids in particular, within cell membranes has been implicated in homeoviscous adaptation. Compared to shallow-water fishes, the brain of the benthopelagic morid *Anitmora rostrata* contains gangliosides, lipids important in cellular recognition and communication, that are highly enriched in mono-unsaturated fatty acids and low in saturated fatty acids (Avrova, 1984). Similarly, Cossins and Macdonald (1986) found that mitochondria of the liver in deep-sea teleosts contains greater proportions of unsaturated fatty acids relative to shallow species.

One of the more important membrane-mediated functions potentially compromised by higher pressures is osmorgulation. To mitigate this, deep benthic fishes have less pressure-sensitive forms of the sodium ion pump, Na<sup>+</sup> K<sup>+</sup>-ATPase, that maintain their activity and membrane fluidity and proper osmoregulatory function Gibbs and Somero (1989, 1990). Transmembrane signaling pathways are also subject to perturbations from high hydrostatic pressures, (e.g., G-protein coupled receptors) and these, too, show similar modifications and insensitivities to depth in some of their important protein and enzymatic components (Siebenaller and Garrett, 2002; Siebenaller, 2000).

In addition to modifications to the proteins themselves, deep-sea fishes increase the concentration of protein-stabilizing osmolytes. Trimethylamine N-oxide (TMAO), in particular, has been implicated in the protection of both ligand binding and protein stability. The counteracting effects of TMAO has been confirmed in a broad range of proteins, including restoration of activity in NADH and LDH (Gillett *et al.*, 1997; Yancey and Siebenaller, 1999; Yancey *et al.*, 2001). The very clear positive relationship between TMAO levels and increased depth of occurrence in fishes reveals how integral TMAO is to the invasion of deep-sea habitats (Figure 12). There is an increasing amount of evidence that TMAO may indeed be a limiting factor in the bathymetric distribution of fishes. (Yancey *et al.*,

2014). Because TMAO is an osmolyte, its increased level in the tissues of fishes inhabiting great depths also increases osmolality. Marine teleosts are hypoosmotic and must remain so to maintain proper homeostatic balance. Muscle TMAO levels among the deepest teleost fishes increase body osmolalities that approach isosmotic conditions (Gillett *et al.*, 1997; Yancey and Siebenaller, 1999; Samerotte *et al.*, 2007). This has led to the prediction that fishes face a limit to their bathymetric distribution: 8000–8500 m, a depth at which TMAO levels would reach a threshold, pushing osmolalities beyond hypo- into isosmoticity (Jamieson and Yancey, 2012; Samerotte *et al.*, 2007). This predicted depth limit corresponds to the maximum depth of fishes either caught in sampling gear or observed *in-situ* (Jamieson *et al.*, 2010; Jamieson and Yancey, 2012; Fujii *et al.*, 2010). The hypothesis that a TMAO-osmoregulatory tradeoff may limit maximum depth of fishes was strengthened by Yancey *et al.* (2014) when they reported on the osmolality and TMAO levels of the second-deepest known fishes, *Notoliparis kermadecensis*, the hadal snailfish (family Liparidae; Figure 12). At 7000 m, *N. kermadecensis* has TMAO and total osmolyte levels that are congruent with model predictions of an isosmotic state at 8200 m.

## Conclusions

Relative to shallow-water taxa, the physiology of deep-sea pelagic fishes has been modified by the adaptive process of natural selection to permit existence in a realm that is unparalleled in its demands on life. In nearly every physiological system considered here, there have been repeated, independent solutions to the problems of limited light, biomass, and high hydrostatic pressure. This high degree of convergence in fishes inhabiting the deep pelagic underscores the highly adaptive nature of their physiologies. From the scope and depth of scientific research reviewed here, it is evident that our knowledge of the biology of deep-sea fishes is increasingly detailed and the proximate and evolutionary forces driving adaptive evolution in the deep sea are becoming more clear. If the disciplines of deep-pelagic ecophysiology and ecomorphology are to continue to advance, there are two primary hurdles that must be overcome: (1) limited fine-scale phylogenetic hypothesis for major taxonomic components of this ecosystem and (2) a near lack of *in-situ* experimentation.

Progress in both of these directions is promising. The recent implementation of densely-sampled, multi-locus molecular phylogenies have, in addition to largely corroborating morphology-based hy-

pothesis, provided robust estimations of phylogenetic history at low taxonomic scales (e.g., Kenaley *et al.*, 2014; Davis and Fielitz, 2010; Denton, 2014). Continued resolution of the interrelationship of deep-sea fishes will continue to be crucial in comparative studies, constituting the means by which researchers reveal the effects of phylogeny in physiological and morphological studies (e.g., see Lisney and Collin, 2007; Busserolles *et al.*, 2013; Davis *et al.*, 2014; Claes *et al.*, 2014). Solutions to the other major challenge, collection of organismal data in a native environment, show promise as well. The continued rapid pace of development in undersea-vehicle technology now allows access to depths and sampling capabilities never before realized Robison (2004). Advancement in vehicle development may soon transform the deep pelagic into field laboratories that permit repeated, rigorous experiments like those undertaken in the laboratory.

