Reference: *Biol. Bull.* **201:** 301–318. (December 2001)

Hidden in Plain Sight: The Ecology and Physiology of Organismal Transparency

SÖNKE JOHNSEN*

Biology Department, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts

Abstract. Despite the prevalence and importance of transparency in organisms, particularly pelagic species, it is a poorly understood characteristic. This article reviews the current state of knowledge on the distribution, ecology, and physical basis of biological transparency. Particular attention is paid to the distribution of transparent species relative to their optical environment, the relationship between transparency and visual predation, the physics of transparency, and what is known about the anatomical and ultrastructural modifications required to achieve this condition. Transparency is shown to be primarily a pelagic trait, uncommon in other aquatic habitats and extremely rare on land. Experimental and theoretical studies in terrestrial, freshwater, and marine ecosystems have shown that transparency is a successful form of camouflage, and that several visual adaptations seem to counter it. The physical basis of transparency is still poorly understood, but anatomical observations and mathematical models show that there are various routes to transparency. Future avenues for research include examination of the ultrastructure and optical properties of transparent tissue, exploring the link between transparent species and special visual modifications in the species they interact with, and analysis of the evolution of transparency using comparative methods.

Introduction

Transparency is a fascinating and surprisingly common characteristic that has received little attention because the majority of transparent species are found only in the pelagic regions of the open ocean. In these regions, however, the prevalence and diversity of transparent species is remarkable, ranging from the relatively well-known medusae and ctenophores to transparent polychaetes, gastropods, and fish (Fig. 1). Transparency is one of the few forms of camouflage possible in a habitat with no surfaces to match or hide behind. It is also the only form of camouflage, and one of the few adaptations, that involve the entire organism. Although the importance of transparency has been mentioned many times by pelagic ecologists, it is a relatively unstudied characteristic (Hardy, 1956; Fraser, 1962; McFall-Ngai, 1990; Meyer-Rochow, 1997).

This review synthesizes the current knowledge on the distribution, ecology, and physical basis of biological transparency. It is divided into five sections. The first section reviews the phylogenetic distribution of transparent species. The second section reviews and attempts to explain the relationship between transparent species and their optical environment. The third section links transparency to visibility; reviews terrestrial, freshwater, and marine studies of transparency and visual predation, including the use of special visual adaptations; and lists known active uses of transparency. The fourth section presents the underlying optical principles of transparency and then applies these principles to the various anatomical and ultrastructural modifications seen in transparent tissues. The final section suggests several avenues for future research.

Phylogenetic Distribution

The phylogenetic distribution of transparent animals is diverse, uneven, and strongly influenced by environment. Although significant levels of tissue transparency are found in a wide array of organisms (Figs. 1, 2), most transparent species are found in the following 10 groups, all of which are pelagic: cubozoans, hydromedusae, non-beroid ctenophores, hyperiid amphipods, tomopterid polychaetes, pterotracheid and carinariid heteropods, pseudothecosomatous pteropods, cranchiid squid, thaliaceans, and chaetognaths.

Received 30 May 2001; accepted 30 August 2001.

* Current address: Biology Department, Box 90338, Duke University, Durham, NC 27708. E-mail: sjohnsen@duke.edu

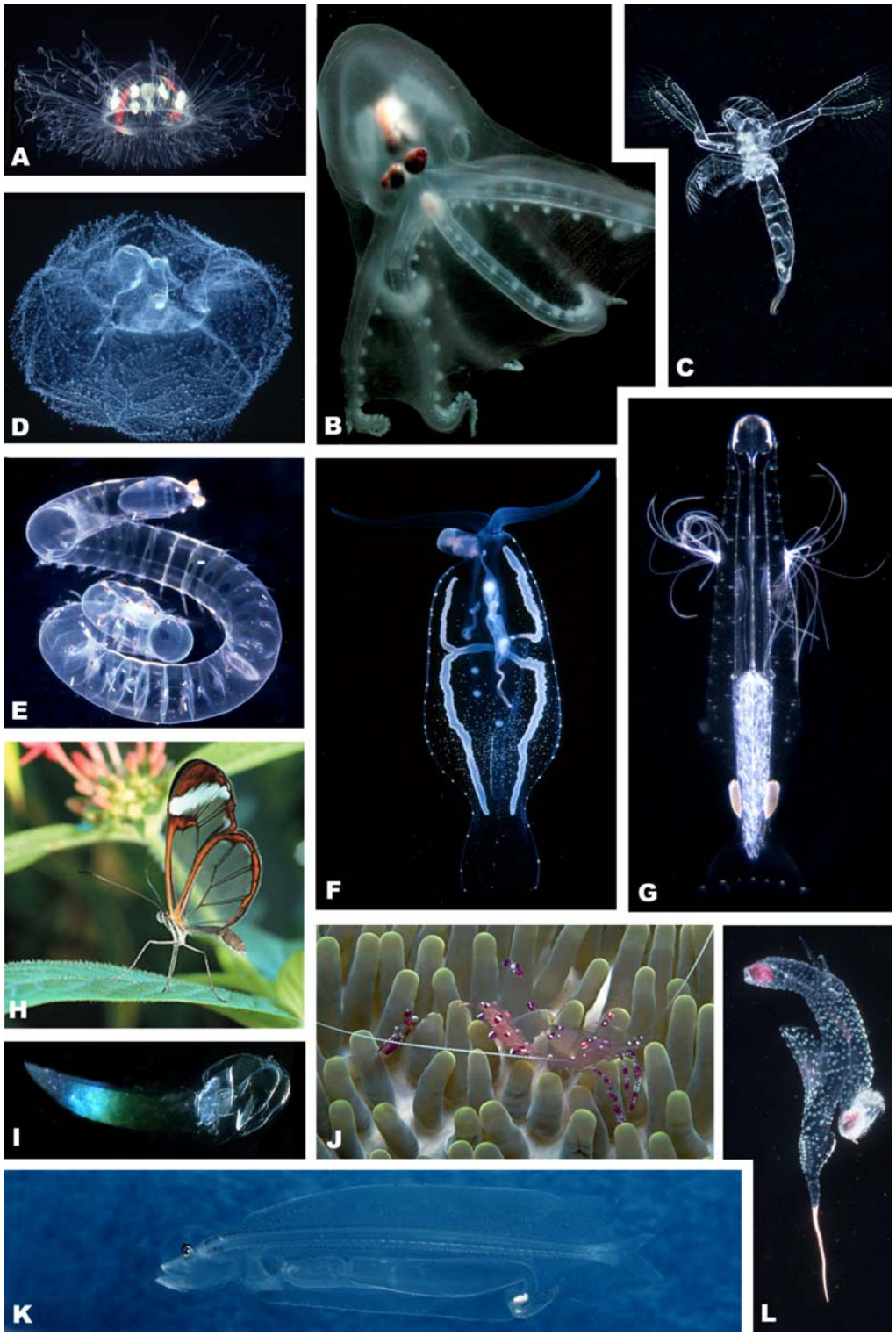

Figure 1: Assemblage of transparent animals. A) *Amphogona apicata* (hydromedusa), B) *Amphitretus pelagicus* (octopus), C) *Leptodora kindtii* (freshwater cladoceran), D) *Planctosphaera pelagica* (hemichordate larva), E) *Naiades cantrainii* (polychaete), F) *Phylliroë bucephala* (nudibranch), G) *Pterosagitta draco* (chaetognath), H) *Greta oto* (neotropical butterfly), I) *Bathochordeus charon* (larvacean), J) *Periclimenes holthuisi* (shrimp), K) *Bathophilus sp.* (larva of deep-sea fish), L) *Cardiopoda richardi* (heteropod). Images credits as follows: A, D, E, G, I, K, L - Laurence P. Madin, B, F - Steven Haddock. C - Wim Van Egmond, H - Randy Emmitt, J – Jeff Jeffords.

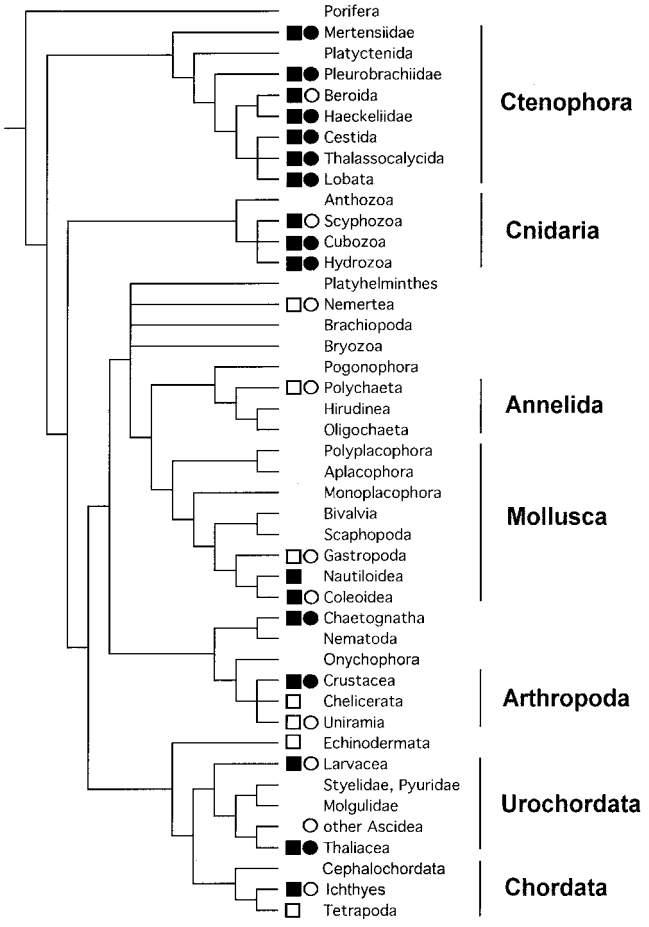

Figure 2. Transparency and pelagic existence mapped onto a phylogeny of the major phyla in the Animalia. Open square indicates pelagic existence is rare within adults of the group; filled square indicates pelagic existence is common. Open circle indicates transparency is rare within adults of the group; filled circle indicates transparency is common. Interrelationships of phyla taken from Halanych and Passamaneck (2001). Relationships within phyla taken from the following: Cnidaria (Bridge *et al.*, 1995), Ctenophora (Podar *et al.*, 2001), Annelida (McHugh, 2000), Mollusca (Wingstrand, 1985; Scheltema, 1993), Urochordata (Swalla *et al.*, 2000), Chordata (Nelson, 1994). The phylogeny of the Arthropoda is controversial and so is left as a polytomy. Taxa are resolved to different levels to maximize information about the distribution of transparency. Therefore Ctenophora is resolved to family level, while Nematoda, which has no transparent members, is unresolved. Gastropoda and Polychaeta are left unresolved because a resolution showing the distribution of transparency would make the figure too complex.

Most benthic, neustonic, and terrestrial groups have very few transparent members, although there are exceptions.

The following phyletic review of transparency was compiled with the aid of specialists in different taxa and environments (see acknowledgments) and is subject to several constraints. First, because nearly all small, unpigmented objects are transparent (for reasons described later), this section considers only species with transparent regions larger than 5 mm. Therefore certain phyla (*e.g.*, Rotifera, Gastrotricha) and most larvae and freshwater taxa are not covered. Second, because aquatic species from transparent groups that are found at aphotic depths tend to be strongly pigmented (usually red, orange, or black) (Hardy, 1956; Herring and Roe, 1988), only terrestrial taxa and aquatic taxa at euphotic and dysphotic depths are considered. Euphotic and dysphotic regions possess enough solar radiation for photosynthesis and vision, respectively. In the clearest waters, the lower bounds of the two regions are 200 and 1000 m. Finally, infaunal or endoparasitic species, in which transparency could not have any optical function (*e.g.*, Echiura, Sipuncula, Nematomorpha), are not covered.

Eight phyla—Porifera, Nematoda, Pogonophora, Onycophora, Brachiopoda, Bryozoa, Platyhelminthes, and Echinodermata—appear to have no transparent adults. The first seven of these are exclusively benthic, neustonic, or terrestrial (Faubel, 1984; May, 1994). Echinodermata is benthic with few exceptions (Miller and Pawson, 1990). Possible examples of transparency in these phyla, such as hexactinellid sponges and certain benthopelagic holothurians (*e.g.*, *Peniagone diaphana, Irpa ludwigi*) are better described as unpigmented and translucent (*i.e.*, milky) rather than transparent.

With the exception of the beroids, ctenophores at euphotic and dysphotic depths are generally transparent (Mayer, 1912; Harbison *et al.*, 1978). Guts, papillae, and other small features are sometimes strongly pigmented, and the comb rows iridesce in directional illumination, but the bulk of the body is often extraordinarily transparent. Beroid ctenophores tend to be opaque, due to the presence of thousands of giant muscle fibers within the mesoglea (Hernandez-Nicaise, 1991), though smaller specimens of certain species (*e.g., Beroe gracilis*) can be transparent.

