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Visual Adaptations in Crustaceans: Chromatic, Developmental, and Temporal Aspects

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Abstract

Crustaceans possess a huge variety of body plans and inhabit most regions of Earth, specializing in the aquatic realm. Their diversity of form and living space has resulted in equally diverse eye designs. This chapter reviews the latest state of knowledge in crustacean vision concentrating on three areas: spectral sensitivities, ontogenetic development of spectral sensitivity, and the temporal properties of photoreceptors from different environments. Visual ecology is a binding element of the chapter and within this framework the astonishing variety of stomatopod (mantis shrimp) spectral sensitivities and the environmental pressures molding them are examined in some detail. The quantity and spectral content of light changes dramatically with depth and water type and, as might be expected, many adaptations in crustacean photoreceptor design are related to this governing environmental factor. Spectral and temporal tuning may be more influenced by bioluminescence in the deep ocean, and the spectral quality of light at dawn and dusk is probably a critical feature in the visual worlds of many shallow-water crustaceans. Plasticity in photoreceptor tuning is a recently emerging theme both in crustaceans and other animals. The seasonal variation in crayfish spectral sensitivity and spectral sensitivity change in single stomatopod species from different depths provide two examples of this. Other oddities such as the need to see the heat from hydrothermal vents, color dances in water-fleas, and the possible influences of temperature on the spectral tuning of visual pigments are also discussed.

1. Introduction

Crustaceans possess a greater variety of eye types than any other invertebrate group (Land, 1984; Fig. 18.1 [see color plate]). They inhabit all the zones of the aquatic realm and some, such as the woodlice (*Armadillidium* sp.), have ventured permanently onto land. The optical design of their eyes includes "simple" or "camera" eyes like our own; compound eyes (apposition, refracting superposition) similar to the insects; eyes with reflecting superposition or