In parallel to the development of *in-situ* technology, methods and instruments to capture and maintain fishes within the laboratory continue to be refined (see Drazen and Seibel, 2007); however, the transfer of fishes to the laboratory has largely been restricted to less fragile demersal and bathybenthic fishes. There is no doubt, however, that many species may be too fragile or rare to be captured or observed in the field and thus crucial physiological and behavioral data will remain elusive. For these taxa, ecophysicist and ecomorphologist should look to closely related taxa that can be more easily studied and develop computational and biophysical models (e.g., biorobotic models) to generate data and test hypotheses.

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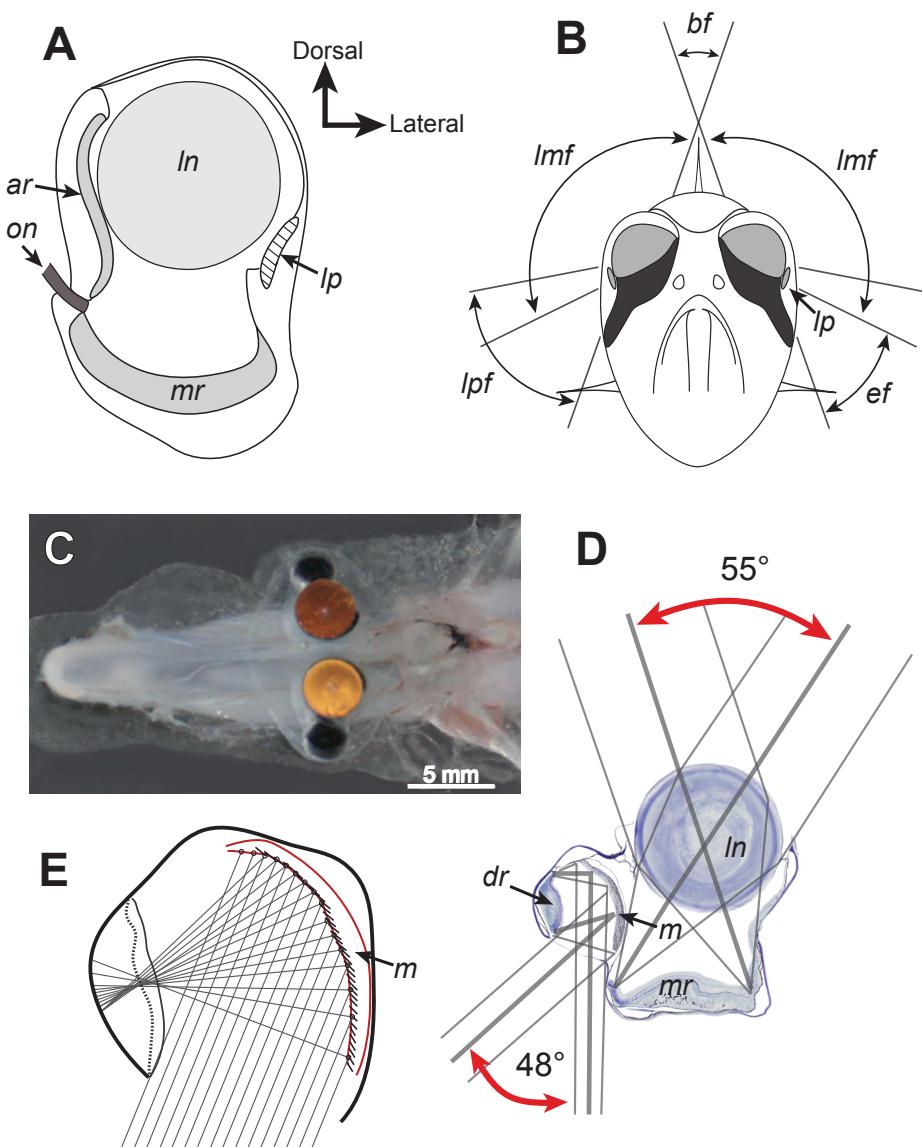


Figure 1: caption on next page

Figure 1: (From previous page) Examples of optical adaptations of deep-sea fishes to increase sensitivity and the visual field. (A) Vertical cross section of the right dorsally directed tubular eye of *Scopelarchus analis* demonstrating its structure including the distended position of the lens (*ln*), the accessory retina (*ar*) lining the tube of the eye, the main retina (*mr*), and optic nerve *on* positioned ventrally, and lens pad (*lo*) that directs light to the dorsal *ar*. Modified from Partridge *et al.* (1992). (B) The visual field from anterior view of a scopelarchid fish demonstrating how its tubular eyes extend the two lateral monocular fields (*lmf*) into a dorsal binocular field (*bf*) and how the lens-pad field (*lpf*) extends the visual field beyond the normal lateral monocular field (*ef*). Modified from Warrant and Locket (2004). (C) Dorsal view of the head and eyes of *Dolichopteryx longipes*, an opisthoproctid fish with effectively four eyes. (D) Vertical cross section of the left eye of *D. longipes* showing how the dorsal tubular eye extends to a 55° field and the diverticulum permits a ventral field of view of about 48°. The dorsal eye of *D. longipes* uses the optics typical of other fishes with a tubular eye, including a focusing lens (*ln*) and main retina (*mr*); however, the second eye, composed of a diverticulum, focuses light on the retina of the diverticulum (*dr*) via a refracting mirror (*m*) that lines the medial surface. (E) Detailed schematic view of the lateral eye diverticulum in *D. longipes*. Incoming ventral light is reflected by the mirror (*m*) which is composed of reflective plates (small black lines) oriented at different angles. Thus, light is focused on the retina of the diverticulum (*dr*) and an image can be formed. C–D modified from Wagner *et al.* (2009).