Transparency in the Cnidaria is mostly found in cubozoans, hydromedusae, and siphonophores. Cubozoans are all highly transparent (Matsumoto, 1995). Hydromedusae tend to be highly transparent, though often with pigmented guts or gonads (Russell, 1953; Kramp, 1959) (Fig. 1A). Siphonophores follow a similar pattern with the exception of neustonic species (*e.g., Physalia*), which are often blue, and members of the benthic family Rhodaliidae, which are opaque (Totton, 1965; Herring, 1967; Pugh, 1983). Scyphozoans, in contrast and for unknown reasons, are generally opaque and pigmented (Mayer, 1910; Russell, 1970; Wrobel and Mills, 1998). No anthozoans are transparent.

Among the Annelida, transparency is found only among the pelagic polychaetes (Fig. 1E). Five phyllodocidacean families (Alciopidae, Lopadorrhynchidae, Pontodoridae, Tomopteridae, and Typhloscolecidae) and two flabelligerid families (Flotidae and Poeobiidae) are dominated by transparent species (Uschakov, 1972; Glasby *et al.*, 2000). The degree of transparency varies between the different families, with the tomopterids and alciopids highly transparent and the flabelligerids less so. The remaining pelagic family,

Isopilidae, apparently does not have transparent members (Uschakov, 1972; Glasby *et al.,* 2000).

Several genera of polystiliferous pelagic nemerteans are transparent (Pelagonemertes, Pilonemertes) (P. Roe, California State University Stanislaus, pers. comm.). However, pigmented food in their highly branched guts often seriously reduces any cryptic benefit. No species of benthic nemerteans is known to be transparent (Roe, pers. comm.).

Transparency in the Mollusca is complex. Although the phylum as a whole is overwhelmingly benthic and opaque, it contains several pelagic groups that are dominated by transparent species (Van der Spoel, 1976; Lalli and Gilmer, 1989). The Mollusca also contains pelagic groups that are entirely opaque, and at least one transparent benthic genus. The Aplacophora, Monoplacophora, Polyplacophora, Bivalvia, and Scaphopoda are exclusively benthic and opaque. Among gastropods, the exclusively pelagic pterotracheid and carinariid heteropods, pseudothecosomatous pteropods, and phylliroid nudibranchs are highly transparent (Figs. 1F, L). However, the janthinid snails, atlantid heteropods, euthecosomatous and gymnosomatous pteropods, and glaucid nudibranchs are all opaque, despite also being pelagic taxa (Van der Spoel, 1976; Lalli and Gilmer, 1989). Benthic gastropods are opaque, with the exception of several species of the nudibranch *Melibe,* which have transparent oral hoods that are used to catch crustaceans (Von W. Kjerschow-Agersborg, 1921). Among cephalopods, transparency is found only in octopus and squid. Although no benthic octopi are transparent, the pelagic families Amphitretidae and Vitreledonellidae are highly transparent (Ijema and Ikeda, 1902; Joubin, 1918) (Fig. 1B). None of the genera of the four families of the pelagic argonautoid octopods are transparent, and the pelagic Bolitaenidae are better described as translucent (Nesis, 1982). The benthopelagic cirrate octopods are all opaque and often strongly pigmented. Among the exclusively pelagic squid, only the Cranchiidae and small specimens of certain chiroteuthids (*e.g., Chiroteuthis*) display any significant transparency. *Vampyroteuthis* and the Sepioidea are opaque.

Species in the Chaetognatha are pelagic and highly transparent, with the exception of the benthic Spadellidae and certain species at the lower end of the dysphotic zone (Fig. 1G). The spadellids are opaque due to the presence of transverse muscles and pigmentation (Bone and Duvert, 1991).

With the exception of the wings of certain satyrid and ithomiid butterflies and sphingid moths (*e.g., Greta oto, Cephonodes hylas*) (Papageorgis, 1975; Yoshida *et al.,* 1997) (Fig. 1C) and the large pelagic larvae of certain freshwater insects (*e.g., Chaoborus*), transparency in the Arthropoda appears to be limited to aquatic crustaceans. As in the Mollusca, the distribution of transparency in crustaceans is complex, with many major groups containing both transparent and non-transparent forms. The only group that is truly dominated by transparent forms is the exclusively pelagic Hyperiidea (Amphipoda) (Bowman and Gruner, 1973; Vinogradov *et al.,* 1996). The hyperiids, which are commensal on gelatinous zooplankton (Madin and Harbison, 1977; Laval, 1980), can be extraordinarily transparent and often have special modifications to increase their transparency (*e.g.,* Land, 1981; Nilsson, 1982). The generally benthic or terrestrial groups (*e.g.,* Decapoda, Gammaridea, Cirripedia, Stomatopoda, Isopoda) are primarily opaque, but with many exceptions among pelagic and benthopelagic subgroups (*e.g.,* some Pasiphaeaid shrimp, various species of cleaner shrimp, the sergestid *Lucifer,* the isopod *Astacilla,* the phyllosoma larvae of *Palinurus,* the anemone shrimp *Periclimenes*) (Fig. 1J). As is true of cnidarians and ctenophores, many transparent pelagic crustaceans have red-pigmented guts and gonads, particularly at dysphotic depths (Hardy, 1956; Herring and Roe, 1988). Transparency is fairly common in freshwater crustaceans, but only a few species, mostly highly modified cladocerans, are larger than 5 mm (*e.g., Leptodora, Bythotrephes*) (Fig. 1C).

Most transparent urochordates are found in the exclusively pelagic Thaliacea, which comprises the pyrosomids, salps, and doliolids (Godeaux *et al.,* 1998). Pyrosomids are opaque, while salps and doliolids, excepting large individuals of *Thetys vagina,* are highly transparent. Among the exclusively benthic Ascidea, transparency is observed in several genera of the order Enterogona (*e.g., Ciona, Clavelina*), some of which are predatory (*e.g., Megalodicopia hians*) (Sanamyan, 1998). The larvaceans generally have small opaque bodies and long transparent tails, but with few exceptions (*e.g., Bathochordeus*) are smaller than 5 mm (L. P. Madin, Woods Hole Oceanographic Institution, pers. comm.) (Fig. 1I).

Although adults in the Hemichordata are infaunal and opaque, the larval form of *Planctosphaera pelagica* has a diameter of 25 mm and is highly transparent (Hart *et al.,* 1994) (Fig. 1D). This organism, known only in this form, appears to have a prolonged larval stage and is well adapted to a pelagic existence.

No tetrapod chordate is transparent, but a number of fish are. Transparent adults are scattered throughout marine and freshwater teleosts, but are common only in the freshwater family Ambassidae (glassfish) (Johnson and Gill, 1995). Commonly known examples from other families include the glass catfish *Kryptopterus bicirrhis* (Siluridae) and *Parailia pellucida* (Schilbeidae), the cardinalfish genus *Rhabdamia* (Apogonidae), the clingfish *Alabes parvulus* (Cheilobranchidae), and the glass knifefish *Eigenmannia virescens* (Sternopygidae) (Briggs, 1995; Ferraris, 1995; Johnson and Gill, 1995). In addition, the pelagic larvae of many freshwater and marine fish are often highly transparent (Breder, 1962; Meyer-Rochow, 1974) (Fig. 1K). The most striking of these are the leptocephalous larvae of elopomorphs. These leaf-shaped larvae incorporate gelatinous material in

their bodies and quickly grow to lengths of up to 50 cm (Pfeiler, 1986). Most larval fish lose their transparency upon metamorphosis, some within 24 hours. The only possible tetrapod candidates, the glass frogs (Centrolenidae), have transparent skin on their ventral side, but opaque organs and a strongly pigmented dorsal surface (reviewed by McFall-Ngai, 1990).

Transparency and Environment

As can be seen from Figure 2 and the previous section, transparency has evolved multiple times and is almost exclusively a pelagic trait. Organismal transparency (rather than simply ocular) is extremely rare on land, rare in the aquatic benthos, uncommon in aphotic regions, somewhat more common in dysphotic and neustonic habitats, and ubiquitous at euphotic depths in clear water. The rarity of terrestrial transparency is probably due to the low refractive index of air, the presence of gravity, and high levels of ultraviolet radiation. The distribution of transparency in aquatic habitats appears to be correlated with the distribution of successful visual predation and crypsis strategies.

Terrestrial transparency

The extreme rarity of terrestrial transparency is probably due to the problem of reflections. The invisibility of a transparent object depends in part on the difference between its refractive index and the refractive index of the surrounding medium. A large difference causes surface reflections that substantially increase visibility. For example, an ice sculpture, while transparent, is highly visible due to surface reflections. At normal incidence, the fraction of incident light that is reflected (R) is

$$R = \left(\frac{n_1 - n_2}{n_1 + n_2}\right)^2, \qquad (1)$$

where n_1 and n_2 are the refractive indices of the object and the surrounding medium. The refractive index of biological tissue is roughly proportional to density and ranges from 1.35 (cytoplasm) to about 1.55 (densely packed protein) (Charney and Brackett, 1961; Chapman, 1976). The refractive index of seawater depends on temperature and salinity, but is about 1.34. For these values, the surface reflection of a transparent organism in air (2%–5%) is roughly 10-fold to 2000-fold greater than its surface reflection in seawater (0.001%–0.7%). Although some nongaseous compounds with refractive indices slightly less than that of seawater exist (*e.g.,* trifluoroacetic acid, $n = 1.28$), the refractive index of water is the lower limit for biological materials. Therefore successful crypsis using transparency is unlikely in terrestrial habitats. Other likely contributing factors are the increased levels of ultraviolet radiation on land, which require protective pigmentation, and the need for supporting skeletal structures that are often opaque.

Distribution of aquatic transparency

Transparency is common in pelagic species at euphotic and dysphotic depths. Almost all non-transparent pelagic taxa are either camouflaged by small size (*e.g.,* atlantid heteropods, euthecosomatous and gymnosomatous pteropods, glaucid nudibranchs, copepods, ostracods) or mirrored surfaces (*e.g.,* fish, cephalopods), or are protected by fast swimming speeds (*e.g.,* fish, cephalopods, shrimp) or chemical or physical defenses (*e.g.,* scyphozoans, janthinid snails, *Nautilus*) (Hamner, 1996). The primary explanation for the prevalence of transparency in this environment is that it is the only form of camouflage in the pelagic realm that is successful from all viewpoints and at all depths. Cryptic coloration (*e.g.,* countershading) is generally successful only from a given viewpoint and at a given depth (Munz and McFarland, 1977; Johnsen, 2002). Mirrored sides are successful at euphotic and upper dysphotic depths and for most viewpoints, although not from directly above or below (Herring, 1994; Denton, 1990). Counterillumination tactics are metabolically expensive and successful only during moonlit nights or at dysphotic depths.

The relative rarity of transparency in benthic and neustonic habitats is puzzling. Both benthic and neustonic species tend to be pigmented to match the surface below them—benthic animals matching the substrate and neustonic species matching the upwelling radiance (deep blue in oceanic water, brown in shallow freshwater) (David, 1965; Herring, 1967; Cheng, 1975; Guthrie, 1989). The rarity of transparency in benthic habitats is possibly due to two factors. First, pigmentation may be less costly to the animal than transparency, since it requires fewer modifications. However, a varied background requires the ability to detect and match a range of patterns and colors, a process done automatically by transparency camouflage. A second possibility is that even perfectly transparent objects tend to cast highly conspicuous shadows, due to distortion of the light by the higher refractive index of the tissue. These shadows, invisible in pelagic habitats, may render transparency ineffective for benthic species.

Neither of these factors, however, can account for the relative rarity of transparency in neustonic species. The two major hypotheses for the pigmentation of neustonic species are photo-protection and crypsis (Herring, 1967; Zaitsev, 1970). Although ultraviolet (UV) radiation is quite high at the surface of any aquatic habitat, there is no evidence that the pigmentation in neustonic species absorbs strongly at UV wavelengths. In addition, there are compounds, such as mycosporine-like amino acids, that strongly absorb at UV but not visible wavelengths (Karentz *et al.,* 1991). The fact that neustonic pigmentation often matches the upwelling

radiation strongly suggests that at least part of its function is crypsis. However, the blue or brown pigmentation is successfully cryptic only from above, or possibly from the side (Munz and McFarland, 1977; Johnsen, 2002), whereas neustonic individuals are most likely to be viewed from below. From this angle, any individual is silhouetted by the bright downwelling light, rendering cryptic coloration useless. Predation from above (*e.g.,* avian) appears to mostly involve larger species (Zaitsev, 1970). As Herring (1967) concluded, no functional explanation of pigmentation in neustonic species is entirely satisfactory, and more data on the UV absorption of the pigments and the structure of the neustonic food web is needed.

