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Transparency and Visibility of Gelatinous Zooplankton from the Northwestern Atlantic and Gulf of Mexico

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Abstract. Transparency measurements (at 400 to 700 nm) were made on living specimens of 29 common species of gelatinous zooplankton from the Northwestern Atlantic Ocean and Gulf of Mexico. Percent transparency ranged from 91% for the hydromedusa *Sibogota typa* to 0.51% for the pteropod *Clione limacina.* Percent transparency was linearly and positively correlated with wavelength, with slopes of the regression lines (normalized to the percent transparency at 480 nm) ranging from 0.027%/nm for *Sibogota typa* to 0.51%/nm for the ctenophore *Mnemiopsis macrydi* (average 0.17 ± 0.019%/nm). There was no significant correlation between the percent transparency of an animal and its daytime depth distribution. The relationship between percent transparency and sighting distance when viewed from below was modeled and showed that, due to the increase of the minimum contrast threshold for object detection at lower light levels, the usefulness of transparency as camouflage increases dramatically with depth. A preliminary account of these results was presented by the authors at the fourteenth meeting of the Ocean Optics Society in November 1998.

Introduction

Transparency is an important, but understudied, characteristic of many oceanic zooplankton. A large percentage of oceanic zooplankton are transparent, some achieving almost complete invisibility (Davis, 1955; Hardy, 1956; McFall-Ngai, 1990), and it is generally assumed that transparency is an important method of camouflage from visual predators and prey in the optically featureless open-ocean environment, particularly in the euphotic region (reviewed in McFall-Ngai, 1990; Hamner, 1996). Indeed, it is difficult to explain the prevalence of transparency in epipelagic and mesopelagic environments and its relative rarity in bathypelagic and coastal environments (McFall-Ngai, 1990) without assuming that it functions as a form of camouflage. Some degree of transparency is found in almost all oceanic zooplankton that are not camouflaged by small size or mirrored surfaces, or protected by fast swimming speeds or chemical defenses. Although these transparent, mostly gelatinous animals are poorly represented in trawls, research using blue-water diving and submersibles has shown they are extremely diverse and abundant (Hamner *et al.,* 1975). However, despite the prevalence and presumed ecological importance of transparency, little work has been done in this area (McFall-Ngai, 1990). In particular, few measurements of the degree of transparency of these animals have been made (Greze, 1963, 1964; Chapman, 1976a, b). This information could help answer several important questions related to the ecological function and importance of transparency. What is the relationship between percent transparency and wavelength? Are animals in shallow water more or less transparent than animals at depth? For a given visual system, what is the maximum distance at which various transparent animals are still detectable?

In this study, 29 species of oceanic zooplankton from seven phyla (Cnidaria, Ctenophora, Annelida, Mollusca, Crustacea, Chaetognatha, and Chordata) were collected from six sites in the Northwestern Atlantic Ocean and Gulf of Mexico. The degree of transparency of various tissues of the animals from different depths was measured at wavelengths ranging from 400 to 700 nm. In addition, the relationship between an animal's degree of transparency and its sighting distance when viewed from below was modeled.

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A preliminary account of these experiments was presented at the fourteenth meeting of the ocean optic society in November 1998 (Johnsen and Widder, in press).

Materials and Methods

Source of animals and description of tissues examined

Animals were obtained from the following six locations: Georges Bank; Oceanographer Canyon (on the southern edge of Georges Bank); Tongue of the Ocean (Bahamas); eastern Gulf of Mexico; Panacea, Florida; and Woods Hole, Massachusetts. Animals from the first four locations were obtained during cruises of the RVs *Oceanus* (April 1998), *Edwin Link* (September 1997), *Seward Johnson* (February 1998), and *Pelican* (June 1998) respectively. The animals obtained from Georges Bank were collected using a MOCNESS net system (five nets, 10-m^2 opening, 3-mm mesh). About half the animals obtained from Oceanographer Canyon were collected at depth using the *Johnson Sea-Link* (*JSL*) research submersible. These animals were captured in 1-liter clear acrylic cylinders with hydraulically activated, sliding lids. The remaining animals from Oceanographer Canyon were collected using an opening/closing Tucker trawl (4.3-m^2 opening, $^1/_4$-inch knotless nylon mesh) fitted with a thermally insulated collecting container that could be closed at depth. The animals collected from Tongue of the Ocean were caught in a surface plankton net (0.2-m^2 opening, 335-μm mesh). Animals from the eastern Gulf of Mexico were collected either with the above-mentioned Tucker trawl or in jars by divers using blue-water diving techniques (Hamner, 1975). Animals from Panacea and Woods Hole were obtained from Gulf Specimen Marine Supply Inc. and the Aquatic Resources Division at The Marine Biological Laboratory respectively. Table I lists the animals collected, their dimensions, and their source and method of collection. The table also lists the conditions of the animals at the times of measurement. Animals listed as "good" were intact and mobile and appeared healthy. Animals listed as "unknown" appeared to be healthy and intact but showed no movement (one of these, *Pyrosoma atlanticum,* generally makes no easily observable movements). Animals collected on cruises were measured within an hour of collection. Animals obtained from the two marine specimen supply companies were measured upon arrival.

Several animals had large regions of obviously different transparency. Therefore, several tissues were measured from these animals. Mesoglea measurements were taken through portions of mesoglea that had no other visible structure. Comb-row measurements in ctenophores were taken through portions of the mesoglea containing one comb row. Lobe measurements in *Bolinopsis infundibulum* were taken through the mesoglea and one of the large oral lobes. Siphosome measurements in *Agalma okeni* were taken through the siphosome of the animal. Center measurements in *Bathocyroe fosteri* were taken through the translucent region surrounding the gut. Canal measurements in *Sibogita typa* were taken through the mesoglea and a number of the radial canals. Body measurements were taken through the thickest unpigmented portion of the body. All measurements were taken along an axis perpendicular to the longest axis of the animal. Therefore, ctenophores were measured perpendicular to the oral-aboral axis; hydromeduse were measured perpendicular to the plane of the bell; molluscs, tunicates, crustaceans, and annelids were measured perpendicular to the anterior-posterior axis; etc.