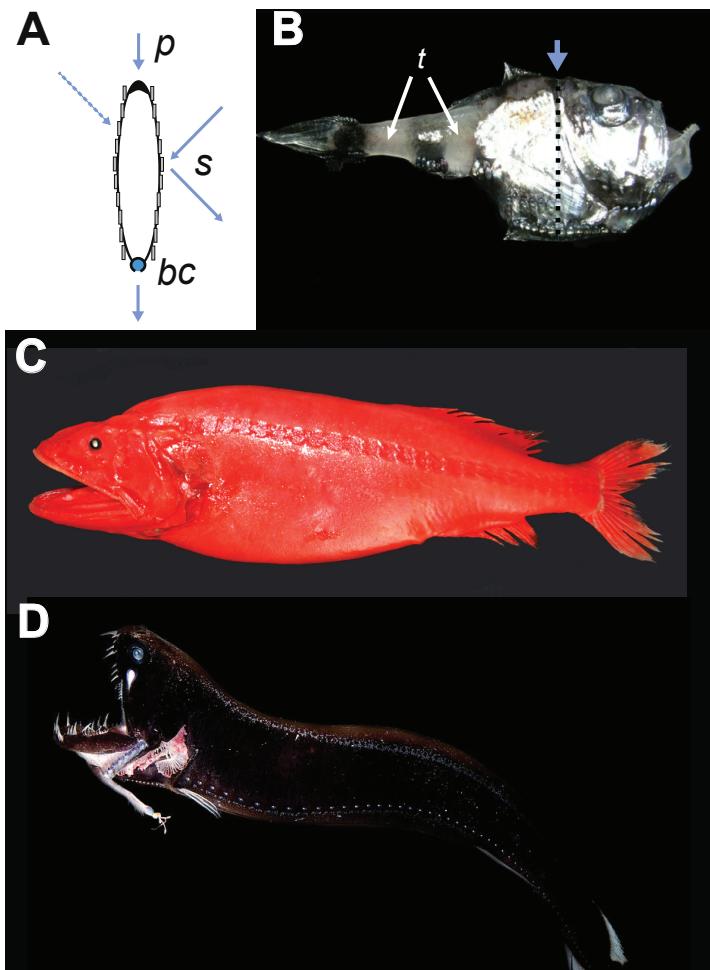


Figure 2: Optical and color-based strategies for crypsis in mesopelagic fishes. (A) Cross-sectional schematic view of *Argyropelecus hemigymnus* showing dorsal pigmentation (*p*), silverying (*s*), and ventral bioluminescent countershading (*bc*). Modified from Land and Osorio (2011). (B) Lateral view of *A. hemigymnus* demonstrating transparent ((*t*) caudal region. Dashed line and arrow represent approximate location of A. Photo from Fotoshow: Kreaturen der Tiefe. (C) The red-velvet whalefish, *Barbourisia rufa* (courtesy of Julian Finn). (D) A bathypelagic dragonfish, *Echiostoma barbatum* demonstrating black pigmentation. The species in C and D are visually similar in that their red or black pigments absorb blue light. Thus, both would appear black in the short-wave photic environment of the mesopelagic ocean or if illuminated by blue bioluminescence