As mentioned above, transparent species are rare at aphotic depths, generally being replaced by species with whole-body red or black pigmentation (Hardy, 1956; Herring and Roe, 1988; McFall-Ngai, 1990). At these depths, visual predation by solar light is sometimes replaced by visual predation based on directed bioluminescence. Because the spectra of photophores are generally void of red wavelengths (Widder *et al.,* 1983), neither red nor black surfaces can be seen by bioluminescent "searchlights." If the red or black coloration absorbs more than 99.5% of the directed bioluminescence, it may be more cryptic than transparency because even a perfectly transparent object causes surface reflections. However, because the reflected light is a small fraction of a dim source, the background light levels must be extremely low for the reflection to be visible. For example, the radiant intensity of the suborbital photophores of the Panama snaggletooth (*Borostomias panamensis*) is on the order of 10^{10} photons $\cdot$ s^{-1} $\cdot$ sr^{-1} (Mensinger and Case, 1997). If this light strikes a transparent individual with a refractive index of 1.37 (10% protein), one can determine from equation (1) that about 0.01% of the photons are reflected back to the viewer. Therefore the background light levels must be 10^6 photons $\cdot$ s^{-1} or lower. For upward viewing this occurs at about 750 m in oceanic water (using absorption and attenuation values from the equatorial Pacific (Barnard *et al.,* 1998) and radiative transfer software (Hydrolight 4.1, Sequoia Scientific)). At these depths, horizontal and upward radiances are 3% and 0.5% of the downward radiance (Denton, 1990), so the equivalent depths for successful viewing using horizontal and downward bioluminescence are 650 and 600 m. For viewers with brighter bioluminescent "searchlights" or targets with higher refractive index, the depths are less. For example, the chitinous cuticle of a transparent hyperiid amphipod (n = 1.55) reflects 0.5% of the light and would be visible at 625, 525, and 475 m for upward, horizontal, and downward-directed bioluminescence, respectively. Truly opaque objects, such as guts and digestive organs, reflect a much higher percentage of light and are visible at even shallower depths. This may explain why many opaque and high refractive index organs are pigmented at shallower depths than those at which whole-body pigmentation is observed.

Visibility and Visual Predation

Although some transparent species may only have trophic interactions with blind taxa, the majority either prey on or are preyed upon by at least some species with well-developed visual systems (Harbison *et al.,* 1978; Alldredge and Madin, 1982; Alldredge, 1984; Madin, 1988; Lalli and Gilmer, 1989; Pages *et al.,* 1996; Baier and Purcell, 1997; Madin *et al.,* 1997; Purcell, 1997; Harbison, unpublished literature review of gelatinivory in vertebrates). Since transparent animals are often more delicate and less agile than their visually orienting predators or prey, their success in predator/prey interactions with these animals depends critically upon their visibility and in particular their sighting distance (the maximum distance at which they are detectable by an animal relying on visual cues). Prey with short sighting distances reduce their encounters with visually orienting predators (Greene, 1983). "Ambush" predators (*e.g.,* medusae, siphonophores, cydippid ctenophores) with short sighting distances increase their chances of entangling visually orienting prey before being detected and avoided. Raptors (*e.g.,* chaetognaths, heteropods) with short sighting distances increase their chances of getting within striking distance without being detected.

Transparency and contrast

The visibility of a transparent individual generally depends more on its contrast than on its size (Mertens, 1970; Hemmings, 1975; Lythgoe, 1979). The inherent contrast (contrast at zero distance) at wavelength λ is defined as

$$C_o(\lambda) = \frac{L_o(\lambda) - L_b(\lambda)}{L_b(\lambda)}, \tag{2}$$

where $L_o(\lambda)$ is the radiance of the object and $L_b(\lambda)$ is the radiance of the background, both viewed a short distance from the object (Hester, 1968; Mertens, 1970; Jerlov, 1976). The absolute value of contrast decreases exponentially with distance according to

$$|C(\lambda)| = |C_o(\lambda)| \cdot e^{(K_L(\lambda) - c(\lambda))d}, \tag{3}$$

where $|C(\lambda)|$ is the absolute value of apparent contrast at distance d from the object, $K_L(\lambda)$ is the attenuation coefficient of the background radiance, and $c(\lambda)$ is the beam attenuation coefficient of the water (adapted from Mertens, 1970; Lythgoe, 1979). The maximum distance at which the object is still detectable is

$$d_{\text{sighting}}(\lambda) = \frac{\ln\left(\frac{|C_o(\lambda)|}{C_{\min}(\lambda)}\right)}{c(\lambda) - K_L(\lambda)}, \tag{4}$$

where $C_{\min}(\lambda)$ is the minimum contrast threshold of the viewer. An animal can indirectly affect $c(\lambda) - K_L(\lambda)$ by moving into a different water type or controlling the angle from which it is viewed, but it can only directly decrease its sighting distance by decreasing its inherent contrast. The inherent contrast of a transparent organism from an arbitrary viewpoint depends on its light-scattering properties and the characteristics of the underwater light field (Chapman, 1976), so it is difficult to model exactly. In general, however, pelagic objects have the greatest sighting distances when viewed from below, and are often viewed from this angle (Mertens, 1970; Munz, 1990; Johnsen, 2002). The transparency, $T(\lambda)$, of an object is the fraction of light of wavelength λ that passes unabsorbed and unscattered through it. Therefore, for the upward viewing angle

$$T(\lambda) = \frac{L_o(\lambda)}{L_b(\lambda)}, \; |C_o(\lambda)| = 1 - T(\lambda),$$

$$\text{and } d_{\text{sighting}}(\lambda) = \frac{\ln\left(\dfrac{1 - T(\lambda)}{C_{\min}(\lambda)}\right)}{c(\lambda) - K_L(\lambda)}. \quad (5)$$

Thus, the relationship between transparency and sighting distance is not linear and depends also on the contrast sensitivity of the viewer. Optimal minimum contrast thresholds have been determined for man (0.01), cat (0.01), goldfish (0.009–0.05), cod (0.02), rudd (0.03–0.07), roach (0.02), and bluegill (0.003–0.007) (Lythgoe, 1979; Douglas and Hawryshyn, 1990). It is important to note, however, that because these values depend on many aspects of the experimental situation (*e.g.*, temperature, target size, position of stimulus on retina, whether one eye or two was used, assessment method), they are not directly comparable (Douglas and Hawryshyn, 1990). For example, the minimum contrast threshold increases as the light level decreases. For example, the minimum contrast threshold of cod (*Gadus morhua*) increases from 0.02 at the surface to nearly 0.5 at 650 m in clear water (10^{-7} W sr^{-1} m^{-2}) (Anthony, 1981). Therefore, animals that are detectable near the surface may become undetectable at depth.

Empirical studies

The only empirical research on terrestrial transparency is a study on predation of neotropical butterflies showing that transparent species were mostly found near the ground, where they were presumably maximally cryptic (Papageorgis, 1975). A subsequent study, however, did not confirm this (Burd, 1994).

Most of the research on the relationship between transparency and visual predation has been performed in freshwater systems. Early studies by Zaret (1972) on fish predation on two morphs of transparent daphnia (*Ceriodaphnia cornuta*) showed that predation was higher on the morph with larger eyes. When the "small-eye" morph was then fed India ink, creating a "super eye spot" in the gut, the predation preferences of the fish switched. Zaret also found that the small-eye morph had a greatly reduced reproductive potential and hypothesized that it was maintained in natural populations due to its reduced visual predation pressure. Later Zaret and Kerfoot (1975) showed that predation on a different transparent cladoceran (*Bosmina longirostris*) did not depend on body size but on the size of the opaque eye spot; they concluded that the important variable in visual predation was not body size, as previously assumed, but apparent body size. This conclusion has been supported by several subsequent studies (*e.g.*, Confer *et al.*, 1978; Wright and O'Brien, 1982; Hessen, 1985). Kerfoot (1982) measured the transparency, palatability, and sighting distances (for pumpkinseed fish) of several species of transparent freshwater zooplankton and found that transparency was correlated with palatability and inversely correlated with sighting distance. He proposed that visual predation by freshwater fishes has driven zooplankton in two opposing directions—palatable groups being selected for decreased visibility through decreased size, increased transparency, or both; unpalatable groups being selected for increased visibility through increased size, intense pigmentation, or both. O'Brien and Kettle (1979) examined the countervailing selective pressures of tactile predation (selecting for large prey) and visual predation (selecting for small prey) on two species of *Daphnia.* They found that these species increased their actual size, but not their apparent size, by developing morphs with large transparent armored sheaths. Giguere and Northcote (1987) repeated the India ink studies of Zaret (1972) in a more natural way by examining the effect of a full gut on the predation of transparent prey. They found that ingested prey increased the predation of *Chaoborus* larvae by 68% and suggested that this increased risk was at least partially responsible for the sinking of the animals after nocturnal feeding.

In contrast to the relatively abundant freshwater studies, fewer feeding studies on transparency exist for marine ecosystems. Tsuda *et al.* (1998), in a feeding study similar to Giguere and Northcote's, found that predation on transparent copepods roughly doubled when their guts were full; he also suggested that predation risk due to gut visibility may be an important factor contributing to vertical migration in transparent zooplankton. Brownell (1985) and Langsdale (1993) both found that eye pigmentation significantly increased the vulnerability of transparent fish larvae to predation. Thetmeyer and Kils (1995) examined the effect of attack angle on the visibility of transparent mysids to herring predators and found that they were most visible when viewed from above or below and least visible when viewed horizontally. Finally, Utne-Palm (1999) found that the sighting distances for transparent copepods (to goby pred-

ators) were significantly lower than the sighting distances for pigmented copepods.

Most of the research on transparency in marine ecosystems has concentrated on physical measurements of transparency and modeling its relationship to visibility. Greze (1963, 1964) was the first to describe the importance of transparency in visual predation. Using relatively crude equipment, he measured the average transparency of various dinoflagellates, siphonophores, copepods, and larvaceans and presented a model, which, unfortunately, was inaccurate, relating the measurements to sighting distance. Using a spectrophotometer, Chapman (1976) measured the transparency of several medusae (*Polyorchis, Chrysaora, Aurelia*) as a function of wavelength (from 200 to 800 nm). He found that transparency was relatively constant over the visual and infrared range and then dropped dramatically at ultraviolet wavelengths. Chapman also modeled the relationship between transparency, reflectivity, and visibility as a function of viewing angle, showing that the visibility of any object that is not 100% transparent depends strongly on the viewing angle and the underwater radiance distribution. Forward (1976), in a study of shadow responses in crab larvae, measured the transparency of the larvae's ctenophore predator, *Mnemiopsis leidyi*, and showed that the ctenophores were sufficiently opaque to cause a defensive response in individuals below them. More recently, Johnsen and Widder (1998, 2001) measured the ultraviolet (280–400 nm) and visible (400–700 nm) transparency of 50 epipelagic and mesopelagic Atlantic species from seven phyla (Cnidaria, Ctenophora, Annelida, Mollusca, Crustacea, Chaetognatha, Chordata) and modeled the relationship between transparency and sighting distance using analyses similar to those given in the previous section. They found that transparency is generally constant over the visual range, with longer wavelengths slightly more transparent. Deep-water animals tended to have constant and high transparency at UV wavelengths, whereas near-surface animals showed rapidly decreasing and low transparency in the UV. The relationship between transparency and visibility was complex and depended strongly on the contrast sensitivity of the viewer. Many mesopelagic animals were found to be far more transparent than necessary for complete invisibility.

Visual adaptations to increase contrast of transparent animals

The importance of transparency in predator/prey interactions is also demonstrated by the special visual adaptations seen in pelagic animals. The three best studied of these are UV vision, polarization vision, and viewing at certain angles. In addition to their possible other functions, all three of these can "break" the camouflage of transparency.

UV vision (documented down to ~320 nm) has been demonstrated in many aquatic species; it has been conservatively estimated that there is sufficient UV light for vision down to 100 m in clear ocean water (reviewed by Losey *et al.*, 1999, and Johnsen and Widder, 2001). Visual pigments with UV sensitivity have been found in dozens of species of marine and freshwater fish (reviewed by Douglas and Hawryshyn, 1990; Jacobs, 1992; Goldsmith, 1994; and Johnsen and Widder, 2001). Among arthropods, UV vision has been demonstrated in stomatopods, cladocerans, copepods, decapods, and horseshoe crabs (Wald and Krainin, 1963; Marshall and Oberwinkler, 1999; Flamarique *et al.*, 2000). Finally, and surprisingly, UV sensitivity is found in at least one mesopelagic alciopid polychaete and four mesopelagic decapod crustaceans (Wald and Rayport, 1977; Frank and Case, 1988).