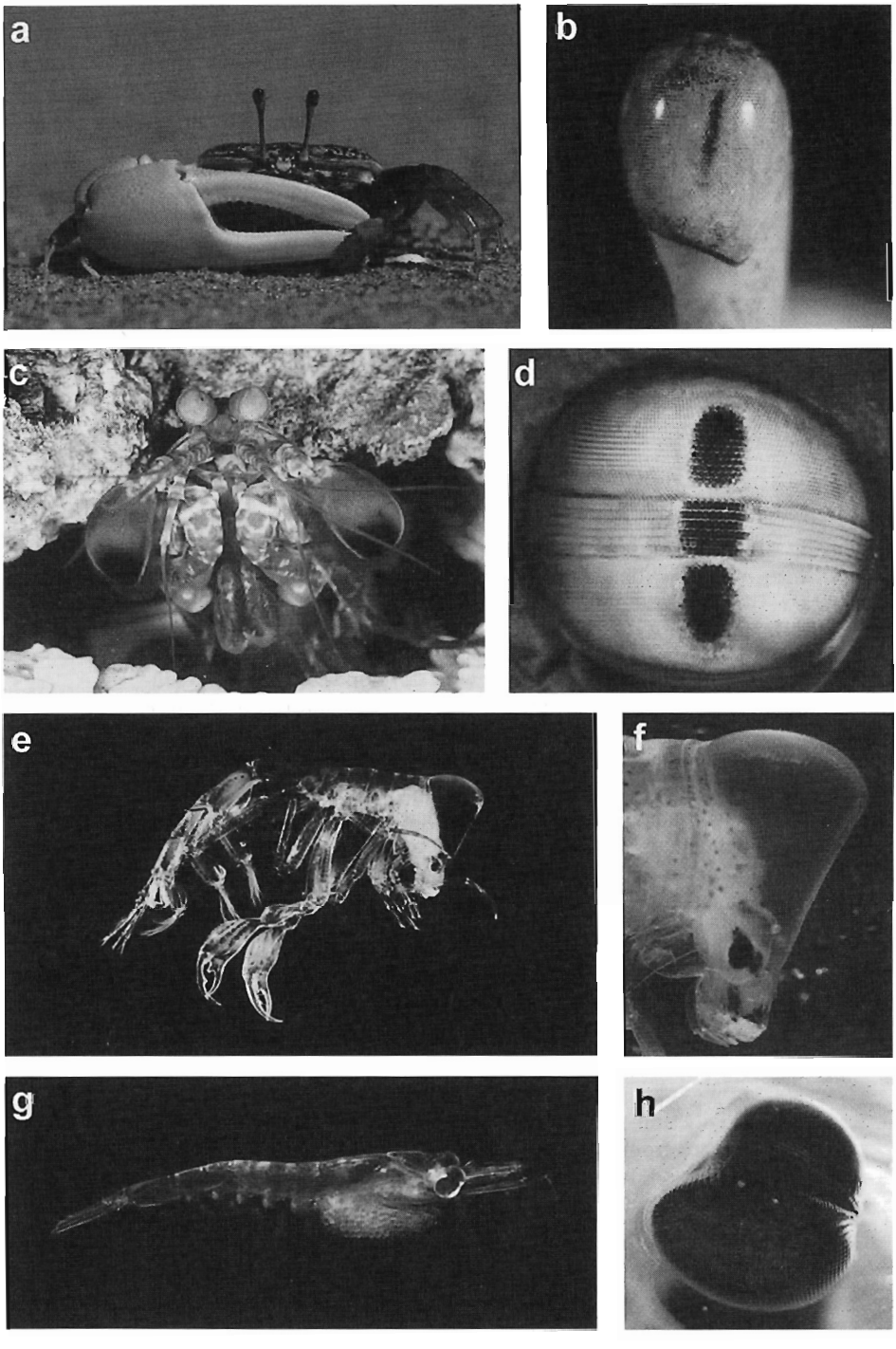


FIGURE 18.1. Crustaceans and their eyes. The fiddler crab *Uca polita* and closeup view of front of eye (a, b), (a—photograph by Jochen Zeil.) The stomatopod *Odontodactylus scyllarus* and closeup view of front of eye (c, d). The hyperiid amphipod *Phronima sedentaria* and closeup view of lateral aspect of head and eyes (e, f), (e—photograph by Mike Land.) The euphausiid *Nematobrachion megalops* and closeup view of lateral aspect of eye (g, h). Note the eye subdivisions in the last three examples. (See color plate)

mirrored optics that may just gather light or form perfect images; and even eyes that possess no optics at all (Land, 1981a, 1984; Land and Nilsson, 2002). This diversity of light-gathering mechanisms partially reflects the range of light intensities that crustaceans experience (10^{13} to 10^{1} photons $cm^{-1} sr^{-1} nm^{-1}$) but is to some extent phylogenetic (Land, 1981a; Cronin, 1986; Marshall et al., 1999a,b). A cursory glance at the spread of peak spectral sensitivities (315–710 nm, Table 18.1; Fig. 18.2) suggests a similar diversity in visual pigments and color vision potential. However, much of the variety seen comes from our knowledge of an isopod (*Ligia*) (Hariyama et al., 1993), a water-flea (*Daphnia*) (Smith and Macagno, 1990), and the mantis shrimps (stomatopods) (Cronin and Marshall, 1989a,b), which possess tri-, tetra-, and polychromatic color vision, respectively. Other crustaceans examined possess one or two spectral mechanisms, usually with one placed close to 400 nm and the other between 450 nm and 550 nm depending on habitat.

It is clear that our knowledge of crustacean spectral mechanisms still has many holes in it (Table 18.2) and there are likely to be many interesting surprises for anyone exploring these fascinating animals. One purpose of this chapter is to rekindle some of the interest in crustacean visual mechanisms, a declining discipline in these days of more applied biology. Interested readers are directed to two recent reviews in this area, Marshall et al. (1999b) and Cronin and Hariyama (2002).

The relationship between eye design constraints, such as the habitat light environment of different species, and their resulting spectral sensitivities, forms a major theme of this chapter. We also examine changes in spectral sensitivity during the development of single species, as many crustaceans shift from shallow-living planktonic larval stages to deeper-living adults and this involves substantial changes in habitat and therefore light regime and way of life. By way of comparison, and within the same framework of visual ecology, our knowledge of the temporal properties of crustacean photoreceptors is also reviewed. All photoreceptors face the dual task of catching enough photons and processing the information fast enough to eat or avoid being eaten. In light-limited habitats, such as deep-oceans or turbid waters, this results in compromises in temporal and optical aspects of photoreceptor design that mirror changes in spectral sensitivity (Land, 1981a,b; Warrant, 1999).

2. A Note on Methods

Five technical methods have been used to gather the data reviewed here. Spectrophotometry of retinal extracts and microspectrophotometry (MSP) of intact photoreceptors and optical filters are the two most common methods of determining spectral sensitivity. Extraction of visual pigment from the retina and its cellular environment can result in changes in the position of the sensitivity maximum (λ_{max}), so these results need to be treated with the caution of hindsight. Intracellular or extracellular electrophysiological recording from intact eyes provide two even more precise measures of eye spectral sensitivity, and these methods are also the ones used most extensively for determining temporal properties of photoreceptors. While recording from individual cells is desirable, for practical reasons (such as the need to conduct experiments onboard vibrating ships in order to work on live animals), the extracellular electroretinogram (ERG) is often used. Finally, in this scale of visual system "dissection," behavioral determination of both spectral sensitivity and flicker fusion frequency (a measure of photoreceptor temporal properties—see Section 5) gives the closest approximation of the parameters of an animal's visual system. Again, for a variety of practical reasons, this may not be possible. One result of this variety of techniques is that some caution is needed in cross comparisons between data gathered with different methods.

Molecular genetics is now being used to examine fish (Carleton et al., 2000) and mammalian (Jacobs and Deegan, 2000) visual pigments, for example, with fascinating results. The target molecule of this method is the opsin or protein component of the visual pigment. All visual pigments are composed of a

TABLE 18.1. Spectral sensitivities in crustaceans.