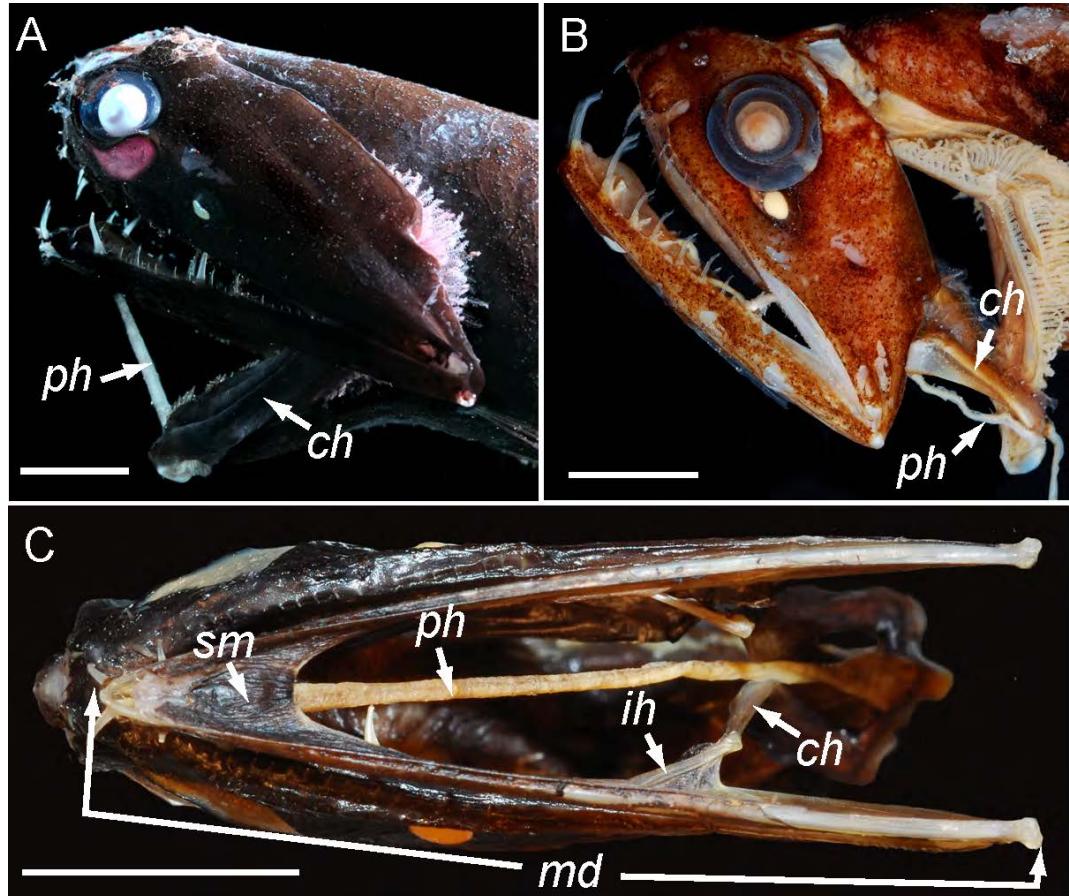


Figure 3: Two species of loosejaw dragonfishes. (A) *Malacosteus niger*, left lateral view of head. (B) *Aristostomias scintillans*, left lateral view of head. (C) ventral view of lower-jaw system and hyoid apparatus of *M. niger*. Note the lack of intermandibular membrane as indicated by the exposed protractor hyoideus muscle. ph, protractor hyoideus; ch, ceratohyal; ih, interhyal; md, mandible (i.e., articular + dentary); sm, symphyseal membrane. Scale bars in the lower left of each field represent 1 cm.

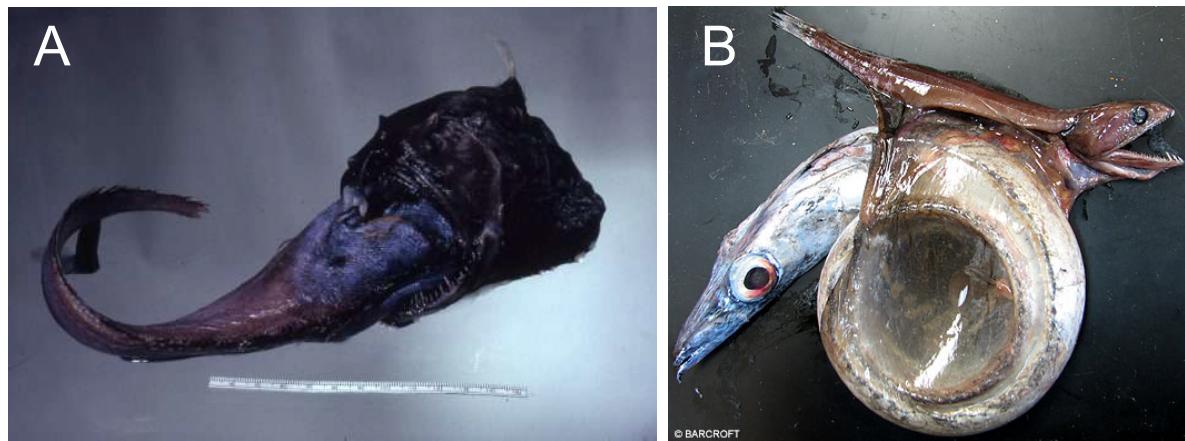


Figure 4: Two gut-limited bathypelagic predatory fishes presumably killed by their prey. (A) A 112-mm specimen of *Diceratias trilobus* partially engulfing a rattail of the genus *Ventrifossa* that measures at least 369 mm (from Paxton and Lavenberg, 1973). (B) The black swallower (*Chiasmodon niger*) with its stomach pierced by the lower jaw of a snake mackerel (*Gempylus serpens*) (courtesy of P. Bush, Barcroft Media).