Apparatus and procedure for measurement of transparency

Transparency was measured with an apparatus (Fig. 1) similar to those used for measuring the wavelength dependence of light transmission in human lenses and corneas (Farrell *et al.,* 1973). The light source was a stabilized tungsten halogen source (LSI, Ocean Optics Inc.) coupled to a 1-mm fiber optic and a 200-μm precision pinhole. The beam was collimated with an achromatic triplet lens and reduced to a diameter of 3 mm with an iris diaphragm. The beam passed through the specimen (held in a glass cuvette) and was focused by an achromatic lens onto a fiber-optic cable (diameter 2 mm) coupled to the detector of an optical multichannel analyzer (OMA-detector model 1420, detector interface model 1461, EG&G Princeton Applied Research). The detector was wavelength calibrated using a low-pressure mercury spectrum lamp (Model 6047, Oriel Inc.). For further details on the theory of operation and calibration of the OMA detector, see Widder *et al.* (1983). Due to space restrictions on the RVs *Oceanus* and *Pelican,* the OMA was replaced with a more compact multichannel spectrometer (PS1000, Ocean Optics Inc.). An iris diaphragm was placed in front of the collection optics to limit the angle of acceptance of scattered light from the sample. The diaphragm was set at a diameter of 3.5 mm, the minimum aperture required to pass the complete uninterrupted beam. Since the base of the sample was 0.07 m from the collection aperture, the detector received forward-scattered light within a cone of half-angle of 1.05° (angle equals arctan (r/d), where r is the radius of the aperture and d is the distance from the sample to the aperture. Angle is corrected for refraction at the air-water surface in the cuvette). Because the collection optics must always have a finite aperture, the detector always collects forward-scattered light in addition to directly transmitted light. There is no standard aperture angle for measuring transmitted light, though a half-angle of approximately 1° is common (Mertens, 1970; Farrell *et al.,* 1973). The angle used was the minimum possible given the problems caused by ship motion. The entire apparatus was placed in a dark room on the ship to eliminate stray light.

Table I

Dimensions, source, and condition of the animals used for transparency measurements

Animal	Specimens (no.)	Optical thickness (mm)	Length* (mm)	Collection		Condition
				Site†	Method‡	
Cnidaria						
Agalma okeni§	8	16 ± 1.2	42 ± 2.5	OC/EGM	T	good/unknown
Athorybia rosacea	1	10	11	EGM	D	good
Cyclocanna welshi	1	15	50	OC	S	good
Halistemma cupulifera§	3	8 ± 0.58	42 ± 1.7	EGM	T	good/unknown
Nemopsis bachei	4	7.3 ± 0.25	7.3 ± 0.25	PFL		good
Orchistoma pileus	4	18 ± 1.7	29 ± 3.3	EGM	D	good
Physophora hydrostatica	1	29	45	GB	T	good
Sibogita typa	1	24	24	OC	T	unknown
Ctenophora						
Bathocyroe fosteri	2	24 ± 4.0	38 ± 2.5	OC	S	good
Beroe cucumis	4	10 ± 0.0	14 ± 0.0	GB	T	good
Bolinopsis infundibulum	2	22 ± 2.0	83 ± 2.5	OC	S	good
Hormiphora sp.	3	17 ± 1.3	35 ± 6.7	EGM	T	good
Mnemiopsis macrydi	11	13 ± 1.0	25 ± 1.3	PFL		good
Ocyropsis maculata	1	10	30	TO	T	good
Pleurobrachia bachei	10	16 ± 0.63	18 ± 0.55	WH		good
Annelida						
Tomopteris sp.	2	3.0 ± 1.0	30 ± 9.5	GB	T	good
Mollusca						
Carinaria lamarcki	4	11 ± 0.88	43 ± 1.7	EGM	T/D	good
Clinoe limacina	1	4	23	OC	T	good
Corolla spectabilis	5	39 ± 6.4	13 ± 2.9	OC/EGM	S/D	good
Phylliroe atlantica	4	1.9 ± 0.13	25 ± 2.0	EGM	D	good
Pterotrachea coronata	4	8.0 ± 1.2	85 ± 4.6	OC/EGM	S/D/T	good
Crustacea						
Cystosoma cystosoma	2	7.5 ± 0.50	53 ± 6.5	EGM	T	good
Chaetognatha						
Sagitta hexaptera	8	3 ± 0.19	45 ± 2.5	GB	T	good/unknown
Sagitta maxima	1	4	55	OC	T	good
Chordata						
Cyclosalpa affinis#	1	35	33	EGM	D	good
Pegea conferedata	4	20 ± 0.48	39 ± 1.9	TO	T	good
Pyrosoma atlanticum	5	10 ± 1.2	32 ± 4.9	OC/EGM	T/D	unknown
Salpa cylindrica	8	16 ± 0.90	38 ± 1.5	EGM	D	good
Salpa maxima	1	13	30	TO	T	good

* Measured along the axis of greatest length.

† OC, Oceanographer Canyon; GB, Georges Bank; EGM, Eastern Gulf of Mexico; PFL, Panacea, FL; WH, Woods Hole; TO, Tongue of the Ocean.

‡ T, trawl; S, submersible; D, scuba diving.

§ *Agalma* and *Halistemma* (physonect siphonophores) lacked several nectophores and bracts, but still exhibited movement and high transparency.

The salp *Cyclosalpa affinis* is an aggregate of seven individuals.

Each animal to be measured was placed in an appropriately sized cuvette. The water level in the cuvette was slightly greater (<2 mm) than the thickness of the animal. A reference measurement of the water was taken, followed by 4–10 (usually 5) measurements of a given tissue of the animal. Each measurement consisted of 3000 consecutive 0.1-s exposures. The exposures were averaged to reduce noise due to ship motion and other sources. The animal was moved slightly between measurements to get an average value for the tissue measured. Transmission values were calculated by dividing the intensity of the beam after it passed through the tissue by the intensity of the reference beam (that had passed through an equivalent distance of water). Although both the OMA and PS1000 detectors were calibrated from 350 to 700 nm, the values from 350 to 400 nm were unreliable due to the small output of the tungsten light source in this region. Therefore, only values from 400 to 700 nm are discussed.

The repeatability of the measurements was confirmed by measuring the transmission of a sample of water 15 times and then calculating the standard error. The standard error ranged from 1.00% of the mean value at 700 nm to 1.25% of the mean value at 400 nm.