Species	λ_{max} (MSP) S-max /nm	Method of study	Author(s)	Year
Subphylum Crustacea				
Class Branchiopoda				
Subclass Diplostraca				
Order Cladocera				
Daphnia magna	348,434,525, & 608	EON	Smith & Macagno	1990
Subclass Sarsostraca				
OrderAnostraca				
Artemia salina	410	ERG	Hertel	1972
Class Maxillopoda				
Subclass Copepoda				
Acartia tonsa	450–520	BP	Stearns & Forward	1984
Subclass Cirripedia				
Order Thoracica				
Suborder Balanomorpha				
Balanus amphitrite	532	ERG	Hillman, Dodge, Hochstein, Knight & Minke	1973
	532	MSP	Minke & Kirschfield	1978
Balanus balanoides (nauplius)	510–530	BP	Barnes & Klepal	1972
Balanus eburneus	532	ERG	Hillman, Dodge, Hochstein, Knight & Minke	1973
	532	MSP	Minke & Kirschfield	1978
Class Malacostraca				
Subclass Eumalacostraca				
Superorder Holpocarida				
Order Stomatopoda				
Superfamily Squilloidea				
Cloridopsis dubia	510	MSP	Cronin, Marshall & Caldwell	1994b
Squilla empusa	517	MSP	Cronin, Marshall & Caldwell	1994b
	360 & 500	OP	Cronin	1985
Squilla mantis	535–555	IC	Schiff	1963
Superfamily Gonodactyloidea				
Gonodactylus oerstedii	400–551 (11)	MSP	Cronin & Marshall	1989a&b
	325	MSP	Cronin, Marshall, Quinn, & King	1994d
	400–695 (11)	CS	Cronin, Marshall, Caldwell & Shashar	1994c
	312–710	IC	Marshall & Oberwinkler	1993
	312–410	IC	Marshall & Oberwinkler	1999
Gonodactylaceus aloha	400–551 (11)	MSP	Cronin, Marshall & Caldwell	1996
Neogonodactylus curacaoensis	400–520 (8)	MSP	Cronin, Marshall & Caldwell	1996
Psuedosquilla ciliata	400–539 (11)	MSP	Cronin & Marshall	1989b
	400–680 (11)	CS	Cronin, Marshall, Caldwell & Shashar	1994c
Hemisquilla ensigera	414–535 (11)	MSP	Cronin, Marshall, Caldwell & Shashar	1994c
	440–625 (11)	CS	Cronin, Marshall, Caldwell & Shashar	1994c
	330	MSP	Cronin, Marshall, Quinn, & King	1994d
Odontodactylus brevirostris	402–535 (11)	MSP	Cronin, Marshall, Caldwell & Shashar	1994c
	400–623 (11)	CS	Cronin, Marshall, Caldwell & Shashar	1994c
Odontodactylus scyllarus	400–546 (11)	MSP	Cronin, Marshall & Caldwell	1994b
	425–655 (11)	CS	Cronin, Marshall & Caldwell	1994b
Odontodactylus havanensis	407–520 (8)	MSP	Cronin, Marshall & Caldwell	1996
Superfamily Lysiosquilloidea				
Coronis scolopendra	407–533 (11)	MSP	Cronin, Marshall, Caldwell & Shashar	1994c
	425–620 (11)	CS	Cronin, Marshall, Caldwell & Shashar	1994c
Lysiosquilla maculata	330	MSP	Cronin, Marshall, Quinn, & King	1994d
Lysiosquilla sulcata	397–538 (11)	MSP	Cronin, Marshall, Caldwell & Shashar	1994c
	410–620 (11)	CS	Cronin, Marshall, Caldwell & Shashar	1994c

TABLE 18.1. *Continued*

Species	λ_{max} (MSP) S-max /nm	Method of study	Author(s)	Year
Superorder Eucarida				
Order Euphausiacea				
Euphausia pacifica	462	EX	Kampa	1955
	483	MSP	Widder, Hiller-Adams & Case	1987
Euphausia superba	462	EX	Denys	1982
	485	EX	Denys & Brown	1982
	487	ERG	Frank and Widder	1999
Meganyctiphanes norvegica	460–465	EX	Fisher & Goldie	1959
	460–515, 490	ERG	Boden, Kampa & Abbott	1961
	488	MSP	Denys & Brown	1982
	490	ERG	Frank and Widder	1999
Nematobrachion sexpinosus	478	ERG	Frank and Widder	1999
Nematobrachion boopis	487	ERG	Frank and Widder	1999
Nematoscelis megalops	465	EX	Fisher & Goldie	1961
	490	ERG	Frank	unpubl.
Stylocheiron maximum	470	EX	Fisher & Goldie	1961
	479	ERG	Frank and Widder	1999
Thysanoessa raschii	460–465	EX	Fisher & Goldie	1961
Thysanopoda acutifrons	480	EX	Fisher & Goldie	1961
Thysanopoda orientalis	478	ERG	Frank and Widder	1999
Suborder Pleocyemata				
Order Decapoda				
Suborder Dendrobranchiata				
Penaeus duorarum	516	EX	Fernandez	1965
Family Oplophoridae				
Acanthephyra curtirostris	510	ERG	Frank & Case	1988a
	485	MSP	Hiller-Adams, Widder & Case	1988
Acanthephyra smithi	510	ERG	Frank & Case	1988a
	491	MSP	Hiller-Adams, Widder & Case	1988
Janicella spinacauda	400 & 500	ERG	Frank & Case	1988a
Notostomus gibbosus	490	ERG	Frank & Case	1988a
Notostomus elegans	490	ERG	Frank & Case	1988a
Oplophorus gracilirostris	400 & 500	ERG	Frank & Case	1988a
Oplophorus spinosus	400 & 500	ERG	Frank & Case	1988a
Systellaspis debilis	400 & 500	ERG	Frank & Case	1988a
	493	MSP	Hiller-Adams, Widder & Case	1988
	410 & 498	MSP	Cronin & Frank	1996
Family Pasiphaedae				
Paciphaea multidentata	497	ERG	Frank and Widder	1999
Family Penaeidae				
Funchalia villosa	489	ERG	Frank and Widder	1999
Faimly Sergestidae				
Sergestes tenuiremis	495	MSP	Hiller-Adams, Widder & Case	1988
Sergestes similis	495	MSP	Lindsay et al	1999
Sergestes arcticus	495	ERG	Frank and Widder	1999
Sergestes corniculum	500	ERG	Frank and Widder	1999
Sergia grandis	500	ERG	Frank and Widder	1999
Suborder Pleocyemata				
Infraorder Caridea				
Family Palaemonidae				
Palaemonetes palludosus	539	EX	Fernandez	1965
Palaemonetes vulgaris	390 & 540	ERG	Wald & Seldin	1968
Family Bresiliidae				
Rimicaris exoculata	500	EX	vanDover, Szuts, Chamberlain, Cann	1989