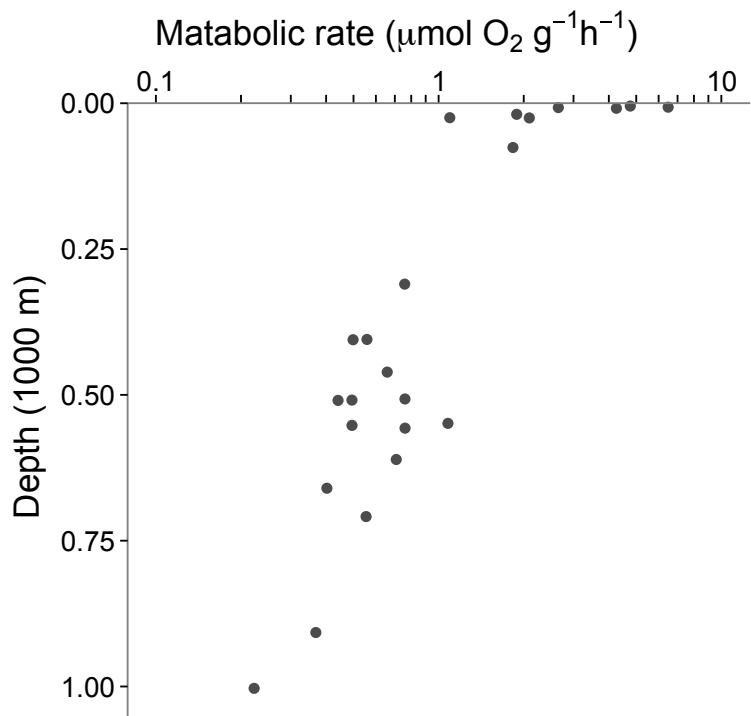


Figure 5: Matabolic rate of mesopelagic fishes as it relates to depth of minimum occurrence. Data are from fishes off California at 5°C (after Cowles and Childress, 1995)

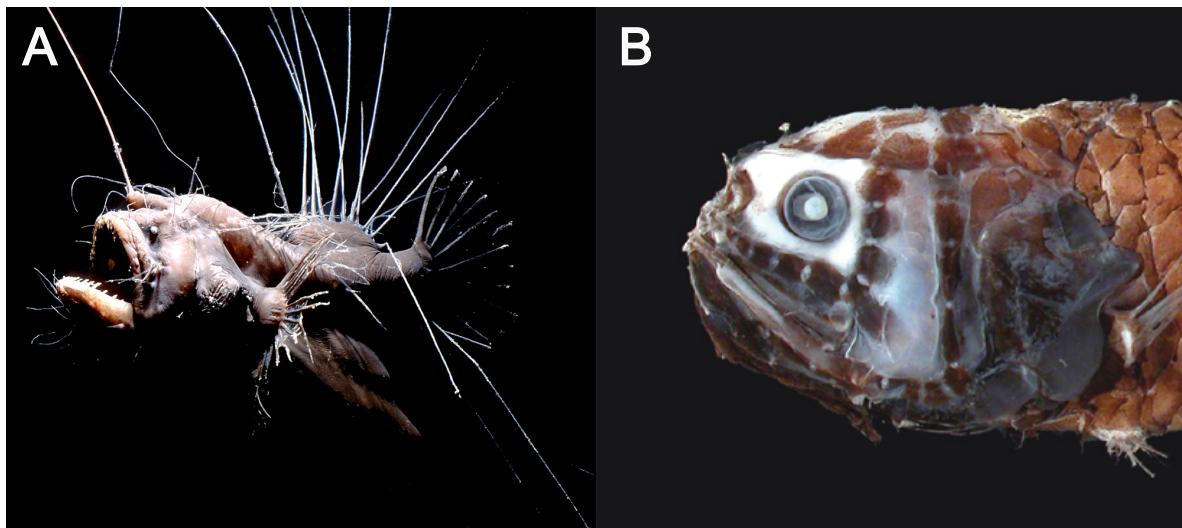


Figure 6: Specializations of the lateral-line system in deep-sea fishes. (A) A species of the ceratioid anglerfish genus *Caulophryne*, a group with dense superficial neuromasts mounted on hair-like papillae and fin fin rays (courtesy of J. Marshall). (B) The head of *Poromitra crassiceps*, a melamphaid fish with expanded lateral-line canals that permit ultra-sensitivity to low-frequency stimuli (courtesy of the President and Fellows of Harvard University).