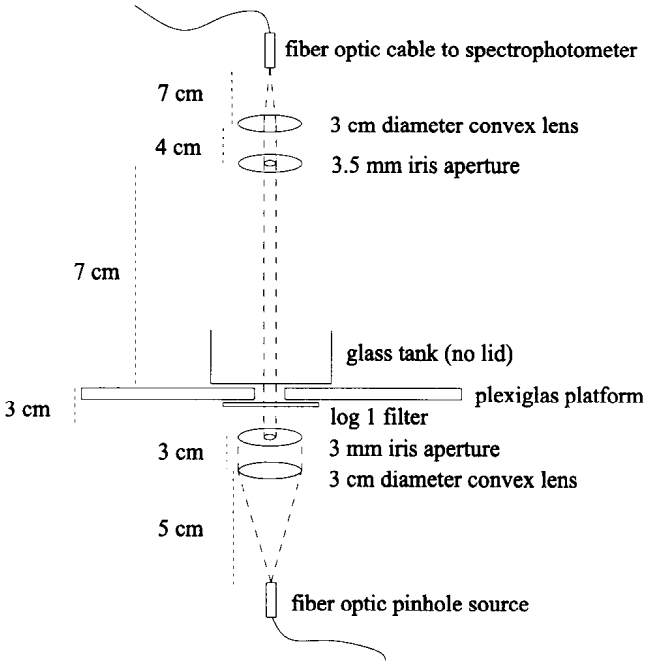

Figure 1. Diagram of the apparatus used to measure transparency.

Calculating the effect of tissue transmission spectra on the spectrum of downwelling light

Unless the percent transmission of a tissue is constant with respect to wavelength, the tissue will have an effect on the spectrum of the downwelling light that passes through it. In general, percent transparency was positively and linearly proportional to wavelength (see *Results*). Hereafter, the slope of the regression of percent transparency on wavelength is referred to as the T-W slope. The alteration of the spectrum of downwelling light after passing through materials with different T-W slopes was calculated. The downwelling spectrum was taken in Oceanographer Canyon at 260 m and 60 m, using the PS1000 multichannel spectrometer. These two depths were chosen because they represent a near-surface and an asymptotic light field. An underwater light field is referred to as asymptotic when the position of the sun has no effect on the light field's spatial characteristics (Jerlov, 1976). Light was transmitted to the PS1000, operated from the back dive chamber of the *JSL* submersible, via a 1-mm fiber-optic through-hull penetrator. To calculate the effects of tissues with different T-W slopes on the downwelling light spectrum, a spectrum with a given slope was multiplied by the measured downwelling light spectrum and the resultant spectrum was divided by its peak value. To factor out the absolute value of the T-W slope, the slopes used were normalized by percent transmission at 480 nm. Therefore, a normalized T-W slope of 1%/nm describes a linear transmission spectrum that has a value 1% greater than the percent transmission at 480 nm for every nanometer greater than 480 (*e.g.*, if $T_{480} = 30\%$, $T_{490} = 30\% + [10 \times (1\% \times 30\%)] = 33\%$).

Modeling of relationship between percent transparency and sighting distance

The visibility of an object depends upon its contrast with the background. Contrast is defined as $(L_o - L_b)/L_b$, where L_o is the radiance of the background (Mertens, 1970; Jerlov, 1976). Contrast values range from -1 to ∞. An object of zero radiance on a luminous background has a contrast value of -1. A luminous object on a background of zero radiance (*e.g.*, a bioluminescent source in the deep ocean) has a contrast value of ∞. An object whose radiance matches the radiance of the background has a contrast value of zero. In the asymptotic light field that most of the collected animals commonly inhabit, the upward and horizontal radiances are only a small fraction of the downward radiance (*ca.* 0.5% and 3% respectively), and downward irradiance approximates vertical downward radiance (Denton, 1990). Therefore, animals are most visible when viewed from below. Since $(L_o - L_b)/L_b = L_o/L_b - 1$, and $L_o/L_b = T/100$ (where T is the percent transparency of a given object), the contrast of an animal viewed from below ranges from 0 to -1 and is equal to $T/100 - 1$.

The absolute value of contrast decreases exponentially with distance. When viewed from below, the attenuation coefficient (of contrast) is equal to the beam attenuation coefficient minus the diffuse attenuation coefficient of the water (Mertens, 1970; Jerlov, 1976); *i.e.*,

$$C = C_o \times e^{-(c-K)d}, \qquad \text{(Equation 1)}$$

where C is the apparent contrast at distance d, C_o is the inherent contrast of the viewed object (contrast at zero distance, $C_o = T/100 - 1$) of the object, and c and K are the beam and diffuse attenuation coefficients of the water. One can determine the maximum distance at which an object is still detectable by setting C equal to $C_{\min}$ (the minimum contrast threshold for object detection for a given visual system) and solving equation (1) for d. This gives

$$d = \ln(C_{\min}/C_o)/(c - K)$$
$$= \ln(C_{\min}/(T/100 - 1))/(c - K). \qquad \text{(Equation 2)}$$

The sighting range, d_{opaque}, of an opaque object ($T = 0$) is

$$d_{\text{opaque}} = \ln(C_{\min}/(0/100 - 1))/(c - K)$$
$$= \ln(-C_{\min})/(c - K). \qquad \text{(Equation 3)}$$

By dividing equation (2) by equation (3), one can factor out the two attenuation coefficients and express the sighting distance as a fraction of the sighting distance of an opaque object of the same size and shape in the same water and light field. This gives

$$d/d_{\text{opaque}} = \ln(C_{\min}/(T/100 - 1))/\ln(-C_{\min}).$$

This ratio gives an estimate of the advantage of a given percent transparency over opacity for a prey item attempting to hide from a visual predator with a given

minimum contrast threshold (the argument, of course, is identical for a predator attempting to hide from a visual prey item). A ratio of zero implies that the object cannot be seen at any distance and can only be detected by nonvisual means. A ratio near one implies that the object is detected at a distance only slightly less than that at which an opaque object of the same size is detected and therefore gains only a slight advantage by being transparent. The ratio d/d_{opaque} as a function of T was calculated for C_{min} values of −0.005 (best value reported for fish), −0.02 (human underwater vision), −0.1, −0.2, −0.5 (cod vision at 650 m), and −0.75 (Douglas and Hawryshyn, 1990).