Three primary functions for UV vision have been hypothesized (Losey *et al.*, 1999): (1) intraspecific communication, (2) enhanced detection of opaque prey (silhouetted against the relatively bright UV background), and (3) enhanced detection of transparent prey. Due to higher light scattering or the presence of UV-protective compounds, many visibly transparent tissues are opaque at UV wavelengths (Douglas and Thorpe, 1992; Thorpe *et al.*, 1993; Johnsen and Widder, 2001). Several researchers have hypothesized that UV vision is primarily used to improve detection of transparent prey (Loew *et al.*, 1993; Cronin *et al.*, 1994; McFarland and Loew, 1994; Loew *et al.*, 1996; Sandstroem, 1999), and Browman *et al.* (1994) have shown that the presence of UV light improves the search behavior of certain UV-sensitive zooplanktivorous fish. The presence of UV sensitivity in planktivorous but not in non-planktivorous life stages of salmonids (reviewed by Tovee, 1995) and the correlation between UV vision and planktivory in coral reef fish (McFarland *et al.*, unpubl. data) suggest that UV vision is often used to increase the contrast of transparent planktonic prey.

Therefore, near-surface transparent species may have to satisfy the conflicting selective pressures of camouflage and protection from radiation damage. The increased visibility due to photo-protective carotenoid and melanin pigmentation in high-UV freshwater environments has been studied for many years (Hairston, 1976; Luecke and O'Brien, 1981, 1983; Byron, 1982; Hobaek and Wolf, 1991; Hansson, 2000; Miner *et al.*, 2000). These studies have shown several novel solutions, such as inducible pigmentation mediated by the relative levels of UV radiation and visual predation, restriction of pigmentation to vital organs, and the use of a photoprotective compound that also decreases visibility. Only two studies have examined marine systems (Morgan and Christy, 1996; Johnsen and Widder, 2001), and only the latter has explored the effect of nonvisible UV protective pigments on UV visibility. In this study, near-surface zooplankton displayed significantly greater UV absorption than deep-dwelling zooplankton, but the effect of UV absorption on UV visibility was less than expected because the mea-

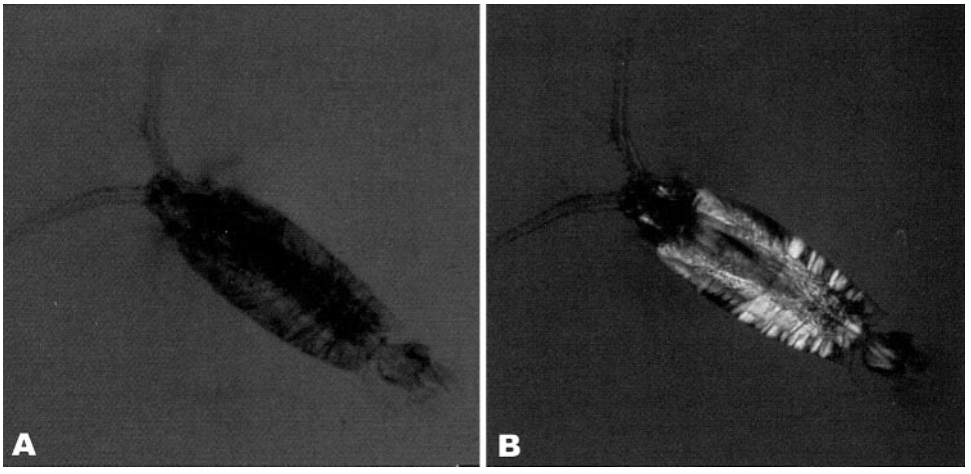

Figure 3. Copepod (*Labidocera*) viewed under (A) unpolarized transmitted light, and (B) crossed polarizers. The copepod is more distinct in (B) due to the presence of birefringent muscle and connective tissue. Because the background underwater illumination is polarized, a viewer with polarization vision may be able to visualize the contrast increase from (A) to (B). Courtesy of Nadav Shashar.

sured UV absorption was generally significantly greater in the UVB than in the UVA (where UV vision occurs), and because the highest UV absorption was often found in less transparent individuals.

The conflict between UV protection and UV concealment may have important ecological implications in light of reports of decreasing ozone levels at polar, temperate, and tropical latitudes and concomitant increases in UVB radiation (measured at 10%–20% per decade at temperate latitudes) (Solomon, 1990; Smith *et al.,* 1992; Stolarski *et al.,* 1992). A responsive increase in UV-protective pigmentation (at either an individual or population level) increases visibility at UV and possibly visible wavelengths, potentially resulting in increased predation or decreased feeding success. A responsive increase in depth may decrease access to prey, phytoplankton, or warmer water. Given the importance of transparent zooplankton to the trophic ecology of the pelagic realm (*e.g.,* Madin *et al.,* 1997; Purcell, 1997), either response may have significant effects.

A second visual adaptation that can increase the contrast of transparent predators or prey is polarization vision. Underwater light is polarized, particularly in the horizontal direction (Waterman, 1981). A transparent object can affect this polarization in two ways: it can depolarize it entirely or, if the object is birefringent, it can rotate the plane of polarization (Lythgoe and Hemmings, 1967; Fineran and Nicol, 1978). Either change is potentially detectable by a polarization-sensitive visual system (Fig. 3), which may explain the prevalence of polarization sensitivity in underwater crustaceans and cephalopods (Waterman, 1981). Despite the enormous potential of this field, only one study has tested this possibility (Shashar *et al.,* 1998). This study showed that squid (*Loligo pealei*) preferentially attacked birefringent plastic beads over non-birefringent beads, although they were otherwise indistinguishable.

The final adaptation is behavioral rather than physiological and relies on the special optical properties of the air-water interface. Due to refraction at the water's surface, the hemispherical sky is compressed into a region 97 ° across, known as Snell's window. Any transparent object just outside the edge of this window is more conspicuous because it refracts and reflects some of the light from within the window, but is seen against the relatively dark background of water outside the window (Lythgoe, 1979). As with polarization sensitivity, this contrast enhancer, while potentially quite important, has only been tested once. Janssen (1981) showed that the attack angles of the blueback herring (*Alosa aestivalis*) were closely distributed around the outside edge of Snell's window.

Active uses of transparency

Although transparency seems to be primarily designed for passive crypsis, a few examples exist of more active uses of this trait. The physonect siphonophores *Athorybia rosacea* and *Aglama okeni* are mostly transparent, but they have pigmented regions mimicking copepods and larval fish that are apparently used as lures (Purcell, 1980, 1981). Therefore, animals approaching the small lures cannot detect the large individual that is also present. Other siphonophores appear to have exploited temporal changes in transparency for defense. The calycophoran siphonophores *Hippopodius hippopus* and *Vogtia* are normally transparent, but they rapidly become opaque when disturbed, presumably as a defensive startle response (Mackie, 1996).

The Physical Basis of Transparency

General principles

Transparency differs from other forms of crypsis and most adaptations in general in that it involves the entire organism. Therefore, many or all the tissues must be specialized for transparency. How this is achieved and how the modifications are compatible with life are only just beginning to be understood. The following sections explain the physics of transparency and then discuss the few theoretical and fewer empirical biological studies that have been performed.

An organism or tissue is transparent if it neither absorbs nor scatters light (Kerker, 1969). The majority of organic molecules do not absorb visible light (Tardieu and Delaye, 1988), and measurements of the wavelength dependence of light attenuation in 52 species of transparent zookplankton show no evidence of visible absorption bands in the transparent regions (Chapman, 1976; Johnsen and Widder, 1998, 2001). Therefore, except for necessarily opaque tissues (*e.g.*, gut, retina) and the special case of UV transparency, the primary barrier to transparency in organic tissue appears to be light scattering.

Scattering is caused by discontinuities in refractive index. A nonabsorbing substance with a homogeneous refractive index is transparent. Biological tissue has many refractive-index discontinuities, due to the varying proportions and densities of its components. For example, the refractive index of lipids is higher than that of cytoplasm (Meyer, 1979). Therefore, plasma membranes, lipid droplets, and organelles with extensive folded membranes (*e.g.*, mitochondria, Golgi apparatus, and endoplasmic reticulum) have a higher refractive index than the surrounding cytoplasm. Organelles with dense protein concentrations, such as peroxisomes and lysosomes, also have a higher refractive index than the surrounding cytoplasm, as do nuclei, due to their high concentrations of nucleic acids. Even gelatinous organisms containing large amounts of water have sufficient complexity to scatter light, as evidenced by their opacity after death. In addition to these internal discontinuities, there is also the large discontinuity defined by the surface of the organism. As a photon passes through regions of different refractive indices, its direction is altered. Given enough direction changes, the tissue, though nonabsorbing, will be opaque. Common examples of nonabsorbing, highly scattering, opaque substances are milk, clouds, snow, and the sclera (white) of the eye.

Therefore, transparent animals must be adapted to scatter as little light as possible. Because the refractive indices of organic molecules are generally closely correlated with density (Ross, 1967), chemical adaptations are unlikely, and the problem is essentially a structural one.

Anatomical adaptations

Although most of the adaptations for transparency are observable only at the electron microscopy level, some are visible to the naked eye. These can be divided into the cloaking of tissues that cannot be made transparent and body flattening (Fig. 4).

Eyes and guts cannot be made transparent. Eyes must absorb light to function and guts are betrayed by their contents, since even transparent prey become visible during digestion. The eyes of transparent animals have been camouflaged in various ingenious ways. Many hyperiid amphipods have enormous eyes, covering most of their head, and could be betrayed by their large, pigmented retinas. However, the retinal signature is masked using either of two strategies. In some hyperiids (*e.g., Phronima*), the light is directed from the large eyes to highly compact retinas using transparent fiber optic cables of complex optical design (Land, 1981; Nilsson, 1982) (Fig. 4B). Conversely, the retina of the hyperiid *Cystisoma* is thinned, expanded, situated directly behind the cornea, and therefore indistinct (Fig. 4A). Many transparent molluscs camouflage their eyes with mirrors, because mirrors in the open ocean reflect only more ocean and so are invisible (Herring, 1994). Others, particularly the transparent cranchiid squid, use counterillumination to mask the shadows of their eyes seen from below (Fig. 4D) (Voss, 1980). Land (1992) suggested that the elongated eyes of transparent octopi function to minimize the shadow of the eye from below. A final adaptation that has not been explored is the separation of the eyes using long stalks (*e.g.*, cranchiid and phyllosoma larvae), thereby minimizing the characteristic signature of two eyes side by side (Fig. 4F).

Similarly ingenious adaptations exist for minimizing the visibility of the opaque guts. Many transparent animals have elongated, vertically oriented, and sometimes reflective guts, including pterotracheid heteropods, cranchiid squid, transparent octopi, and hyperiid amphipods (Seapy and Young, 1986; Land, 1992; Vinogradov *et al.*, 1996; Young *et al.*, 1998). The shape and orientation minimizes the profile of the gut when viewed from above or below. The reflective coating minimizes the contrast of the gut when viewed from other angles. Seapy and Young (1986) showed that pterotracheids and cranchiids actively maintained the vertical orientation of their guts while altering the orientation of their bodies (Fig. 4C, D). A converse approach, seen in many salps, ctenophores, and medusae, is the possession of compact, spherical guts. Although not as cryptic from below, a sphere has the minimum average projected area when averaged over all potential viewing angles (Johnsen and Widder, 1999). Finally, as is found in eyes, the shadows of the opaque guts of certain species are masked using counterilluminating bioluminescence. For example, the mostly transparent midwater shrimp *Sergestes similis* masks

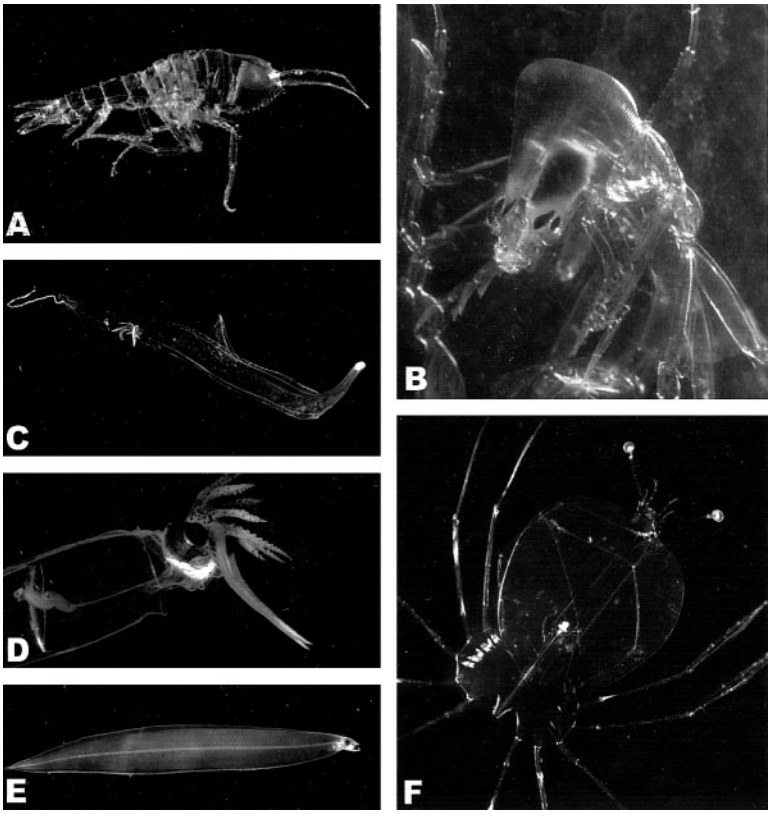

Figure 4. Various anatomical modifications that reduce the visibility of transparent animals. (A) Thin and extended retina directly behind cornea reduces the opacity of the eyes of the hyperiid amphipod *Cystisoma.* (B) Although the eyes of the hyperiid *Phronima* are large, the light is directed to the compact retinae using transparent fiber optic guides. (C) and (D) The guts of the heteropod *Pterotrachea* and the cranchiid squid *Taonius pavo* are elongated, mirrored, and vertical to minimize their visibility. (E) and (F) The bodies of leptocephalous and phyllosoma larvae are highly flattened to minimize light attenuation. Credits: A, B, E—Laurence Madin; C, D—Edith Widder; F—Tamara Frank.

the shadow of its digestive organs in this fashion (Warner *et al.*, 1979).