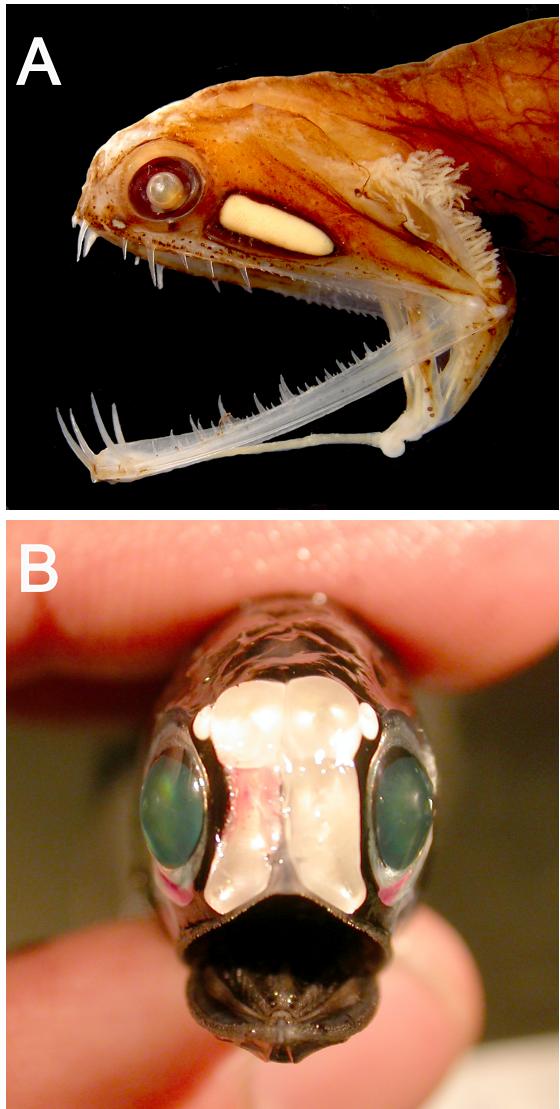


Figure 7: Luminescent organs that illuminate prey. (A) the postorbital photophore of *Photostomias lucingens*. (B) The suborbital organ of a headlight fish, genus *Diaphus*.

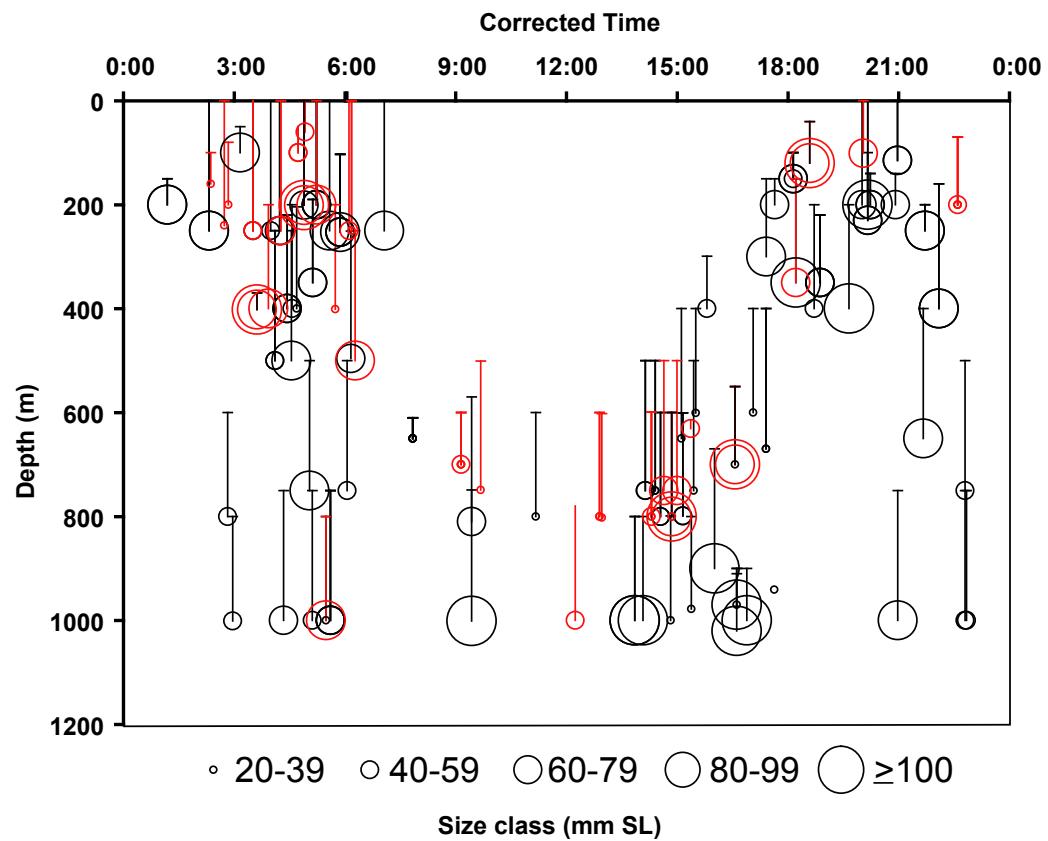


Figure 8: Vertical distribution of species of *Photostomias* in the North Atlantic Ocean relative to corrected local time where 12:00 represents solar noon, 6:00 solar dusk, 18:00 solar dusk and 0:00 solar midnight. Size of circles represent standard length classes in mm according to the bottom legend. Red symbols represent *P. goodeyari* and black symbols represent *P. guernei*. From Kenaley (2008)