Results

Percent transparency values

Figure 2 shows three typical traces of percent transparency *vs.* wavelength. Table II is a summary of measured percent transparency values. In general, percent transparency was linearly and positively proportional to wavelength. The slopes of the linear regressions of transparency on wavelength (normalized by dividing by the percent transparency at 480 nm) ranged from 0.027%/nm to 0.51%/nm (average 0.17 ± 0.019%/nm), with most r^2 values approaching unity. The slopes in all animals were significantly different from zero ($P < 0.0005$). The most transparent tissues (at 480 nm) were hydromedusa mesoglea (66%), followed by *Cystosoma* (42%), ctenophore mesoglea (41%), siphonophore mesoglea (39%), pelagic tunicates (excluding *Pyrosoma*) (33%), *Sagitta* (24%), and the translucent portions of the hydromedusae and ctenophores (24%). The least transparent tissues were from the pelagic gastropods (excluding *Clione*) (17%) and *Tomopteris* (9.1%). *P. atlanticum* and *C. limacina* were essentially opaque, with percent transparencies of 1.6% and 0.51% respectively.

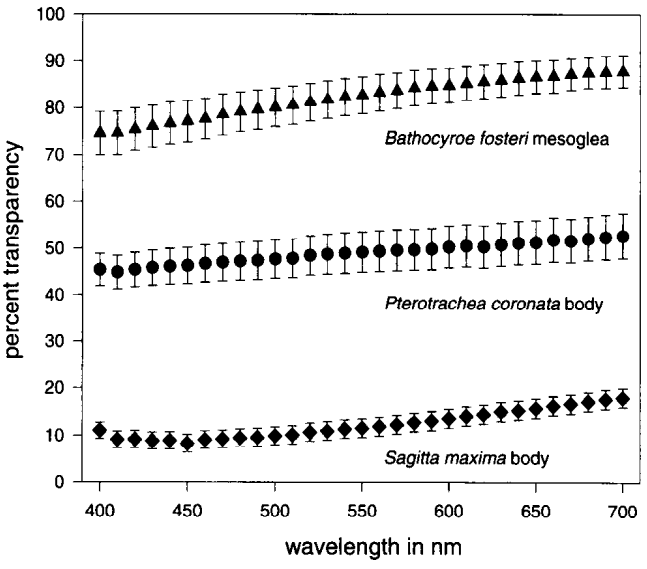

Figure 2. Percent transparency *vs.* wavelength for individual specimens of *Bathocyroe fosteri, Pterotrachea coronata,* and *Sagitta maxima.* The error bars denote standard deviation of the mean.

Transmission values vs. *depth*

Because the optical properties of the collecting sites differed greatly and the largest variety of animals was collected from Oceanographer Canyon, data from animals collected at that site were used to evaluate the relationship between the percent transparency (of the major tissue in the animal) and its average daytime depth (Fig. 3). No significant relationship was found ($r = 0.39$, $n = 11$, $P > 0.2$). Highly transparent animals were found at all depths, and nearly opaque animals were found at all depths.

Effect of tissue transmission spectra on the spectrum of downwelling light

The spectrum of downwelling light and the altered spectra after passing through tissues with linear relationships between percent transparency and wavelength with normalized slopes of 0.5%, 2%, 5%, and 10%/nm was analyzed for two depths in Oceanographer Canyon. At 260 m the peak wavelength shifts from 489.5 nm to 489.5, 492.0, 492.5, and 495.0 (Fig. 4a). At 60 m the peak wavelength shifts from 489.5 nm to 492.5, 494.0, 498.0, and 505.0 (Fig. 4b).

Relationship between percent transparency and sighting distance

Figure 5 shows the ratio of sighting distance of a transparent object to sighting distance of an opaque object *vs.* percent transparency of the transparent object for visual systems with different minimum contrast thresholds. For predators with a low minimum contrast threshold, the sighting distance decreases slowly until high transparency values are reached, after which it decreases rapidly. For high absolute minimum contrast thresholds, the sighting distance decreases rapidly and linearly with increasing transparency. At percent transparencies higher than $100 \times (1 - C_{min})$, the sighting distance is zero and the tissue is essentially invisible.

Discussion

Transparency and predator/prey relationships among gelatinous zooplankton

Although the effects of prey transparency on visually mediated predation have often been examined in freshwater systems (Zaret and Kerfoot, 1975; Greene, 1983; reviewed in McFall-Ngai, 1990), less work has been done in marine systems (McFall-Ngai, 1990). In addition, the effects of predator transparency on successful capture of visually oriented prey are largely unexplored (Purcell,

Table II

Transparency values (percent transparency: T_λ, at wavelength λ) measured at three wavelengths (λ) for animals and tissues; values are given as mean ± standard deviation of the mean