Many guts of transparent animals, if not mirrored, are pigmented. This is hypothesized to mask the presence of bioluminescent prey but may also serve as cryptic coloration, particularly since the color often approximates the optimally cryptic shade for a given depth (Johnsen, 2002).

Finally, some animals simply ingest substances that remain clear. The highly transparent larva of the phantom midge (*Chaoborus*) sucks out clear fluids from its prey (Kerfoot, 1982). Therefore, the gut remains transparent and does not need to be camouflaged.

Light attenuation in tissue, whether due to absorption or scattering, is exponential. For example, if a 1-cm-thick section of tissue is 60% transparent, then 2 cm is 36% transparent, and 3 cm is 22% transparent. Conversely, a 1-mm-thick section of the same tissue is 95% transparent. Therefore, transparency can be achieved through extreme body flattening. This adaptation has the additional advantage of also camouflaging the animal when it is observed edge-on. Flattening is observed in many transparent animals including cestid ctenophores, phylliroid nudibranchs, many freshwater cladocerans, hyperiid amphipods, phyllosoma and stomatopod larvae, and the leptocephalous larvae of fish (Mayer, 1912; Zaret, 1981; Pfeiler, 1986; Lalli and Gilmer, 1989; Vinogradov *et al.*, 1996) (Fig. 4E, F). In certain cases, the flattening is extreme. The phyllosoma larvae of *Palinurus* are about 50 mm across and less than 1 mm thick (Fig. 4F). In many cases, body flattening may serve additional functions, such as more efficient swimming in fish and phylliroid nudibranchs, or increased surface area for gas exchange in cestid ctenophores.

Transparency and ultrastructure

The primary modifications for transparency, however, are ultrastructural and can only be seen with electron microscopy. The modifications depend on the tissue, which can be divided into three groups: external surface, extracellular matrix, and cellular tissue.

As mentioned above, the external surface of even a perfectly transparent organism reflects light due to the change

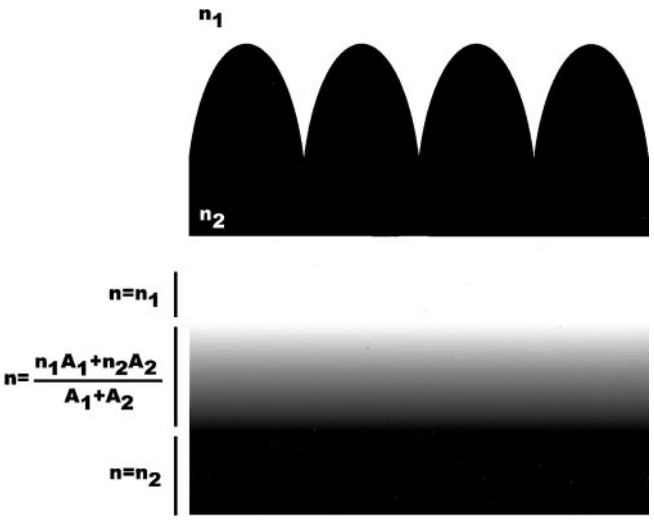

Figure 5. Photons impinging from above on an irregular surface with protrusions smaller than half a wavelength of light experience a gradual change in refractive index rather than a sharp discontinuity. n_1 is the refractive index of the external medium, n_2 is the index of the surface of the organism (*e.g.*, cuticle). The refractive index at a given horizontal plane within the protrusion layer equals the average refractive index, which is given by the equation in the figure, where A_1 and A_2 are the respective areas of the external and organismal regions in that plane. The gradual shift in refractive index can reduce or eliminate surface reflections.

in refractive index. These reflections can be reduced or eliminated by covering the surface with submicroscopic protrusions (Miller, 1979; Wilson and Hutley, 1982). Because the protrusions are submicroscopic, they do not scatter light, but instead mimic a material of an intermediate refractive index. At the tips of the protrusions, the refractive index is that of the external medium. At the base, the index is that of the organism. At intermediate heights, the index varies smoothly and depends on the relative projected areas of the protrusions and the external medium (Fig. 5). These structures, known as "moth eye" surfaces, are found on the eyes of certain, particularly nocturnal, lepidopterans, dipterans, and caddisflies, where they are believed to camouflage the large eyes and increase sensitivity (by reducing reflected light) (reviewed by Miller, 1979; Parker *et al.*, 1998). They are also found on the wings of transparent lepidopterans, and in certain species (*e.g.*, *Cephonodes hylas*) have been shown to reduce their visibility (Yoshida *et al.*, 1997).

The transparency of many extracellular tissues may depend on the counterintuitive notion that, although a completely homogeneous refractive index is sufficient for transparency, it is not always necessary. A transparent tissue can have components with many different refractive indices, so long as the average refractive index is constant over distances equal to half the wavelength of the incident light or more (Benedek, 1971). More precisely, scattering and light attenuation are low if the spatial distribution of refractive index has no Fourier components with wavelengths greater than one half the wavelength of light. This low scattering is due to extensive destructive interference of the scattered light from the various scatterers. What is observed instead is a slower speed of light through the material. In short, scattering (in the presence of heavy destructive interference) is the source of refractive index. In glass, for example, each of the various molecules scatter light, but due to destructive interference no scattered light is observed and the beam is not attenuated. This theory has been invoked to explain the transparency of the mammalian cornea and lens (Benedek, 1971; Tardieu and Delaye, 1988; Vaezy and Clark, 1994). In both tissues, a substance with a high refractive index (collagen fibers in the cornea and crystalline proteins in the lens) is embedded within a substance with a low refractive index. The substance with the high refractive index is packed so densely that steric and other repulsive interactions force a local ordering of the scatterers (Tardieu and Delaye, 1988). The ordering exists only over distances on the order of several diameters of the scatterers, but it is sufficient to drastically reduce scattering. In the case of N identical scatterers, the total scattering cross-section, C_{total}, is given by

$$C_{\text{total}} = NC_{\text{sca}}S(\phi), \tag{6}$$

where C_{sca} is the scattering cross-section of an individual scatterer, ϕ is the volume concentration of the scatterers ($V_{\text{scatterers}}/V_{\text{total}}$), and $S(\phi)$ is the structure factor. The structure factor gives the amount of reduction in total scattering due to destructive interference caused by local ordering. In general, $S(\phi)$ is complex or unknown (see Benedek, 1971), but in the simpler case of small scatterers (radius $\leq$ 70 nm) it is

$$S(\phi) = \frac{(1-\phi)^4}{1 + 4\phi + 4\phi^2 - 4\phi^3 + \phi^4}$$

(Delaye and Tardieu, 1983). (7)

A concentration of scatterers of 30% reduces the total scattering to 10% of the value calculated under the assumption of no destructive interference of scattered light. A concentration of 60% reduces the scattering to less than 1% of the value calculated assuming no destructive interference. Figure 6 shows the total scattering cross-section of a solution of small particles plotted against their volume concentration. As the volume concentration increases there are more scatterers, but also more destructive interference. The maximum light scattering occurs at 13% concentration and then decreases as the concentration increases (see Benedek (1971) and Tardieu and Delaye (1988) for further details). This theory has been experimentally confirmed using solutions of lens proteins (Bettleheim and Siew, 1983). The solution becomes cloudier with increasing concentration, until a volume concentration of about 13%, after which it becomes clearer.

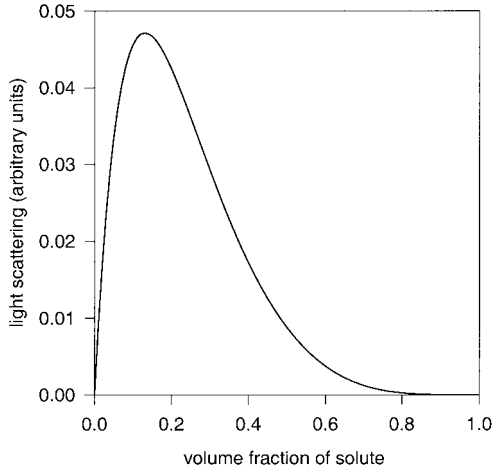

Figure 6. The amount of light scattering of a solution of small, identical scatterers plotted against their concentration (by volume). The scattering peaks when the concentration equals 13%.

Many extracellular and some cellular tissues (*e.g.,* muscle) of transparent organisms may meet these requirements. Although studies of the extracellular matrices and muscle of transparent animals are fairly rare, ultrastructural data exist for hydromedusae, siphonophores, ctenophores, chaetognaths, transparent ascidians, pyrosomas, doliolids, and salps (De Leo *et al.*, 1981; Weber and Schmid, 1985; Franc, 1988; Hernandez-Nicaise, 1991; Shinn, 1997; Hirose *et al.*, 1999). The fact that all of these appear homogeneous under light microscopy strongly suggests that they have few Fourier components greater than one half the wavelength of light. However, rigorous analyses have not been performed.

Although the above theory may explain the transparency of extracellular structures, it cannot adequately account for the transparency of cellular tissue. Reduction of scattering by destructive interference relies on dense packing of similar objects. In the two cases where this theory has been successfully applied (lens and cornea), the tissues are highly simplified. The mammalian lens, in particular, has been drastically modified for transparency (Goldman and Benedek, 1967; Philipson, 1973; Tardieu and Delaye, 1988). Most of the lens cells lack nuclei, mitochondria, and other organelles and, in fact, are little more than containers for dense concentrations of a few different proteins. The cells rely entirely on the surrounding cells for metabolic support and maintenance. Similarly, the cornea is a tightly packed array of collagen fibers with very few support cells and cannot maintain itself. These modifications are obviously incompatible with life when employed throughout an entire organism.