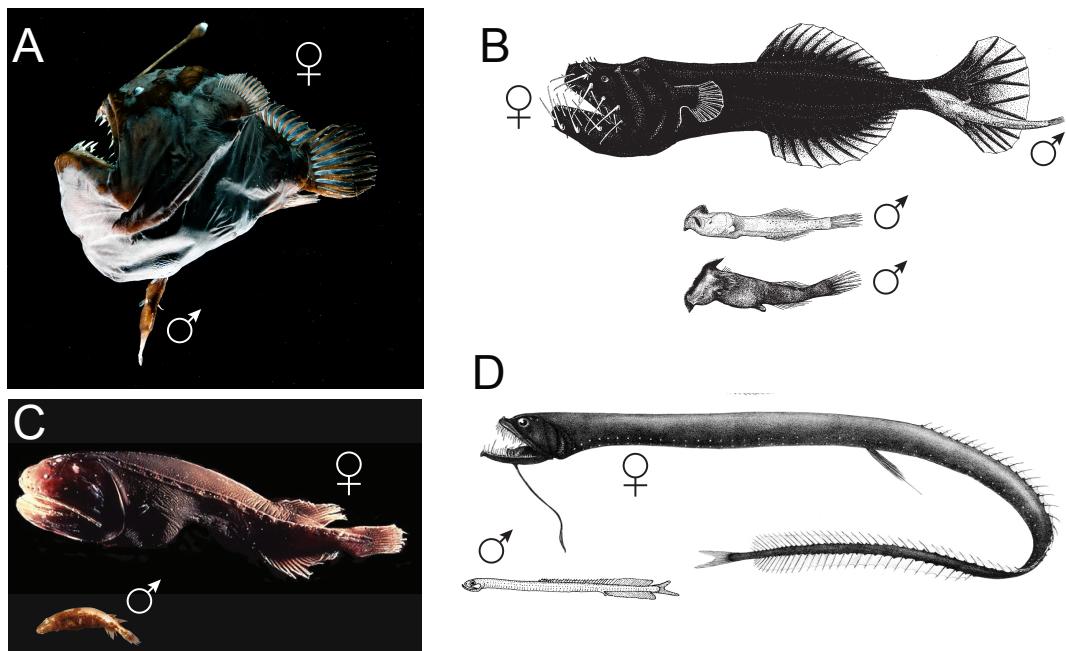


Figure 9: Examples of size sexual dimorphism in deep-sea fishes presented in relative scale. (A) An attached pair of the ceratioid anglefish *Melanocetus johnsoni* (courtesy of E. Widder, ORCA). (B) Male and female pairs and attached males of *Neoceratias spinifer* (modified from Pietsch, 2009). (C) Cetomimid whalefishes (female courtesy of Bruce Robison, MBARI; male courtesy of President and Fellows of Harvard University) (D) The stomiid dragonfish genus *Idiacanthus* (from Brauer, 1906)

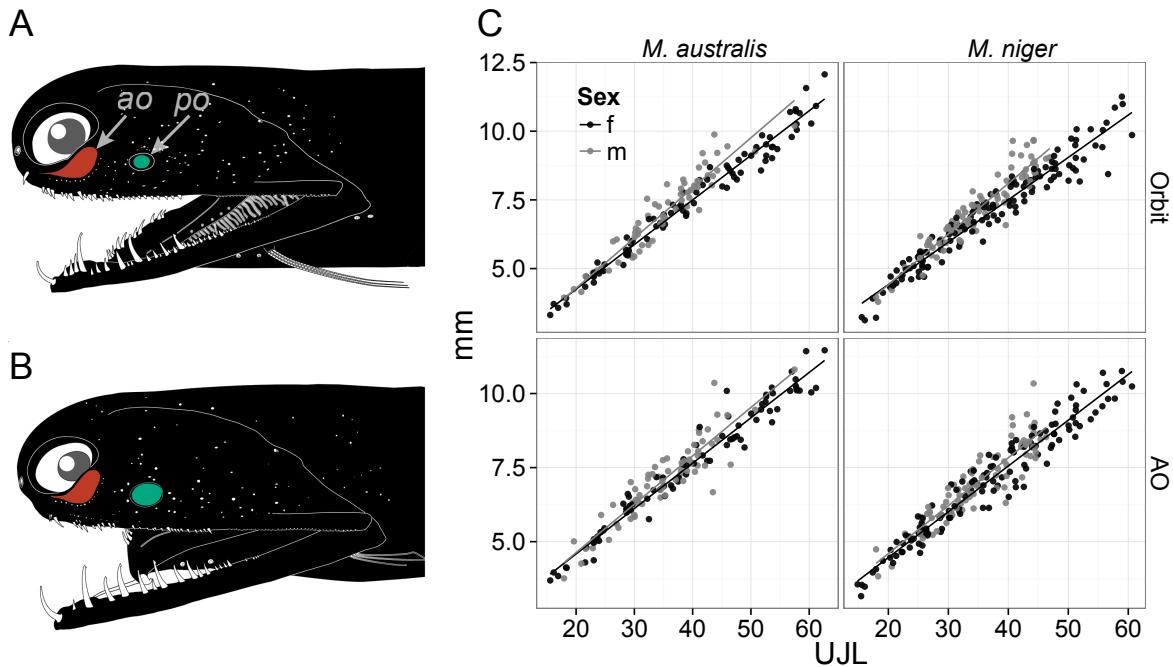
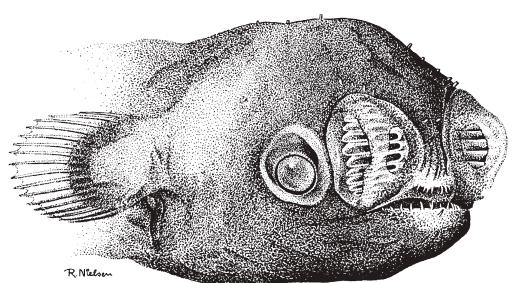


Figure 10: Subtle sexual dimorphism in bioluminescent and visual systems of the genus *Malacosteus*. The female of *M. niger* (A) possesses a smaller blue-green glowing postorbital photophore (*po*) than the male of the species (B). However, the female of this and its only known congener, *M. australis*, also possesses a very slightly smaller orbit and far-red glowing accessory orbital photophore (*ao*)—regressed here against upper jaw length—relative to the males of the species (C). This thus suggests that both far-red and blue-green visual systems play a role in sexual communication in the genus. (A) and (B) modified from Kenaley (2007), (C) from Kenaley (In Prep.).