Animal	Tissue	n	T_λ			Regression parameters*	
			λ = 400	λ = 480	λ = 700	$\frac{dT/d\lambda}{T_{480}}$	r^2
Cnidaria							
A. okeni	mesoglea	8	40 ± 4.0	48 ± 4.1	56 ± 4.8	0.11	0.95
	siphosome	1 (4)	3.7 ± 1.4	3.9 ± 1.4	4.5 ± 1.4	0.15	0.99
A. rosacea	mesoglea	1 (5)	47 ± 7.1	53 ± 8.1	59 ± 9.7	0.068	0.94
C. welshi	mesoglea	1 (5)	55 ± 7.2	64 ± 7.0	80 ± 8.7	0.13	0.98
H. cupulifera	mesoglea	3	36 ± 7.7	44 ± 8.8	53 ± 8.3	0.10	0.95
N. bachei	mesoglea	4	50 ± 8.6	56 ± 8.7	68 ± 8.8	0.10	0.99
O. pileus	mesoglea	4	49 ± 8.2	52 ± 7.9	59 ± 7.9	0.071	0.97
P. hydrostatica	mesoglea	1 (10)	6.1 ± 2.4	11 ± 2.5	14 ± 2.6	0.21	0.88
S. typa	mesoglea	1 (5)	89 ± 0.91	91 ± 1.0	96 ± 1.8	0.027	0.99
	canal	1 (5)	20 ± 1.4	22 ± 1.5	39 ± 1.6	0.31	0.98
Ctenophora							
B. fosteri	mesoglea	2	70 ± 4.9	75 ± 4.0	85 ± 2.8	0.069	0.98
	center	1 (5)	32 ± 5.6	36 ± 6.3	47 ± 6.9	0.14	0.99
B. cucumis	mesoglea	4	11 ± 1.7	13 ± 1.3	17 ± 1.5	0.13	0.96
B. infundibulum	mesoglea	2	40 ± 13	45 ± 12	58 ± 9.1	0.13	0.99
	lobe	2	14 ± 2.1	18 ± 1.9	29 ± 1.5	0.27	0.99
	comb row	2	22 ± 7.9	24 ± 7.4	30 ± 8.0	0.12	0.99
Hormiphora sp.	mesoglea	3	27 ± 4.7	33 ± 11	39 ± 7.6	0.11	0.97
M. macrydi	comb row	11	4.8 ± 1.3	7.0 ± 1.5	15 ± 2.2	0.51	0.99
O. maculata	mesoglea	1 (5)	28 ± 12	39 ± 13	48 ± 8.9	0.14	0.97
P. bachei	comb row	10	12 ± 1.2	17 ± 1.6	22 ± 1.8	0.19	0.95
Annelida							
Tomopteris sp.	body	2	7.7 ± 4.5	9.1 ± 3.2	12 ± 0.22	0.12	0.96
Mollusca							
C. lamarcki	body	4	4.3 ± 1.0	8.0 ± 1.4	11 ± 1.7	0.24	0.92
C. limacina	body	1 (5)	0.76 ± 0.031	0.51 ± 0.04	0.93 ± 0.10	0.33	0.72
C. spectabilis	body	5	12 ± 5.0	18 ± 6.2	25 ± 7.3	0.22	0.96
P. atlantica	body	4	4.9 ± 1.7	14 ± 2.8	18 ± 3.5	0.19	0.74
P. coronata	body	4	25 ± 9.0	29 ± 9.0	37 ± 9.2	0.13	0.99
Crustacea							
C. cystosoma	body	2	36 ± 7.1	42 ± 6.5	49 ± 7.4	0.098	0.96
Chaetognatha							
S. hexaptera	body	8	32 ± 4.7	38 ± 5.1	49 ± 5.9	0.15	0.98
S. maxima	body	1 (5)	11 ± 1.7	9.4 ± 1.9	18 ± 2.0	0.44	0.91
Chordata							
C. affinis	body	1 (5)	9.0 ± 2.9	8.4 ± 2.6	8.0 ± 2.6	−0.036	0.79
P. confederata	body	4	39 ± 4.0	42 ± 4.5	47 ± 4.7	0.060	0.97
P. atlanticum	body	5	0.78 ± 0.41	1.6 ± 0.57	2.8 ± 0.8	0.42	0.96
S. cylindrica	body	8	49 ± 3.7	55 ± 3.3	64 ± 3.0	0.078	0.99
S. maxima	body	1 (5)	22 ± 2.0	25 ± 2.3	33 ± 2.9	0.18	0.99

The number of animals measured is represented by n. If n = 1, the number following in parentheses is the number of measurements taken from that animal. When $n > 1$, the reported value for T_λ is the average of the average values for each animal. When n = 1, the reported value is the average of the measurements for that animal.

* $dT/d\lambda/T_{480}$ is the slope of the linear regression of percent transparency on wavelength divided by percent transparency at 480 nm, and r^2 is the coefficient of determination for the regression. In general, percent transparency was linearly proportional to wavelength (see Fig. 2).

1980; Mackie *et al.*, 1987), probably because of the difficulty in determining the predators and prey of gelatinous marine animals. However, due to the increasing use of submersible and scuba-based collecting and observing techniques, the role of gelatinous animals in the trophic ecology of the ocean is becoming clearer (Alldredge, 1984; Madin, 1988; Lalli and Gilmer, 1989). Table III lists documented examples of predator/prey relationships involving transparent animals and animals with well-developed visual systems. Of the phyla containing transpar-

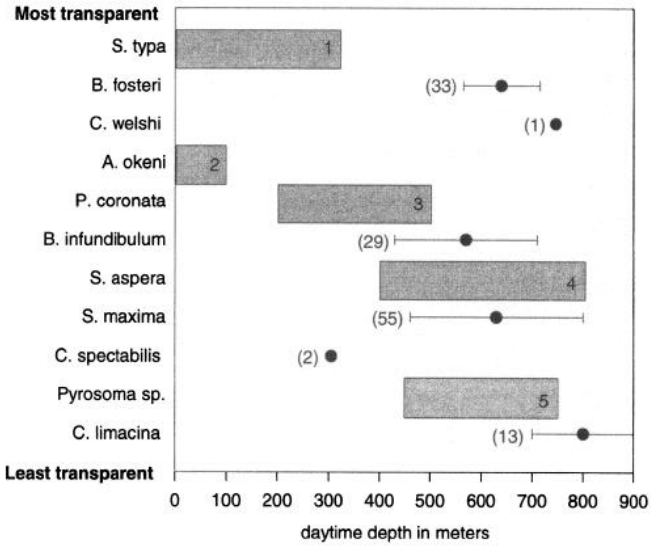

Figure 3. Transparency of species collected from Oceanographer Canyon in relation to depth of daytime distribution. Species are arranged from most transparent (*Sibogita typa*) to least transparent (*Clione limacina*). Transparency values (filled circles) for each species are means of measurements taken from animals collected on the same cruise; bars are standard deviation of the mean, with number of specimens given in parentheses. Daytime depth ranges (bars) are taken from the literature. The number within each bar gives the reference from which it was taken: 1 = Mayer (1910); 2 = Youngbluth (pers. comm.); 3 = Lalli and Gilmer (1989); 4 = Wiebe *et al.* (1979); 5 = Anderson *et al.* (1992).

ent members, all include transparent animals that either prey on, or are preyed upon by animals with well-developed visual systems. In addition, many of these animals (in particular certain cnidarians, ctenophores, and chaetognaths) prey upon copepods (Harbison *et al.,* 1978; Madin, 1988; Baier and Purcell, 1997). Copepods do not have well-developed vision, but have been shown to react defensively to shadows (Buskey *et al.,* 1986), and therefore may react to opaque or translucent predators passing overhead. A large number of transparent animals are thus interacting with animals that respond to visual cues.

Since, in general, transparent animals are more delicate and less agile than their visually oriented predators or prey, their success as predators or prey of such animals depends critically upon their sighting distance (the maximum distance at which they are still detectable by a visually oriented animal). Prey with short sighting distances reduce their number of encounters with visually oriented predators (Greene, 1983). "Ambush" predators (*e.g.,* medusa, siphonophores, cydippid ctenophores) with short sighting distances increase their chances of entangling visually oriented 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.