TABLE 18.1. *Continued*

Species	λ_{max} (MSP) S-max /nm	Method of study	Author(s)	Year
Infraorder Astacidea				
Astacus fluviatilis	530	MSP	Hamacher & Kohl	1981
Astacus leptodactylus	530	MSP	Hamacher & Stieve	1984
Homarus americanus	515	EX	Wald & Hubbard	1957
	515	MSP	Bruno, Barnes & Goldsmith	1977
Orconectes rusticus	530	MSP	Goldsmith	1978
	535	MSP	Cronin & Goldsmith	1982
Procambarus clarkii	640	IC	Nosaki	1969
	530	MSP	Cronin & Goldsmith	1982
	567 (A2)	MSP	Zeiger & Goldsmith	1989
	560,600,640	MSP	Cronin & Hariyama	2002
Procambarus milleri	440 & 530	IC	Cummins & Goldsmith	1981
Camberellus schufeldtii	522	MSP	Crandall and Cronin	1995
Cambarus ludovicianus	526	MSP	Crandall and Cronin	1995
Engaeus cunicularius	529	MSP	Crandall and Cronin	1995
Nephrops norvegicus	522	MSP	Crandall and Cronin	1995
Homarus gammarus	496	MSP	Marshall, Kent & Cronin	1999b
Infraorder Palinura				
Panulirus argus	504	EX	Fernandez	1965
Infraorder Anomura				
Pleuroncodes planipes	503	EX	Fernandez	1973
	523	IC	Fernandez	1973
Superfamily Paguridea				
Family Diogenidae				
Clibanarius vittatus	510	MSP	Cronin & Forward	1988
Dardanus fucosus	511	MSP	Cronin & Forward	1988
Petrochirus diogenes	508	MSP	Cronin & Forward	1988
Family Coenobitidae				
Coenobita clypeatus	508	MSP	Cronin & Forward	1988
Coenobita rugosa	491	MSP	Cronin & Forward	1988
Family Paguridae				
Pagurus annulipes	495	MSP	Cronin & Forward	1988
Pagurus longicarpus	515	MSP	Cronin & Forward	1988
Pagurus pollicaris	515	MSP	Cronin & Forward	1988
Superfamily Galatheoidea				
Family Porcellanidae				
Polyonyx gibbesi	—	MSP	Cronin & Forward	1988
Superfamily Hippoidea				
Family Hippoidae				
Emerita talpoida	—	MSP	Cronin & Forward	1988
Infraorder Brachyura				
Hemigrapsus edwardsii	513	EX	Briggs	1961
Leptograpsus variegtus	513	EX	Briggs	1961
	484	IC	Stowe	1980
Section Oxystomata				
Family Calappidae				
Calappa flammea	486	MSP	Cronin & Forward	1988
Hepatus epheliticus	487	MSP	Cronin & Forward	1988
Section Oxyrhyncha				
Family Majidae				
Libinia dubia	489	MSP	Cronin & Forward	1988
Libinia emarginata	493	MSP	Briggs	1961
	493	MSP	Hays & Goldsmith	1969

TABLE 18.1. *Continued*

Species	λ_{max} (MSP) S-max /nm	Method of study	Author(s)	Year
Section Cancridea				
Cancer irroratus	496	MSP	Cronin & Forward	1988
Pandalus borealis (nauplius)	475–500	ERG	Eaton and Brown	1970
Section Brachyrhyncha				
Family Portunidae				
Arenaeus cribrarius	498	MSP	Cronin & Forward	1988
Callinectes ornatus	501	MSP	Cronin & Forward	1988
Callinectes sapidus	477	EX	Bruno & Goldsmith	1973
	440 & 508	IC	Martin & Mote	1982
Carcinus maenas	503	MSP	Cronin & Forward	1988
	508	B	Horridge	1967
	508	MSP	Bruno, Mote & Goldsmith	1973
Ovipales stephensoni	440 & 508	IC	Martin & Mote	1982
Portunus spinimanus	505	MSP	Cronin & Forward	1988
	483	MSP	Cronin & Forward	1988
Family Xanthidae				
Eurypanopeous depressus	490	MSP	Cronin & Forward	1988
Menippe mercenaria	494	MSP	Cronin & Forward	1988
Panopeus herbstii	493	MSP	Cronin & Forward	1988
Panopeous obesus	493	MSP	Cronin & Forward	1988
Pilumnus sayi	489	MSP	Cronin & Forward	1988
Rhithropanopeus harrisii	495	MSP	Cronin & Forward	1988
Family Geryonidae				
Geryon quinquendens	473	MSP	Cronin & Forward	1988
Family Grapsidae				
Sesarma cinereum	492	MSP	Cronin & Forward	1988
Sesarma reticulatum	508	IC	Scott & Mote	1973
	493	MSP	Cronin & Forward	1988
Family Ocypodidae				
Uca pugilator	508	IC	Scott & Mote	1973
Uca pugnax	508	IC	Scott & Mote	1973
Family Gecarcinidae				
Gecarcinus lateralis	510	ERG	Lall & Cronin	1987
	487	MSP	Cronin & Forward	1988
Superorder Peracaridia				
Order Mysida				
Gnathophausia ingens	490 & 520	ERG	Frank & Case	1988b
Order Isopoda				
Ligia	330,460 & 520	ERG	Hariyama, Tsukahara & Meyer-Rochow	1993
Order Amphipoda				
Suborder Hyperiidae				
Phronima sedentaria	470	ERG	Frank and Widder	1999
	480	MSP	Cronin and Marshall	Unpubl
Recent Reviews			Marshall, Kent Cronin	1999a
			Cronin & Hariyama	2002
			Cronin & Marshall	In Press