A



B

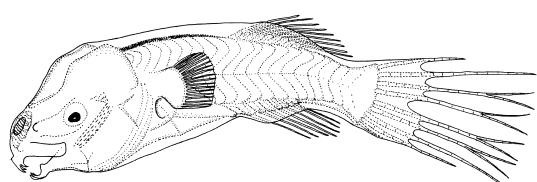


Figure 11: Enlarged olfactory systems of free-living males of ceratioid anglerfishes. (A) *Linophryne arborifer*-group with well-developed semitubular eyes in addition to nostrils (from Bertelsen (1980)). (B) *Gigantactis longicirra* with minute eyes and enlarged nostrils (from Bertelsen *et al.* (1981)).

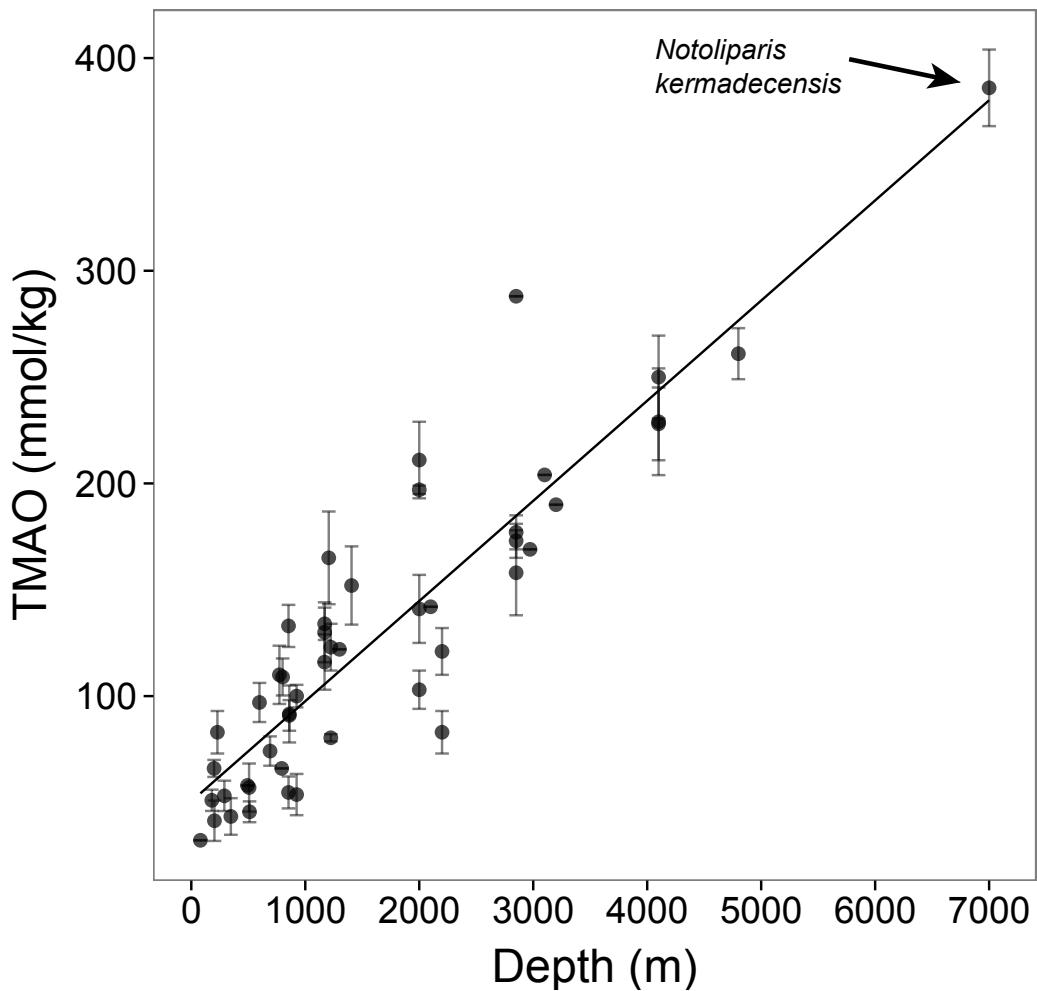


Figure 12: Trimethylamine N-oxide (TMAO) levels in demersal fishes as it relates to capture depth. Each point represents a single species; bars represent standard deviations of species sampled more than once. Capture depth reflects maximum trawl depth. Data from Gillett *et al.* (1997); Kelly and Yancey (1999); Samerotte *et al.* (2007); Yancey *et al.* (2004); Dyer (1952); Yancey *et al.* (2014).