In certain cases, the relationship between transparent animals and visually oriented animals is quite complex. The physonect siphonophores *Athorybia rosacea* and *Agalma okeni* are mostly transparent, but they have pigmented regions that mimic copepods and larval fish and are apparently used as lures (Purcell, 1980). Other animals appear to have exploited temporal changes in transparency for defense. The calycophoran siphonophore *Hippopodius hippopus* is normally transparent, but rapidly becomes opaque when disturbed, presumably as a defense response (Mackie, 1996). Finally, there is evidence that cephalopods use their well-developed polarization vision to break the camouflage afforded by transparency (Shashar *et al.,* 1998). Certain zooplankton, though trans-

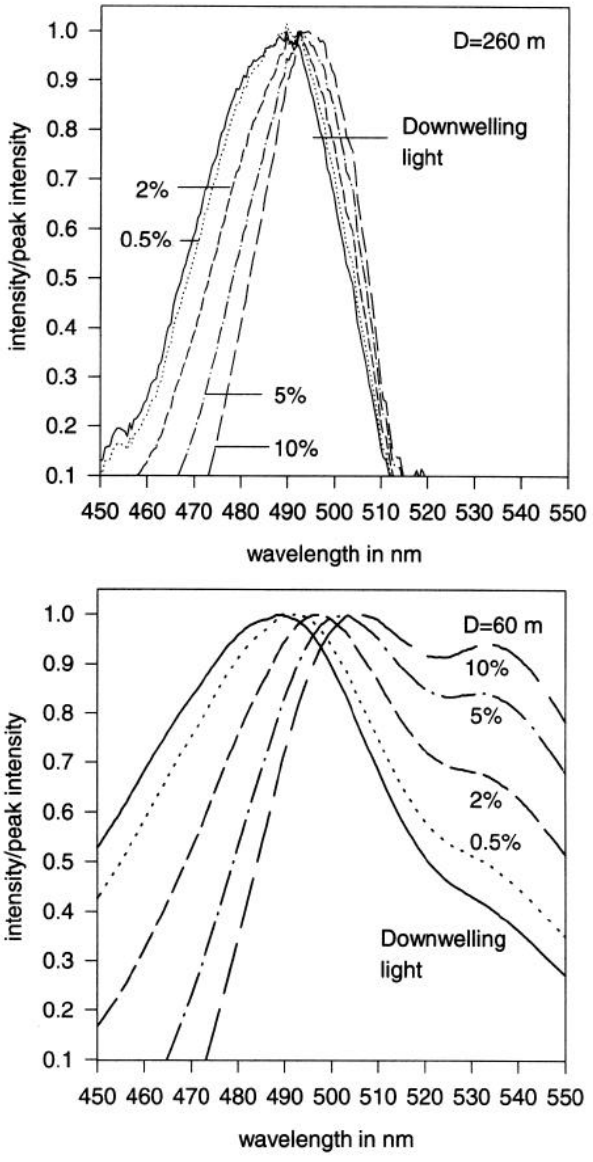

Figure 4. (Top) Spectrum of downwelling light in Oceanographer Canyon at 260 m (solid line) and the spectra after having passed through the tissue with linear transmission spectra with normalized slopes of 0.5%, 2%, 5%, and 10%/nm. All spectra are normalized to have a value of unity at their wavelength of peak intensity. (Bottom) Same as above, but at 60 m.

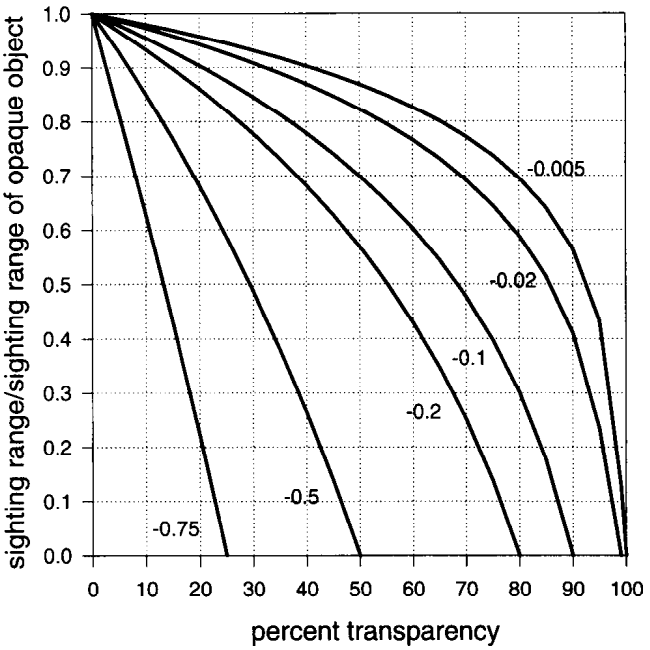

Figure 5. Sighting distance of a prey item *vs.* its percent transparency when viewed from below by predators with visual systems that have different minimum contrast thresholds for object detection. The sighting distance is divided by the sighting distance of an opaque object to control for water clarity, prey shape, size, etc. The ratio gives an estimate of the advantage of transparency for crypsis in a given situation.

parent, alter the polarization characteristics of transmitted light and are therefore detectable by animals that can detect these characteristics (Shashar *et al.,* 1998). Since many crustaceans have polarization vision (Waterman, 1981), this method of detection may be quite common.

Relationship of measured transparency to in situ *light transmission*

The great majority of the collected animals either have a mesopelagic daytime distribution in oceanic water or are found at moderate depths in coastal water (see *Results*). In both cases, the light field has reached an asymptotic state. The asymptotic light field is considerably simpler than its epipelagic counterpart. The intensity and spatial and temporal aspects of the epipelagic light field are strongly influenced by solar elevation and azimuth, waves, and clouds (Jerlov, 1976; Lythgoe, 1979; Loew and McFarland, 1990). In addition, downwelling light has a broad angular distribution. Therefore, it can be difficult to relate percent transmission of a narrow beam of light to percent transmission of the *in situ* light field (Chapman, 1976a). In contrast, while the intensity of the asymptotic light field is affected by surface light levels, its spatial characteristics are essentially constant (Jerlov, 1976; Denton, 1990). Additionally, the angular distribution of most of the light is narrow and centered around the vertical. As mentioned in the *Materials and Methods* section, the vertical upward and horizontal radiances are only 0.5% and 3% of the vertical downward radiance. At asymptotic depths, the vertical downward radiance approximates the downward irradiance (reviewed in Denton, 1990). Therefore, measurements of percent transparency in a light beam are comparable to the *in situ* transparency of an animal viewed from below. Since visual acuity and contrast sensitivity are in general proportional to the amount of available light (Douglas and Hawryshyn, 1990), transparent animals are most visible when viewed from below. Therefore an analysis of visibility from this viewing position provides a conservative estimate of the cryptic abilities of these animals.