λ_{max} from MSP and S-max from a variety of methods. For the stomatopoda, where known, both l-max and S-max calculated from λ_{max} and intrarhabdomal filtering are given. Numbers in brackets are total numbers of visual pigments. Abbreviations as follows: MSP—microspectrophotometry, EX—visual pigment extract, OP—optical physiology, ERG—electroretinogram, EON—extracellular/optic nerve, IC—intracellular electrophysiology, B—behavioral, BP—behavioral/phototaxis, CS—calculated sensitivity.

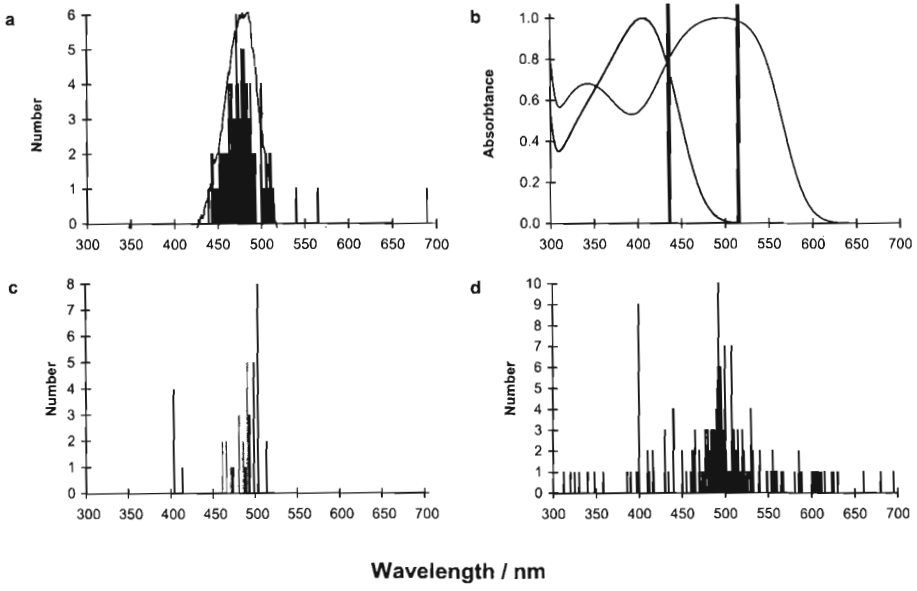


FIGURE 18.2. Spectral sensitivities in crustaceans and the light they may try to capture. (a) The peak wavelengths of bioluminescent emissions plotted as a histogram. (Data from Latz et al., 1988.) Also shown is irradiance at 335 m in clear ocean water near Cuba (solid line—normalized to 6 to fit existing axis). (Widder and Frank, unpublished.) (b) Spectral sensitivities of the midwater oplophorid shrimp *Systellaspis debilis*. Curves are calculated absorptance and therefore take into account photo pigment density and photoreceptor length. (Marshall et al., 1999b.) The vertical bars encompass the spectral region in which most bioluminescent emissions are found (see a). (c) Peak sensitivities of photoreceptors in euphausiids (gray) compared to oplophorids and sergestids (black). (d) Spectral sensitivity maxima of all crustaceans studied thus far. Most of the apparent diversity is from stomatopods. (Data summarized in Marshall et al., 1999b.)

chromophore embedded in the center of a 7-helix transmembrane protein. Changes in either of these two subunits can affect spectral tuning (λ_{max}) and a brief examination of this with respect to chromophore changes is included in Section 3.4. Changes in opsin amino acid sequence have been linked with λ_{max} for some time (e.g., Nathans, 1989); however, little molecular work has been attempted with crustaceans (Sacamoto et al., 1996). Interestingly, in common with some vertebrates, the crab *Hemigrapsus sanguinensis* shows multiple expression of opsin types in one cell type (each of the R1–7 cells; Sacamoto et al., 1996; Shand et al., 2001; Chapter 8). Until more complete genomic libraries and expression systems are developed, the significance of this, and the other revelations this powerful technique is likely to bring, remain in the background for crustaceans. Especially in light of the "natural molecular laboratory" offered by the 16 spectral sensitivities of stomatopods, each possibly based on different opsins (Section 3.5), this is an area in desperate need of further research.