The only investigation of the basis of transparency in more complex cellular tissue is a theoretical treatment by Johnsen and Widder (1999). This study assumed that a cell requires given total volumes of various components. It then determined how to apportion, distribute, and shape the volumes to minimize light scattering. The study found that the size of the components was most important, followed by the refractive index and, distantly, by the shape (Fig. 7; Table 1). A similar analysis was performed assuming that a cell requires a given total surface area of certain components, with similar results. Because a group of smaller particles within a wavelength of light of each other behave roughly like one larger particle (Thiele, 1998), clustering particles can change the total amount of scattering. For example, if several lysosomes have radii near the critical

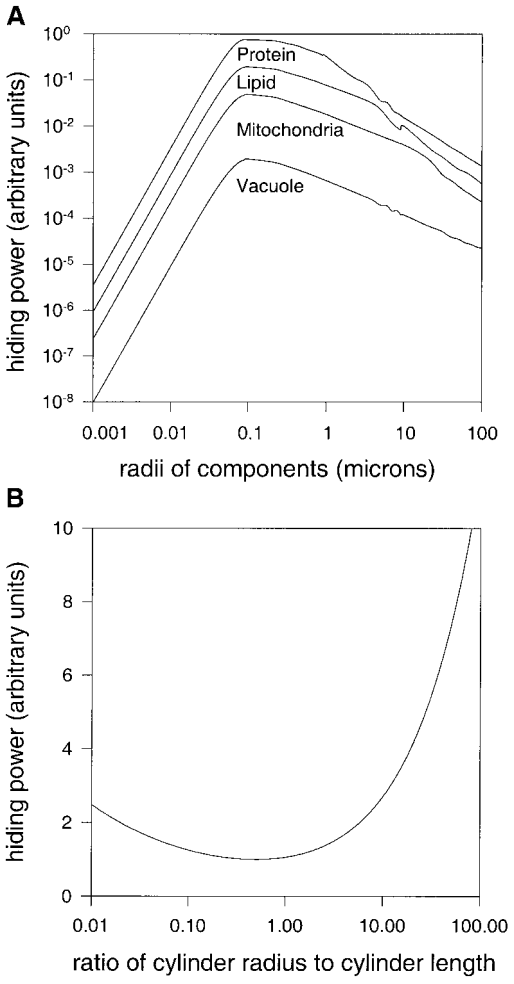

Figure 7. (A) The hiding power (opacity) for a given volume of material as a function of refractive index and the size of the smaller volumes into which it is divided. Hiding power is $S \cdot (1 - \langle \cos \theta \rangle)$, where S is the total amount of light scattering and $\langle \cos \theta \rangle$ is the average cosine of the angle into which the light is scattered. Therefore, backscattered light has a higher hiding power than forward scattered light. Material is assumed to be embedded in cytoplasm ($n = 1.35$). The refractive indices are vacuole—1.34, mitochondria—1.42, lipid—1.49, protein—1.62. (B) Hiding power plotted against shape for a large cylinder of constant volume averaged over all possible orientations relative to the incident light. Shape is given as the ratio between the radius of the cylinder and the length. Scattering is minimal when the radius equals half the length of the cylinder (*i.e.,* when the cylinder is most spherical).

Table 1

Ultrastructural predictions for transparent cellular tissue: the left column lists the various parameters in order of their importance to tissue transparency; the right column lists the predictions for the given parameter under a constant volume constraint; particles are considered clustered if they are within a wavelength of light of each other

Parameter	Predictions
Size of particles into which substance is subdivided	Particles will have radii either greater or less than 100 nm
Clustering or dispersion of particles	Small particles will be dispersed; large particles will be clustered
Refractive index of particles	All particles will have low relative refractive indices
Shape for particles with radii less than the wavelength of light	Particle shape will be arbitrary
Shape for particles with radii comparable to the wavelength of light	Predictions are highly case-specific
Shape for particles with radii greater than the wavelength of light	Particles will be spherical

radius (see Fig. 7; Table 1), they can be clustered to reduce the total amount of light scattering. Shape is surprisingly unimportant. For particles smaller than the wavelength of light, shape is irrelevant (Johnsen and Widder, 1999). For larger particles, the change in scattering as an object shifts from needle-shaped to disk-shaped is quite small relative to the enormous changes due to size (Fig. 7B).

Table 2 lists the predictions for actual cell components to scatter a minimum amount of blue-green light. For each component, a range of size and refractive index is given. All the components are considered to be primarily bound by constant-volume constraints, with the exception of mitochondria. Since mitochondrial functioning depends heavily on membrane surface, it is considered to be bound by constant-surface-area constraints (see above). The refractive index of the cytoplasm is assumed to be 1.35. The refractive indices of the components are highly approximate and based on values of 1.62 for protein, 1.49 for lipid, and 1.34 for saline. In cases where a given prediction cannot be applied (*e.g.*, dividing a nucleus into smaller nuclei, changing the shape of a microtubule), no prediction is made. All predictions assume that the size and refractive index of a given

Table 2

Predictions for a typical cell that scatters a minimum amount of light: the predictions cover the shape, distribution (many and small, few and large), and refractive index of the cellular components

Component	Constraint	Size	Index	Predictions
Actin filaments, intermediate filaments, microtubules	Volume	4 nm, 5 nm, 12 nm	1.55–1.62	Shape: not applicable Distribution: dispersed Refractive index: low
Ribosomes	Volume	15 nm	1.55–1.62	Shape: arbitrary Distribution: dispersed Refractive index: low
Transport vesicles	Volume	15–50 nm	1.49–1.62	Shape: arbitrary Distribution: many, small, and dispersed Refractive index: low
Lysosomes, peroxisomes	Volume	0.1–0.25 μm	1.49–1.62	Shape: difficult to predict Distribution: many, small, and dispersed Refractive index: low
Lipid droplets	Volume	0.1–10 μm	1.49–1.62	Shape: arbitrary (if droplets are large, then spherical) Distribution: many, small, and dispersed Refractive index: low
Mitochondria	Surface area	0.25–10 μm	1.42–1.49	Shape: difficult to predict Distribution: many, small, and dispersed Refractive index: low
Nucleus	Volume	1.5–5 μm	1.42–1.49	Shape: spherical Distribution: not applicable Refractive index: low
Large vacuole	Volume	5–15 μm	1.34–1.62	Shape: spherical Distribution: few, large, and clustered Refractive index: low

component must remain within the range given. None of these predictions have been tested, although the morphological techniques are relatively straightforward.

In summary, although the physics of light scattering is well understood, the field of organismal transparency is still in its infancy. The few theoretical and empirical studies suggest that there are several routes to transparency, many of which probably operate concurrently. For example, the transparency of leptocephalous larvae may be due to body flattening, ordered packing within the gelatinous core, a very thin muscle layer, and possibly modifications within the cellular tissue itself. Other animals, such as phyllosoma larvae, may rely entirely on their extreme flattening. However, the actual modifications and their proximate and ultimate costs are, for the most part, unknown.

Future Directions

Transparency is currently a field with more questions than answers. Almost every major aspect of its study is a fruitful avenue for future research, but several topics are critical for future understanding of this adaptation. First, the structural predictions must be tested using morphological and optical measurements of transparent tissue. The unlikely possibility that organic molecules in transparent organisms have altered their refractive indices needs to be tested. More images of transparent animals under UV and polarized light are needed to evaluate the hypotheses of special camouflage breakers in planktivores, as are more feeding studies in both freshwater and marine ecosystems. Finally, as more phylogenies of pelagic groups become available, comparative methods should be used to explore the evolution of this extraordinary trait.

Acknowledgments

I thank the following for information on the transparency of specific groups: Martin Angel, Daphne Fautin, Tamara Frank, Steven Haddock, Richard Harbison, Peter Herring, Dina Leech, Laurence Madin, Marianne Moore, Karen Osborn, David Pawson, Pamela Roe, Clyde Roper, Michael Vecchione, Janet Voight, and Edith Widder. I also thank Ken Halanych and Yale Passamaneck for pointing out relevant phylogenetic literature and software, and Kristina Fjeld, Tamara Frank, and Laurence Madin for a critical reading of the manuscript. The images for Figures 1, 3, and 4 were generously provided by Tamara Frank, Steven Haddock, Jeff Jeffords, Laurence Madin, Nadav Shashar, and Edith Widder. This work was funded in part by grants to SJ from The Rinehart Coastal Research Center, the Reuben F. and Elizabeth B. Richards Endowed Fund, the Penzance Endowed Fund, and the Grayce B. Kerr Fund. This is contribution number 10555 of the Woods Hole Oceanographic Institution.

Literature Cited

Alldredge, A. L. 1984. The quantitative significance of gelatinous zooplankton as pelagic consumers. Pp. 407–434 in *Flows of Energy and Materials in Marine Ecosystems*, M. J. R. Fasham, ed. Plenum Press, New York.

Alldredge, A. L., and L. P. Madin. 1982. Pelagic tunicates: unique herbivores in the marine plankton. *Bioscience* **32:** 655–663.

Anthony, P. D. 1981. Visual contrast thresholds in the cod *Gadus morhua*. *J. Fish Biol.* **19:** 87–103.

Baier, C. T., and J. E. Purcell. 1997. Trophic interactions of chaetognaths, larval fish, and zooplankton in the South Atlantic Bight. *Mar. Ecol. Prog. Ser.* **146:** 43–53.

Barnard, A. H., W. S. Pegau, and J. R. V. Zaneveld. 1998. Global relationships of the inherent optical properties of the oceans. *J. Geophys. Res.* **103:** 24955–24968.

Benedek, G. B. 1971. Theory of the transparency of the eye. *Appl. Opt.* **10:** 459–473.

Bettleheim, F. A., and E. L. Siew. 1983. Effect of change in concentration upon lens turbidity as predicted by the random fluctuation theory. *Biophys. J.* **41:** 29–33.

Bone, Q., and M. Duvert. 1991. Locomotion and buoyancy. Pp. 32–44 in *The Biology of Chaetognaths*, Q. Bone, H. Kapp, and A. C. Pierrot-Bults, eds. Oxford University Press, New York.

Bowman, T., and H. E. Gruner. 1973. The families and genera of Hyperiidea (Crustacea: Amphipoda). *Smithson. Contrib. Zool.* **146:** 1–60.

Breder, C. M. 1962. On the significance of transparency in osteichthid fish eggs and larvae. *Copeia* **1962:** 561–567.

Bridge, D., C. W. Cunningham, R. DeSalle, and L. W. Buss. 1995. Class-level relationships in the phylum Cnidaria: molecular and morphological evidence. *Mol. Biol. Evol.* **12:** 679–689.

Briggs, J. C. 1995. Clingfishes. Pp. 142–144 in *Encyclopedia of Fishes*, J. R. Paxton and W. N. Eschemeyer, eds. Academic Press, New York.

Browman, H. I., I. Novales-Flamarique, and C. W. Hawryshyn. 1994. Ultraviolet photoreception contributes to prey search behaviour in two species of zooplanktivorous fishes. *J. Exp. Biol.* **186:** 187–198.

Brownell, C. L. 1985. Laboratory analysis of cannibalism by larvae of the Cape anchovy *Engraulis capensis*. *Trans. Am. Fish Soc.* **114:** 512–518.

Burd, M. 1994. Butterfly wing colour patterns and flying heights in the seasonally wet forest of Barro Colorado Island, Panama. *J. Trop. Biol.* **10:** 601–610.

Byron, E. R. 1982. The adaptive significance of calanoid copepod pigmentation: a comparative and experimental analysis. *Ecology* **63:** 1871–1886.

Chapman, G. 1976. Reflections on transparency. Pp. 491–498 in *Coelenterate Ecology and Behavior*, G. O. Mackie, ed. Plenum Press, New York.

Charney, E., and F. S. Brackett. 1961. The spectral dependence of scattering from a spherical alga cell and its implication for the state of organization of the light accepting pigments. *Arch. Biochem. Biophys.* **92:** 1–12.

Cheng, L. 1975. Marine pleuston—animals at the sea-air interface. *Oceanogr. Mar. Biol. Annu. Rev.* **13:** 181–212.

Confer, J. L., G. L. Howick, M. H. Corzette, S. L. Kramer, S. Fitzgibbon, and R. Landerbert. 1978. Visual predation by planktivores. *Oikos* **31:** 27–37.

Cronin, T. W., N. J. Marshall, R. L. Caldwell, and N. Shashar. 1994. Specialization of retinal function in the compound eyes of mantis shrimps. *Vision Res.* **34:** 2639–2656.

David, P. M. 1965. The surface fauna of the ocean. *Endeavour* **24:** 95–100.

Delaye, M., and A. Tardieu. 1983. Short-range order of crystallin proteins accounts for eye lens transparency. *Nature* **302:** 415–417.

De Leo, G., E. Patricolo, and G. Frittitta. 1981. Fine structure of the tunic of *Ciona intestinalis* L. II. Tunic morphology, cell distribution and their functional importance. *Acta Zool.* **62:** 259–271.

Denton, E. J. 1990. Light and vision at depths greater than 200 meters. Pp. 127–148 in *Light and Life in the Sea,* P. J. Herring, A. K. Campbell, M. Whitfield, and L. Maddock, eds. Cambridge University Press, New York.

Douglas, R. H., and C. W. Hawryshyn. 1990. Behavioral studies of fish vision: an analysis of visual capabilities. Pp. 373–418 in *The Visual System of Fish,* R. H. Douglas and M. B. A. Djamgoz, eds. Chapman and Hall, New York.

Douglas, R. H., and A. Thorpe. 1992. Short-wave absorbing pigments in the ocular lenses of deep-sea teleosts. *J. Mar. Biol. Assoc. UK* **72:** 93–112.

Faubel, A. 1984. On the geographical occurrence of pelagic polyclad turbellarians. *Cah. Biol. Mar.* **25:** 153–168.

Ferraris, C. J. 1995. Catfishes and knifefishes. Pp. 106–112 in *Encyclopedia of Fishes,* J. R. Paxton and W. N. Eschemeyer, eds. Academic Press, New York.

Fineran, B. A., and J. A. C. Nicol. 1978. Studies on the photoreceptors on *Anchoa mitchilli* and *A. hepsetus* (Engraulidae) with particular reference to the cones. *Philos. Trans. R. Soc. Lond. B* **283:** 25–60.