Wavelength dependence of light transmission

In all but one of the animals (*C. affinis*), the percent transparency increased linearly with wavelength. This linear wavelength dependence can be a disadvantage to an animal using transparency as camouflage. Unless percent transparency of the animal is independent of wavelength, the spectrum of light passing through the animal will be altered. Whereas the peak wavelength is displaced only slightly, there is a considerable reduction in intensity in shorter wavelengths and an increase in longer wavelengths, even for normalized slopes as small as 2%/nm (see *Results*). Therefore, in addition to creating an intensity contrast against the background, the animal will also appear to be a slightly different color from the surrounding water. Because the spectral distribution of the downwelling light broadens near the surface, this effect is stronger at shallow depths, though the peak displacement remains small (Fig. 4). Since there is evidence that the eyes of some mesopelagic predators have certain characteristics (*e.g.,* pigmented lenses, multibanked retinae) that may give them excellent hue discrimination in the blue-green (Munz, 1976; Denton and Locket, 1989; Douglas and Thorpe, 1992), it is advantageous that the normalized T-W slope of an animal using transparency for camouflage be as small as possible. In the tissues measured, the normalized slopes are all less than 0.5% and average only 0.17%/nm. Therefore, they have a small and probably undetectable effect on the spectrum of the downwelling light.

Constant percent transparency at all wavelengths is not a general characteristic of materials. Light attenuation (100-T) is caused by true absorption and scattering, but scattering dominates in unpigmented organic materials (Chapman, 1976a). The wavelength dependence of attenuation due to scattering depends on the size of the scattering particles, with the general form $S \approx \lambda^k$, where S is the amount of scattering and λ is the wavelength of incident light. For particles with radii that are small relative to λ (Rayleigh scattering), k equals -4. For particles with radii within an order of magnitude of λ (Mie scattering),

Table III

Examples of transparent zooplankton that have prey or predators with well-developed visual systems

Animal	Preys on	Preyed upon by
Cnidaria		
Aegina		hyperiid amphipods[1]
Aglantha	euphausiids[1]	euphausiids,[1] fish[1]
Athorybia	mysids,[2], heteropods[2]	
Aurelia	fish[4]	sea turtles[3]
Carybdea	fish,[5] mysids[5]	
Forskalia	fish[6]	
Laodicea	fish[6]	
Liriope	fish,[6] alciopid worms[6]	
Nanomia		heteropods[7]
cystonect siphonophores	fish[8]	sea turtles[3]
assorted siphonophores		heteropods,[7] sea turtles[3]
assorted hydromedusae		sea turtles[3]
Ctenophora		
Bathocyroe	euphausiids[5]	
Bolinopsis	euphausiids[5]	
Cestum		alciopid worms[9]
Eurhamphaeca		alciopid worms[9]
Hormiphora	fish,[6] heteropods[6]	
Nmemiopsis		alciopid worms,[9] fish[4]
Ocyropsis	fish,[9] euphausiids[9]	alciopid worms[9]
Pleurobrachia	fish[5]	
assorted. ctenophores		hyperiid amphipods,[9] sea turtles[3]
Annelida		
Tomopteris		heteropods,[7] squid[11]
Mollusca		
Carianria	euphausiids,[7] fish[7]	sea turtles,[3] fish[15]
Corolla		hyperiid amphipods[7]
Cymbulia	heteropods[15]	
Phylliroe		heteropods[10]
Pterotrachea		hyperiid amphipods[9]
assorted heteropods	heteropods[7]	heteropods,[7] fish,[7] squid,[11] sea turtles[3]
assorted cranchiid squid		birds[14]
Crustacea		
Lucifer		fish[12]
Phronima		squid[11]
Chaetognatha		
assorted chaetognaths	fish,[12] euphausiids[12]	heteropods,[7] squid,[11] euphausiids,[12] fish,[12] decapods[12]
Chordata		
assorted salps		hyperiid amphipods,[9] heteropods,[7] euphausiids,[13] sea turtles[3]
assorted larvaceans		fish[10]

Sources of the data: [1] Mackie, 1996; [2] Purcell, 1981; [3] Bjorndal, 1997; [4] Alldredge, 1984; [5] Wrobel and Mills, 1998; [6] Madin, 1988; [7] Lalli and Gilmer, 1989; [8] Purcell, 1980; [9] Harbison *et al.*, 1978; [10] Hamner *et al.*, 1975; [11] Hanlon and Messenger, 1996; [12] Pierrot-Bults and Chidgey, 1988; [13] Du and Zhang, 1980; [14] Imber, 1978; [15] Van der Spoel, 1976. Most of the sources are reviews to minimize the number of references.

k ranges from -4 to 0.2. For particles much larger than λ (geometric optics), k equals 0 (see Mertens (1970) for further details). Table IV shows the k values calculated for the transparent tissues by fitting the above power function to $(100 - T)$ *vs.* wavelength. For the most transparent tissues, k ranges from -2 to -1. For moderately transparent tissues, k ranges from -0.78 to -0.11. For the nearly opaque tissues, k approximates zero. Therefore, it is likely that the attenuation of light in the highly and moderately transparent tissues (*e.g., S. typa, P. coronata*) is mostly due to light scattering by medium-size particles and that the attenuation in the nearly opaque tissues (*e.g., C. limacina*) is mostly due to scattering by large particles. In contrast, the k values reported for vertebrate corneas ($T = 90-100\%$) range from -5 to -3, suggesting that attenuation in this tissue is dominated by scattering from small particles (reviewed in Farrell *et al.*, 1973).