3. Crustaceans' Spectral Sensitivity

Before we examine the array of spectral sensitivities crustaceans exhibit and the evolutionary

pressures, environmental and otherwise, which mold them, some discussion of the photoreceptor types in crustacean eyes is worthwhile. Many crustacean compound eyes, including those in most decapod, mysid, and stomatopod species, contain two anatomically distinct photoreceptor classes. Seven retinular cells (therefore called R1–7), construct the main portion of the rhabdom, and a single cell, R8, forms a smaller, usually distally placed part (e.g., Eguchi and Waterman, 1967; Marshall et al., 1991a,b). Both R8 and R1–7 cells contribute microvilli, or membrane tubes, to the rhabdom, and it is within these that the light-absorbing visual pigment molecule is located. All R8 cells known contain relatively short-wavelength, UV- or violet-sensitive visual pigment and R1–7 cells generally contain visual pigments maximally sensitive in the blue/green region of the spectrum. This pattern is found in many decapods including crabs (Martin and Mote, 1982; Cronin and Forward, 1988; Forward et al., 1988), crayfish (Cummins and Goldsmith, 1981), lobsters (Cummins et al., 1984), and decapod shrimps (Frank and Case 1988a; Frank and Widder, 1994a,b; Cronin and Frank, 1996).

R8 cells in some of the deep-sea decapods and other crustaceans are lost or greatly reduced, as the increasingly blue light from the surface or bioluminescent sources becomes the only light available, resulting in these species having monochromatic visual systems (Table 18.1; Fig. 18.2). In addition, R8 cells are small, and many studies including MSP and electrophysiology have probably missed their contribution to the retina, and erroneously concluded that these species have monochromatic visual systems. The crabs and crayfish are good examples, as almost all examined anatomically so far possess R8 cells (Eguchi and Waterman, 1967; Eguchi, 1973; Stowe et al., 1986; Marshall, unpublished; and see brief review in Marshall et al., 1991). The intracellular study of Martin and Mote (1982) found functional R8 cells in two species of crab, *Ovipales stephensoni* and *Callinectes sapidus*, and another intracellular investigation (Cummins and Goldsmith, 1981) revealed its presence in the crayfish *Procambarus milleri* (Table 18.1). Functional ultraviolet (UV)/violet-sensitive R8 cells are likely to be present in many crabs and crayfish and this is not obvious from Table 18.1.

Where examined, the nondecapod crustaceans with the typical R8/R1–7 cell arrangement, such as some squilloid stomatopods, sometimes possess this basic UV-violet + blue-green spectral sensitivity pattern (Cronin, 1985; J. Marshall and T.W. Cronin, unpublished). Seemingly dependent on their habitat, other squilloids reduce or lose their R8 cells (Schiff, 1963; Cronin, 1985). In the gonodactyloid and lysiosquilloid stomatopods, the basic theme is still present but has been greatly expanded upon (Section 3.4). ERG has demonstrated the presence of two spectral sensitivities, peaking at 490 nm and 520 nm, in the deep-sea mysid *Gnathophausia ingens* (Frank and Case, 1988b). Although at least some mysids do possess R8 cells (Hallberg, 1977), the precise anatomical positions of the two spectral mechanisms in *G. ingens*, along with reasons for their rather long-wavelength sensitivity for a deep-sea animal, are yet to be determined (Frank and Case, 1988b).

One other large crustacean order, which has previously received some attention, is the Euphausiacea. Where examined, these oceanic and often deep-living (mesopelagic) shrimp have only seven retinular cells, all with the one spectral sensitivity. It is unknown whether R8 cells in this group were secondarily lost. The flurry of other sensitivities found in *Meganyctiphanes norvegica* in the late 1950s and early 1960s (Table 18.1) is probably due to methodological problems (Frank and Widder, 1999). Isopods and amphipod eyes examined contain five or seven retinular cells, generally in a monomorphic population (Edwards, 1969; Ball, 1977; Hallberg et al., 1980; Hallberg and Nilsson, 1983).

3.1. Spectral Sensitivities in Different Habitats: Comparisons of Freshwater, Shoreline, and Open Ocean

Where spectral sensitivities lie in clusters (Fig. 18.2), functional reasons are often sought as an explanation. Ecological explanations behind λ_{max} positions in several animals, including crustaceans, center around optimization of the photoreceptors for maximum sensitivity according to habitat light regime (Bayliss et al., 1936;

TABLE 18.2. A phylogenetic analysis of current knowledge of crustacean spectral sensitivities.

Class	Subclass	Superorder	Order	Suborder	Infraorder	Spectral sensitivities	Number of spectral sensitivities	Example reference (See Table 18.1 for full listing)
Remipedia			Nectiopoda					
			Enantiopoda					
Cephalocardia								
Branchiopoda	Sarsostraca		Anostraca			*	1	Hertel (1972)
	Calmanostraca		Notostraca					
	Diplostraca		Cladocera			*	4	Smith and Macagno (1990)
			Conchostraca					
Maxillopoda	Ostracoda	Myodocopa						
		Podacopa						
		Palaeocopa						
	Mystacocarida							
	Copepoda		Calanoida			*	1	Stearns and Forward (1984)
			Harpacticoida					
			Cyclopoida					
			Poecilostomatoida					
			Siphonostomatoida					
			Monstrilloida					
			Misophirioda					
			Mormonilloida					
	Branchiura							
	Cirripedia		Thoracica			*	1	Hillman et al. (1973)
			Ascothoracia					
			Acrothoracica					
			Rhizocephala					
	Tantulocarida							
Malacostraca	Phyllocarida		Leptostraca					
	Eumalacostraca	Hoploarida	Stomatopoda			**	1,2,16	Cronin and Marshall (1989a,b)
		Syncarida	Bathynellacea					
			Anaspidacea					