Flamarique, I. N., H. I. Browman, M. Belanger, and K. Boxaspen. 2000. Ontogenetic changes in visual sensitivity of the parasitic salmon louse *Lepeophtheirus salmonis. J. Exp. Biol.* **203:** 1649–1659.

Forward, R. B., Jr. 1976. A shadow response in a larval crustacean. *Biol. Bull.* **151:** 126–140.

Franc, J. M. 1988. The mesoglea of ctenophores. *Bull. Soc. Zool. Fr.* **113:** 347–351.

Frank, T. M., and J. F. Case. 1988. Visual spectral sensitivities of bioluminescent deep-sea crustaceans. *Biol. Bull.* **175:** 261–273.

Fraser, J. 1962. *Nature Adrift: The Story of Marine Plankton.* G. T. Foulis, London.

Giguere, L. A., and T. G. Northcote. 1987. Ingested prey increase risks of visual predation in transparent *Chaoborus* larvae. *Oecologia* **73:** 48–52.

Glasby, C. J., P. A. Hutchings, K. Fauchald, H. Paxton, G. W. Rouse, C. W. Russell, and R. S. Wilson. 2000. Polychaeta. Pp. 1–296 in *Polychaetes and Allies: The Southern Synthesis,* P. L. Beesley, G. J. B. Ross, and C. J. Glasby, eds. CSIRO Publishing, Melbourne.

Godeaux, J., Q. Bone, and J. C. Braconnot. 1998. Anatomy of Thaliacea. Pp. 1–24 in *The Biology of Pelagic Tunicates,* Q. Bone, ed. Oxford University Press, New York.

Goldman, J. N., and G. B. Benedek. 1967. The relationship between the morphology and transparency in the nonswelling corneal stroma of the shark. *Investig. Ophthalmol.* **6:** 574–600.

Goldsmith, T. H. 1994. Ultraviolet receptors and color vision: evolutionary implications and dissonance of paradigms. *Vision Res.* **34:** 1479–1488.

Greene, C. H. 1983. Selective predation in freshwater zooplankton communities. *Int. Rev. Gesamten Hydrobiol.* **68:** 297–315.

Greze, V. N. 1963. The determination of transparency among planktonic organisms and its protective significance. *Dokl. Akad. Nauk. SSSR* **151:** 435–438.

Greze, V. N. 1964. The transparency of planktonic organisms in the equatorial part of the Atlantic Ocean. *Okeanologiya* **4:** 125–127.

Guthrie, M. 1989. *Animals of the Surface Film.* Richmond Publishing, Slough, U.K.

Hairston, N. 1976. Photoprotection by carotenoid pigments in the copepod *Diaptomus nevadensis. Proc. Natl. Acad. Sci.* **73:** 971–974.

Halanych, K. M., and Y. Passamaneck. 2001. A brief review of metazoan phylogeny and future prospects in Hox-research. *Am. Zool.* (In press).

Hamner, W. M. 1996. Predation, cover, and convergent evolution in epipelagic oceans. Pp. 17–37 in *Zooplankton: Sensory Ecology and Physiology,* P. H. Lenz, D. K. Hartline, J. E. Purcell, and D. L. Macmillan, eds. Overseas Publishers Association, Amsterdam.

Hansson, L. 2000. Induced pigmentation in zooplankton: a trade-off between threats from predation and ultraviolet radiation. *Proc. R. Soc. Lond. B.* **267:** 2327–2331.

Harbison, G. R., L. P. Madin, and N. R. Swanberg. 1978. On the natural history and distribution of oceanic ctenophores. *Deep-Sea Res.* **25:** 233–256.

Hardy, A. C. 1956. *The Open Sea, Its Natural History: The World of Plankton.* Houghton Mifflin, Cambridge, MA.

Hart, M. W., R. L. Miller, and L. P. Madin. 1994. Form and feeding mechanism of a living *Planctosphaera pelagica* (phylum Hemichordata). *Mar. Biol.* **120:** 521–533.

Hemmings, C. C. 1975. The visibility of objects underwater. Pp. 359–374 in *Light as an Ecological Factor,* G. C. Evans, R. Bainbridge, and O. Rackhman, eds. Blackwell, Oxford.

Hernandez-Nicaise, M-L. 1991. Ctenophora. Pp. 359–418 in *Microscopic Anatomy of the Invertebrates Volume II: Placozoa, Porifera, Cnidaria, and Ctenophora,* F. W. Harrison and J. A. Westfall, eds. John Wiley, New York.

Herring, P. J. 1967. The pigments of plankton at the sea surface. *Symp. Zool. Soc. Lond.* **19:** 215–235.

Herring, P. J. 1994. Reflective systems in aquatic animals. *Comp. Biochem. Physiol. A* **109:** 513–546.

Herring, P. J., and H. S. J. Roe. 1988. The photoecology of pelagic oceanic decapods. *Symp. Zool. Soc. Lond.* **59:** 263–290.

Hessen, D. O. 1985. Selective zooplankton predation by pre-adult roach (*Rutilus rutilus*): the size-selective hypothesis versus the visibility-selective hypothesis. *Hydrobiologia* **124:** 73–79.

Hester, F. J. 1968. Visual contrast thresholds of the goldfish (*Carassius auratus*). *Vision Res.* **8:** 1315–1335.

Hirose, E., S. Kimura, T. Itoh, and J. Nishikawa. 1999. Tunic morphology and cellulosic components of pyrosomas, doliolids, and salps (Thaliacea, Urochordata). *Biol. Bull.* **196:** 113–120.

Hobaek, A., and H. G. Wolf. 1991. Ecological genetics of Norwegian *Daphnia.* 2. Distribution of *Daphnia longispina* genotypes in relation to short-wave radiation and water colour. *Hydrobiologia* **225:** 229–243.

Ijema, I., and S. Ikeda. 1902. Notes on a specimen of *Amphitretus* obtained in the Sagami Sea. *Annot. Zool. Jpn.* **4:** 5–101.

Jacobs, G. H. 1992. Ultraviolet vision in vertebrates. *Am. Zool.* **32:** 544–554.

Janssen, J. 1981. Searching for zooplankton just outside Snell's window. *Limnol. Oceanogr.* **26:** 1168–1171.

Jerlov, N. G. 1976. *Marine Optics.* Elsevier, New York.

Johnsen, S. 2002. Cryptic and conspicuous coloration in the pelagic environment. *Proc. R. Soc. Lond. B* **269**(1). (In press).

Johnsen, S., and E. A. Widder. 1998. Transparency and visibility of gelatinous zooplankton from the northwestern Atlantic and Gulf of Mexico. *Biol. Bull.* **195:** 337–348.

Johnsen, S., and E. A. Widder. 1999. The physical basis of transparency in biological tissue: ultrastructure and the minimization of light scattering. *J. Theor. Biol.* **199:** 181–198.

Johnsen, S., and E. A. Widder. 2001. Ultraviolet absorption in transparent zooplankton and its implications for depth distribution and visual predation. *Mar. Biol.* **138:** 717–730.

Johnson, G. D., and A. C. Gill. 1995. Perches and their allies. Pp. 181–196 in *Encyclopedia of Fishes,* J. R. Paxton and W. N. Eschemeyer, eds. Academic Press, New York.

Joubin, L. 1918. Études preliminaries sur les Cephalopodes recueillis au cours des croisieres de S. A. S. le Prince de Monaco 6e Note: *Vitreledonella richardi* Joubin. *Bull. Inst. Oceanogr.* **340:** 1–40.

Karentz, D., F. S. McEuen, M. C. Land, and W. C. Dunlap. 1991. Survey of mycosporine-like amino acid compounds in Antarctic marine organisms: potential protection from ultraviolet exposure. *Mar. Biol.* **108:** 157–166.

Kerfoot, W. C. 1982. A question of taste: crypsis and warning coloration in freshwater zooplankton communities. *Ecology* **63:** 538–554.

Kerker, M. 1969. *The Scattering of Light and Other Electromagnetic Radiation.* Academic Press, New York.

Kramp, P. L. 1959. The hydromedusae of the Atlantic Ocean and adjacent waters. *Dana-Rep.* **46:** 1–283.

Lalli, C. M., and R. W. Gilmer. 1989. *Pelagic Snails.* Stanford University Press, Palo Alto, CA.

Land, M. F. 1981. Optics of the eyes of *Phronima* and other deep-sea animals. *J. Comp. Physiol. A* **145:** 209–226.

Land, M. F. 1992. A note on the elongated eye of the octopus *Vitreledonella richardi. J. Mar. Biol. Assoc. UK* **72:** 89–92.

Langsdale, J. R. M. 1993. Developmental changes in the opacity of larval herring, *Clupea harengus*, and their implications for vulnerability to predation. *J. Mar. Biol. Assoc. UK* **73:** 225–232.

Larson, R. J. 1976. Cubomedusa: feeding, functional morphology, behavior and phylogenetic position. Pp. 237–246 in *Coelenterate Ecology and Behavior*, G. O. Mackie, ed. Plenum Press, New York.

Laval, P. 1980. Hyperiid crustaceans as parasitoids associated with gelatinous zooplankton. *Oceanogr. Mar. Biol.* **18:** 11–56.

Loew, E. R., and W. N. McFarland. 1990. The underwater visual environment. Pp. 1–44 in *The Visual System of Fish*, R. H. Douglas and M. B. A. Djamgoz, eds. Chapman and Hall, New York.

Loew, E. R., W. N. McFarland, E. L. Mills, and D. Hunter. 1993. A chromatic action spectrum for planktonic predation by juvenile yellow perch, *Perca flavescens. Can. J. Zool.* **71:** 384–386.

Loew, E. R., R. A. McAlary, and W. N. McFarland. 1996. Ultraviolet visual sensitivity in the larvae of two species of marine atherinid fishes. Pp. 195–210 in *Zooplankton: Sensory Ecology and Physiology*, P. H. Lenz, D. K. Hartline, J. E. Purcell, and D. L. Macmillan, eds. Gordon and Breach, Amsterdam.

Losey, G. S., T. W. Cronin, T. H. Goldsmith, D. Hyde, N. J. Marshall, and W. N. McFarland. 1999. The UV visual world of fishes: a review. *J. Fish. Biol.* **54:** 921–943.

Luecke, C., and W. J. O'Brien. 1981. Phototoxicity and fish predation: selective factors in color morphs in *Heterocope. Limnol. Oceanogr.* **26:** 454–460.

Luecke, C., and W. J. O'Brien. 1983. Photoprotective pigments in a pond morph of *Daphnia middendorffiana. Arctic* **36:** 365–368.

Lythgoe, J. N. 1979. *The Ecology of Vision.* Clarendon Press, Oxford.

Lythgoe, J. N., and C. C. Hemmings. 1967. Polarized light and underwater vision. *Nature* **213:** 893–894.

Mackie, G. O. 1996. Defensive strategies in planktonic coelenterates. Pp. 435–446 in *Zooplankton: Sensory Ecology and Physiology*, P. H. Lenz, D. K. Hartline, J. E. Purcell, and D. L. Macmillan, eds. Overseas Publishers Association, Amsterdam.

Madin, L. P. 1988. Feeding behavior of tentaculate predators: in situ observations and a conceptual model. *Bull. Mar. Sci.* **43:** 413–429.

Madin, L. P., and G. R. Harbison. 1977. The associations of Amphipoda Hyperiidea with gelatinous zooplankton—I. Associations with Salpidae. *Deep-Sea Res.* **24:** 449–463.

Madin, L. P., J. E. Purcell, and C. B. Miller. 1997. Abundance and grazing effects of *Cyclosalpa bakeri* in the subarctic Pacific. *Mar. Ecol. Prog. Ser.* **157:** 175–183.

Marshall, N. J., and J. Oberwinkler. 1999. The colourful world of mantis shrimp. *Nature* **401:** 873–874.

Matsumoto, G. I. 1995. Observations on the anatomy and behavior of the cubozoan *Carybdea rastonii* Haacke. *Mar. Freshw. Behav. Physiol.* **26:** 139–148.

May, R. M. 1994. Biological diversity: differences between land and sea. *Philos. Trans. R. Soc. Lond. B.* **343:** 105–111.

Mayer, A. G. 1910. *Medusae of the World III: The Scyphomedusae.* Carnegie Institution of Washington, Washington, DC.

Mayer, A. G. 1912. *Ctenophores of the Atlantic Coast of North America.* Carnegie Institution of Washington, Washington, DC.

McFall-Ngai, M. J. 1990. Crypsis in the pelagic environment. *Am. Zool.* **30:** 175–188.