Relationship of percent transparency to sighting distance

All other factors being equal, a visual predator will spot an opaque animal at a greater distance than it will

Table IV

Exponent values (k), calculated when light attenuation (100 − T) vs. wavelength (λ) is fit to the power function 100 − T ≈ λ^k, that provide information about the size of the ultrastructural components responsible for most of the light scattering; r^2 is the coefficient of determination for the curve fit to the power function

Animal	Tissue	*k*	r^2
Cnidaria			
A. okeni	mesoglea	−0.57	0.98
	siphosome	−0.041	0.99
A. rosacea	mesoglea	−0.052	0.99
C. welshi	mesoglea	−1.5	0.99
H. cupulifera	mesoglea	−0.47	0.99
N. bachei	mesoglea	−0.78	0.99
O. pileus	mesoglea	−0.44	0.99
P. hydrostatica	mesoglea	−0.14	0.92
S. typa	mesoglea	−2.0	0.93
	canal	−0.58	0.97
Ctenophora			
B. fosteri	mesoglea	−1.3	0.99
	center	−0.50	0.99
B. cucumis	mesoglea	−0.11	0.97
B. infundibulum	mesoglea	−0.64	0.99
	lobe	−0.35	0.99
	comb row	−0.21	0.99
Hormiphora sp.	mesoglea	−0.29	0.99
M. macrydi	comb row	−0.21	0.98
O. maculata	mesoglea	−0.43	0.99
P. bachei	comb row	−0.22	0.98
Annelida			
Tomopteris sp.	body	−0.069	0.97
Mollusca			
Carinaria sp.	body	−0.11	0.96
C. limacina	body	−0.007	0.67
C. spectabilis	body	−0.27	0.99
P. atlantica	body	−0.18	0.81
P. coronata	body	−0.30	0.99
Crustacea			
C. cystosoma.	body	−0.40	0.99
Chaetognatha			
S. hexaptera	body	−0.52	0.99
S. maxima	body	−0.19	0.86
Chordata			
C. affinis	body	0.018	0.85
P. confederata	body	−0.24	0.99
P. atlanticum	body	−0.037	0.98
S. cylindrica	body	−0.54	0.99
S. maxima	body	−0.28	0.99

spot a transparent one. Since a shorter sighting distance for a prey item decreases its encounters with visual predators, transparency can be advantageous. The ratio of the sighting distance of a transparent prey item to the sighting distance for a similar opaque prey item gives an estimate of the advantage of transparency as a form of crypsis in a given situation (Fig. 5). The scale is inverted in that a ratio of zero implies a high advantage (the prey item is essentially invisible) and a ratio of one implies no advantage over an opaque object. The model showed that the qualitative and quantitative relationship between the percent transparency of an object and its sighting distance depends critically upon the minimum contrast threshold for object detection in the given visual system. Note that in the preceding and following discussion, the terms predator and prey can be exchanged without loss of meaning.

The minimum contrast threshold is known for only a handful of animals and depends on many variables (Douglas and Hawryshyn, 1990). Optimal minimum contrast thresholds have been determined for several species (reviewed in Lythgoe, 1979, and Douglas and Hawryshyn, 1990); for simplicity, quoted values are unsigned: 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). Because these values depend on many aspects of the experimental situation (temperature, position of stimulus on retina, use of one eye or two, assessment method, etc.), they are not directly comparable (Hester, 1968, cited in Douglas and Hawryshyn, 1990). In addition, studies on cod (*Gadus morhua*) have shown that the minimum contrast threshold increases from the optimum (0.02) at a light level of 10^{-1} W $sr^{-1}m^{-2}$ to nearly 0.5 at a light level of 10^{-7} W $sr^{-1}m^{-2}$ (Anthony, 1981). In general, the minimum contrast threshold of visual systems increases with decreasing light levels (Douglas and Hawryshyn, 1990). The minimum contrast threshold also depends on the relative size of the object. Studies on goldfish (*Carassius auratus*) viewing sine wave patterns have shown that the minimum contrast threshold increases from 0.025 at 0.3 cycles/degree to 0.25 at higher and lower spatial frequencies (Northmore and Dvorak, 1979). The same pattern is found in humans, though the optimal minimum contrast threshold is 4 cycles/degree (Uhlrich *et al.*, 1981). For the above reasons, absolute determination of the sighting distance of these animals by their relevant predators and prey is at present impossible.

Despite this limitation, it can be predicted that the usefulness of transparency as camouflage increases dramatically with depth (up to the depth limit for vision for a given predator). This is because, in general, the minimum contrast threshold of a given visual system increases with decreasing light levels. For example, as mentioned above, the minimum contrast threshold of the cod, *Gadus morhua,* increases to 0.5 at light levels of 10^{-7} W $sr^{-1}m^{-2}$. In clear water, daytime vertical downward radiance has this intensity at about 650 m (Denton, 1990). At this depth, the sighting range decreases rapidly with increasing percent transparency, and tissues with percent transparency greater than 50% are invisible at all distances when viewed from below by *G. morhua* (see Fig. 5). Near the surface, the minimum contrast threshold decreases to 0.02, and the sighting distance of a tissue with 50% transparency is only 27% less than that for an opaque object. An interesting corollary is that, unless they are preyed upon by visual predators whose low-light contrast

sensitivity is extraordinarily better than that of humans, many of the animals measured are far more transparent than is necessary to achieve complete invisibility at their daytime depths (*e.g., Bathocyroe fosteri*).

This analysis, however, is limited to one dimension. An extension would be to consider a critical volume within which a prey item could be detected. If the light field were spherically symmetrical, the volume would equal $4\pi d^3/3$, where d is the sighting distance and the above-mentioned 27% decrease in d would correspond to a 61% reduction in the critical volume. However, due to the asymmetry of the asymptotic light field (Denton, 1990) and the complex relationship between percent transparency and visibility in horizontal and downward lines of sight, a determination of the critical volume is beyond the scope of this paper.

The foregoing analysis does not necessarily predict a simple relationship between percent transparency and depth. Indeed, in this study no relationship was found between the percent transparency of an animal and its daytime depth distribution. High transparency at depth may be a consequence of selection for low backscatter to camouflage animals from predators or prey that use directed bioluminescence to illuminate the environment. Shallow-water animals with a low percent transparency when backlit by a narrow beam may be considerably more transparent in the diffuse epipelagic light environment (see Chapman, 1976a). Finally, of course, some animals may be transparent for reasons unrelated to vision and camouflage—*e.g.*, as a result of having gelatinous flotation devices (Marshall, 1979).

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