Eucarida	Euphausiacea			**	1,(3)	Boden et al. (1961), Frank and Widder (1999)
	Amphionidacea					
	Decapoda	Dendrobranchiata		*	1	Fernandez (1965)
		Pleocyemata	Caridea	**	1,2	Frank and Case (1988a), Marshall et al. (1999b)
			Stenopodidea			
			Thalassinidea			
			Astacidea	*	1,2,4	Cummins and Goldsmith (1981)
			Palinura	*	2	Cummins et al. (1984)
			Anomura	**	1	Cronin and Forward (1988)
			Brachyura	**	1,2	Cronin and Forward (1988)
Peracarida	Mysida			*	2	Frank and Case (1988a), Marshall et al. (1999b)
	Lophogastrida					
	Cumacea					
	Tanaidacea					
	Mictacea					
	Spelaeogriphacea					
	Thermosbaenacea					
	Isopoda	Gnathiidea				
		Anthuridea				
		Flabellifera				
		Oniscidea		*	3	Hariyama et al. (1993)
		Valvifera				
		Phreatoicidea				
		Asellota				
		Epicaridea				
		Calabozoidea				
	Amphipoda	Gammaridea				
		Hyperiidea		*	1	Frank and Widder (1999)
		Caprellidea				
		Ingofiellidea				

*Species examined.
**More than 10 species examined.
Numbers in brackets indicate doubtful results (Frank and Widder, 1999).
Crustacean groups down to infraorder are tabulated and, where known, spectral sensitivities scored. Knowledge exists of spectral sensitivities in only 9 of the existing 36 orders and often these data are from one species only. Best known are the Decapoda, Stomatopoda, and Euphausiacea.

Clarke, 1936; Lythgoe, 1979; Cronin and Forward, 1988; Forward et al., 1988; Marshall et al., 1999b). Light penetrating clear, deep ocean waters is maximally bright, close to 475 nm (Figs. 18.2 and 18.3; Jerlov, 1976; Frank and Widder, 1996). This blue-water environment generally shifts to green closer to the coast, and in fresh waters, yellow light may penetrate further than other wavelengths (Fig. 18.3; Jerlov, 1976; Lythgoe, 1979). As with fishes (Lythgoe, 1979), freshwater crustaceans generally possess longer-wavelength sensitivity than their marine counterparts (Fig. 18.3; Table 18.1). Crustacean R1–7 cell sensitivities in the marine environment lie mostly between 460 and 525 nm, while the range in freshwater crustaceans is 510–567 nm but may go up to 640 nm in winter crayfish (Table 18.1; Fig. 18.3; and see Section 3.3).

Optimization, or at least correlation of spectral sensitivity to habitat, is found within the marine habitat. Crabs are often intertidal coast dwellers or reef dwellers, experiencing the greener water of these habitats (Jerlov, 1976). Their R1–7 spectral sensitivities, having maxima between 473 and 523 nm (average 499 nm, Table 18.1; Figs. 18.2 and 18.3), lie toward the long-wavelength side of those known in crustaceans. The euphausiid shrimps (krill), on the other hand, are open-water, often deep-living crustaceans and their sensitivities peak between 460 and 490 nm (average 475 nm; Table