McFarland, W. N., and E. R. Loew. 1994. Ultraviolet visual pigments in marine fishes of the family Pomacentridae. *Vision Res.* **34:** 1393–1396.

McHugh, D. 2000. Molecular phylogeny of the Annelida. *Can. J. Zool.* **78:** 1873–1884.

Mensinger, A. F., and J. F. Case. 1997. Luminescent properties of fishes from nearshore California basins. *J. Exp. Mar. Biol. Ecol.* **210:** 75–90.

Mertens, L. E. 1970. *In-Water Photography: Theory and Practice.* John Wiley, New York.

Meyer, R. A. 1979. Light scattering from biological cells: dependence of backscatter radiation on membrane thickness and refractive index. *Appl. Opt.* **18:** 585–588.

Meyer-Rochow, V. B. 1974. Leptocephali and other transparent fish larvae from the south-eastern Atlantic ocean. *Zool. Anz.* **192:** 240–251.

Meyer-Rochow, V. B. 1997. Wenn Unsichtbares sichtbar wird: durchsichtige Tiere—transparente Gewebe. *Nat. Mus.* **127:** 121–127.

Miller, J. E., and D. L. Pawson. 1990. Swimming sea cucumbers (Echinodermata: Holothuroidea): a survey, with analysis of swimming behavior in four bathyl species. *Smithson. Contrib. Mar. Sci.* **35:** 1–18.

Miller, W. H. 1979. Intraocular filters. Pp. 69–144 in *Handbook of Sensory Physiology*, Vol. 7/6A, H. Autrum, ed. Springer, New York.

Miner, G. B., S. G. Morgan, and J. R. Hoffman. 2000. Postlarval chromatophores as an adaptation to ultraviolet radiation. *J. Exp. Mar. Biol. Ecol.* **249:** 235–248.

Morgan, S. G., and J. H. Christy. 1996. Survival of marine larvae under the countervailing selective pressures of photodamage and predation. *Limnol. Oceanogr.* **41:** 498–504.

Munz, W. R. A. 1990. Stimulus, environment and vision in fishes. Pp. 491–511 in *The Visual System of Fish*, R. H. Douglas and M. B. A. Djamgoz, eds. Chapman and Hall, New York.

Munz, F. W., and W. N. McFarland. 1977. Evolutionary adaptations of fishes to the photic environment. Pp. 194–274 in *The Visual System in Vertebrates*, F. Crescitelli, ed. Springer-Verlag, New York.

Nelson, J. S. 1994. *Fishes of the World.* John Wiley, New York.

Nesis, K. N. 1982. *Cephalopods of the World.* T. F. H. Publications, Neptune City, NJ.

Nilsson, D. E. 1982. The transparent compound eye of *Hyperia* (Crustacea): examination with a new method for analysis of refractive index gradients. *J. Comp. Physiol. A* **147:** 339–349.

O'Brien, W. J., and D. Kettle. 1979. Helmets and invisible armor: structures reducing predation from tactile and visual planktivores. *Ecology* **60:** 287–294.

Pages, F., M. G. White, and P. G. Rodhouse. 1996. Abundance of gelatinous carnivores in the nekton community of the Antarctic polar frontal zone in summer 1994. *Mar. Ecol. Prog. Ser.* **141:** 139–147.

Papageorgis, C. 1975. Mimicry in neotropical butterflies. *Am. Sci.* **63:** 522–532.

Parker, A. R., Z. Hegedus, and R. A. Watts. 1998. Solar-absorber antireflector on the eye of an Eocene fly (45 Ma). *Proc. R. Soc. Lond. B* **265:** 811–815.

Pfeiler, E. 1986. Towards an explanation of the developmental strategy in leptocephalous larvae of marine teleost fishes. *Environ. Biol. Fishes* **15:** 3–13.

Philipson, B. 1973. Changes in the lens related to the reduction of transparency. *Exp. Eye Res.* **16:** 29–39.

Podar, M., S. H. D. Haddock, M. L. Sogin, and G. R. Harbison. 2001. A molecular phylogenetic framework for the phylum Ctenophora using 18S rRNA genes. *Mol. Biol. Evol.* (In press).

Pugh, P. R. 1983. Benthic Siphonophores: a review of the family Rhodaliidae (Siphonophora, Physonectae). *Philos. Trans. R. Soc. Lond. B* **301:** 165–300.

Purcell, J. E. 1980. Influence of siphonophore behavior on their natural diets; evidence for aggressive mimicry. *Science* **209:** 1045–1047.

Purcell, J. E. 1981. Selective predation and caloric consumption by the siphonophore *Rosacea cymbiformis* in nature. *Mar. Biol.* **63:** 283–294.

Purcell, J. E. 1997. Pelagic cnidarians and ctenophores as predators: selective predation, feeding rates and effects on prey populations. *Ann. Inst. Oceanogr.* **73:** 125–137.

Ross, K. F. A. 1967. *Phase Contrast and Interference Microscopy*. Edward Arnold, London.

Russell, F. R. S. 1953. *The Medusae of the British Isles.* Cambridge University Press, Cambridge.

Russell, F. R. S. 1970. *The Medusae of the British Isles II: Pelagic Scyphozoa.* Cambridge University Press, Cambridge.

Sanamyan, K. 1998. Ascidians from the north-western Pacific region. 5. Phlebobranchia. *Ophelia* **49:** 97–116.

Sandstroem, A. 1999. Visual ecology of fish—a review with special reference to percids. *Fiskeriverk Rapp.* **2:** 45–80.

Scheltema, A. H. 1993. Aplacophora as progenetic aculiferans and the coelomate origin of mollusks as the sister taxon of Sipuncula. *Biol. Bull.* **184:** 57–78.

Seapy, R. R., and R. E. Young. 1986. Concealment in epipelagic pterotracheid heteropods (Gastropoda) and cranchiid squids (Cephalopoda). *J. Zool. Lond.* **210:** 137–147.

Shashar, N., R. T. Hanlon, and A. Petz. 1998. Polarization vision helps detect transparent prey. *Nature* **393:** 222–223.

Shinn, G. L. 1997. Chaetognatha. Pp. 103–220 in *Microscopic Anatomy of Invertebrates, Volume 15: Hemichordata, Chaetognatha, and the Invertebrate Chordates,* F. W. Harrison and E. E. Ruppert, eds. John Wiley, New York.

Smith, R. C., B. B. Prézelin, K. S. Baker, R. R. Bidigare, N. P. Boucher, T. Coley, D. Karentz, S. MacIntyre, H. A. Matlick, D. Menzies, M. Ondrusek, Z. Wan, and K. J. Waters. 1992. Ozone depletion: ultraviolet radiation and phytoplankton biology in Antarctic waters. *Science* **255:** 952–959.

Solomon, S. 1990. Progress toward a quantitative understanding of Antarctic ozone depletion. *Nature* **347:** 347–354.

Stolarski, R. S., R. Bojkov, L. Bishop, C. Zerefos, J. Staehelin, and J. Zawodny. 1992. Measured trends in stratospheric ozone. *Science* **256:** 342–349.

Swalla, B. J., C. B. Cameron, L. S. Corley, and J. R. Garey. 2000. Urochordates are monophyletic within the deuterostomes. *Syst. Biol.* **49:** 52–64.

Tardieu, A., and M. Delaye. 1988. Eye lens proteins and transparency: from light transmission theory to solution x-ray structural analysis. *Annu. Rev. Biophys. Biophys. Chem.* **17:** 47–70.

Thetmeyer, H., and U. Kils. 1995. To see and not be seen: the visibility of predator and prey with respect to feeding behavior. *Mar. Ecol. Prog. Ser.* **126:** 1–8.

Thiele, E. S. 1998. Light scattering by complex microstructures in the resonant regime. Ph.D. dissertation, University of Pennsylvania.

Thorpe, A., R. H. Douglas, and R. J. W. Truscott. 1993. Spectral transmission and short-wave absorbing pigments in the fish lens—I. Phylogenetic distribution and identity. *Vision Res.* **33:** 289–300.

Totton, A. K. 1965. *A Synopsis of the Siphonophora.* British Museum, London.

Tovee, M. J. 1995. Ultra-violet photoreceptors in the animal kingdom: their distribution and function. *Trends Ecol. Evol.* **10:** 455–460.

Tsuda, A., H. Saito, and T. Hirose. 1998. Effect of gut content on the vulnerability of copepods to visual predation. *Limnol. Oceanogr.* **43:** 1944–1947.

Uschakov, P. V. 1972. *Fauna of the U.S.S.R. Polychaetes. Vol. 1. Polychaetes of the Suborder Phyllodociformia of the Polar Basin and the Northwestern Part of the Pacific: Families Phyllodocidae, Alciopidae, Tomopteridae, Typhloscoleicidae, and Lacydoniidae. Akademiya NAUK SSSR,* New Series 102, B. E. Bykhorskii, ed. [Translated from Russian by the Israel Program for Scientific Translations, Jerusalem, 1974.]

Utne-Palm, A. C. 1999. The effect of prey mobility, prey contrast, turbidity and spectral composition on the reaction distance of *Gobiusculus flavescens* to its planktonic prey. *J. Fish Biol.* **54:** 1244–1258.

Vaezy, S., and J. I. Clark. 1994. Quantitative analysis of the microstructure of the human cornea and sclera using 2-D Fourier methods. *J. Microsc.* **175:** 93–99.

Van der Spoel, S. 1976. *Pseudothecosomata, Gymnosomata* and *Heteropoda.* Bohn, Scheltema and Holkema, Utrecht.

Vinogradov, M. E., A. F. Volkov, and T. N. Semanova. 1996. *Hyperiid Amphipods (Amphipoda, Hyperiidea) of the World Oceans.* Smithsonian Institution Libraries, Washington, DC.

Von W. Kjerschow-Agersborg, H. P. 1921. Contribution to the knowledge of the nudibranchiate mollusk, *Melibe leonina* (Gould). *Am. Nat.* **55:** 222–253.

Voss, N. A. 1980. A generic revision of the Cranchiidae (Cephalopoda; Oegopsida). *Bull. Mar. Sci.* **30:** 365–412.

Wald, G., and J. M. Krainin. 1963. The median eye of *Limulus:* an ultraviolet photoreceptor. *Proc. Natl. Acad. Sci.* **50:** 1011–1017.

Wald, G., and S. Rayport. 1977. Vision in annelid worms. *Science* **196:** 1434–1439.

Warner, J. A., M. I. Latz, and J. F. Case. 1979. Cryptic bioluminescence in a midwater shrimp. *Science* **203:** 1109–1110.

Waterman, T. H. 1981. Polarization sensitivity. Pp. 281–469 in *Handbook of Sensory Physiology,* Vol. 7/6B, H. Autrum, ed. Springer, New York.

Weber, C., and V. Schmid. 1985. The fibrous system in the extracellular matrix of hydromedusae. *Tissue Cell* **17:** 811–822.

Widder, E. A., M. I. Latz, and J. F. Case. 1983. Marine bioluminescence spectra measured with an optical multichannel detection system. *Biol. Bull.* **165:** 791–810.

Wilson, S. J., and M. C. Hutley. 1982. The optical properties of 'moth eye' antireflection surfaces. *Optica Acta* **7:** 993–1009.

Wingstrand, K. G. 1985. On the anatomy and relationships of Recent Monoplacophora. *Galathea Rep.* **16:** 7–94.

Wright, D. I., and W. J. O'Brien. 1982. Differential location of *Chaoborus* larvae and *Daphnia* by fish: the importance of motion and visible size. *Am. Midl. Nat.* **108:** 68–73.

Wrobel, D., and C. Mills. 1998. *Pacific Coast Pelagic Invertebrates: A Guide to Common Gelatinous Animals.* Sea Challengers, Monterey Bay Aquarium, Monterey Bay, CA.

Yoshida, A., M. Motoyama, A. Kosaku, and K. Miyamoto. 1997. Antireflective nanoprotuberance array in the transparent wing of a hawkmoth, *Cephanodoes hylas. Zool. Sci.* **14:** 737–741.

Young, R. E., M. Vecchione, and D. T. Donovan. 1998. The evolution of coleoid cephalopods and their present biodiversity and ecology. *S. Afr. J. Mar. Sci.* **20:** 393–420.

Zaitsev, Y. P. 1970. *Marine Neustonology.* Keter Press, Jerusalem.

Zaret, T. M. 1972. Predators, invisible prey, and the nature of polymorphisms in the Cladocera (Class Crustacea). *Limnol. Oceanogr.* **17:** 171–184.

Zaret, T. M. 1981. Lateral compression and visibility in cladocerans. *Limnol. Oceanogr.* **26:** 965–970.

Zaret, T. M., and W. C. Kerfoot. 1975. Fish predation on *Bosmina longirostrus:* body size selection versus visibility selection. *Ecology* **56:** 232–237.