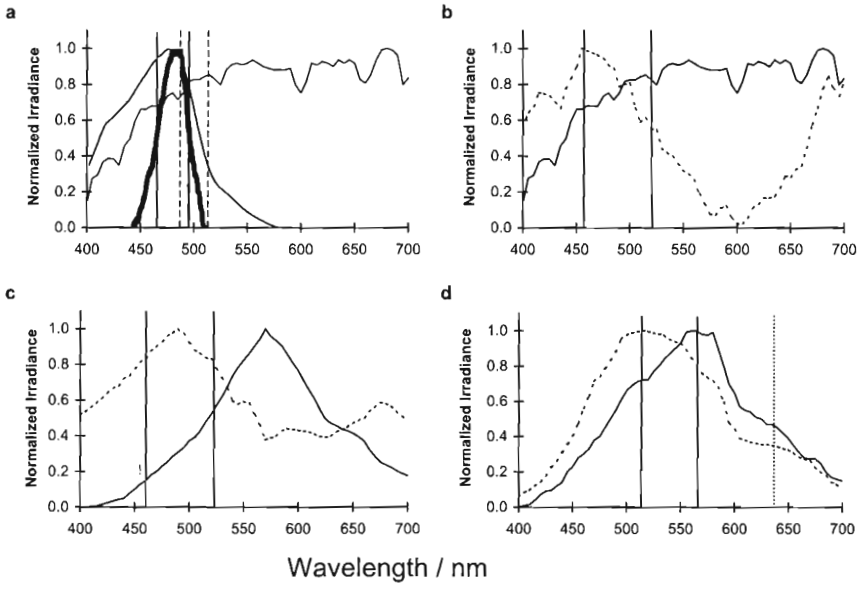


FIGURE 18.3. Light environments and spectral sensitivity ranges of crustaceans in different habitats. (a) Normalized irradiance at 3 m, 60 m, and 335 m (progressively thicker lines) in clear oceanic water. (Deep-water data from the ocean close to Cuba, Widder and Frank, unpublished; 3 m data from Munz and McFarland, 1973.) Solid vertical lines encompass spectral sensitivity maxima of euphausiids; dotted vertical lines encompass spectral sensitivity maxima of oplophorid and sergestid shrimps. (b) Irradiance at 3 m in clear oceanic reef water at noon (solid line) and after sunset (dotted line). (Data from Eniwetok atoll in the Pacific ocean—Munz and McFarland, 1973.) Solid vertical lines encompass all R1–7 cell sensitivities in most monochromatic and dichromatic marine crustaceans. (c) Light at noon (solid line) and just after dark (dotted line) in an estuary. Crab R1–7 spectral sensitivities lie between the vertical lines. (Light data from Munz and McFarland, 1977) (d) Freshwater crustacean light environment (Lake Michigan, from Forward et al., 1988) at noon (solid) and dusk (dotted) and spectral sensitivity range of most R1–7 cells (between vertical solid lines). The vertical dotted line marks the peak sensitivity in winter Japanese crayfish *Procambarus clarkii*.

18.1; Figs. 18.2 and 18.3), closely matching the blue peak transmission of such waters. The non-euphausiid ocean dwellers seem to be exceptions to the "sensitivity rule" for reasons discussed in Section 3.2.

The R1–7 photoreceptors of shallow-living marine crustaceans are perhaps best adapted to the crepuscular light environment (Fig. 18.3; Marshall et al., 1999b) rather than the daytime spectral world of their respective habitats. This is certainly true for coastal crustaceans, such as crabs (Fig. 18.2; Cronin and Forward, 1988), whose spectral sensitivities are better matched to the spectrum of light reaching them at dawn and dusk (Fig. 18.3). This trend, an extension of the sensitivity hypothesis, is also apparent in marine fishes (McFarland and Munz, 1975; McFarland, 1991), and it may be that for many shallow-living marine animals, it is most critical to have good vision during this time of day. On coral reefs it is a period of intense predation (McFarland, 1991), and a variety of crustaceans become more active during these periods (Forward et al., 1988). The day and night light environments in freshwater are more similar to each other than in shallow marine habitats (Fig. 18.3). In freshwater the overriding factor in light quality is the organic and suspended particle content of the water (Jerlov, 1976).

Shallow-water crustaceans, in any habitat other than the most turbid waters, have broad-spectrum light available for vision (Fig. 18.3). In theory, they could place spectral sensitivities almost anywhere and indeed, one group, the stomatopods, have literally done this (Section 3.4). Aside from this exception, however, R1–7 cell sensitivities peak between 460 and 525 nm, a spectral window containing almost 45% of all light at dawn and dusk. It seems that being closely tuned to the light experienced during crepuscular periods is of utmost importance to many crustaceans (Fig. 18.3).

The reason why R8 cell sensitivities are clustered around 400 nm is obscure. For crustaceans in shallow environments, there are certainly plenty of photons available in this spectral region and, in fact, even in clear oceanic waters there may be enough UV photons for effective vision several hundred meters down (Frank and Widder, 1994a,b, 1996; Section 3.2). One advantage of two spectrally distinct sensitivities is that they can form the basis of a color vision system. However, good evidence for this has yet to be conclusively shown in any dichromatic crustacean. Initial suggestions of the existence of color vision in fiddler crabs have not been satisfactorily replicated (Hyatt, 1975). As we shall see in Section 3.4, color vision has been mastered in one crustacean group, the stomatopods.

Finally in this section, the littoral isopod *Ligia exotica* deserves a mention, for this woodlouse-like crustacean is trichromatic, with sensitivities at 330, 460, and 520 nm (Hariyama et al., 1993). *L. exotica* certainly has broad-spectrum light in its habitat, but reasons for its spectral diversity in behavioral or ecological terms remain a tantalizing mystery.

3.2. Spectral Sensitivities in the Open Ocean and Deep-Sea

As we have just seen, the euphausiids seem to have adapted to their blue-water world by maximizing the sensitivity of their eyes to this environment. The spectral sensitivity range of their visual systems is also a good match to bioluminescent sources of light (Fig. 18.2). As shown a number of years ago, the most effective spectral sensitivity position for detecting small spots of light may not be an exact match to the light emitted, but this is critically dependent on background contrast (Lythgoe, 1966, 1968; Loew and Lythgoe, 1978). A spectral sensitivity matched to downwelling light is good for spotting dark targets against the lighter background, such as, for example, looking up from 400 m during the day. A spectral sensitivity offset from the maximum irradiance is more useful for the detection of light objects against a darker background (Lythgoe, 1966). The target could be a bioluminescent flash, which exceeds the intensity of the downwelling light. That many euphausiids seem to favor the former strategy may suggest that, for them at least, detecting small silhouettes overhead, whether they be predator, prey, or conspecifics, is important. Alternatively, at night,

when the background has no photons in it, bioluminescence will always be best detected by a spectral sensitivity matched to it (Land, 1981a; Warrant, 1999; and see Chapter 16). It also seems possible that euphausiid vision may be good for this task; however, other than knowing that they undergo diurnal vertical migration in huge swarms, more needs to be known about euphausiid biology before answering these questions (Frank and Widder, 1999).

It is interesting that one other group of mesopelagic crustaceans, the hyperiid amphipods, also match their spectral sensitivity to the downwelling light or bioluminescence (Table 18.1; Frank and Widder, 1999; T.W. Cronin and J. Marshall, unpublished). Intriguingly, both euphausiids and hyperiids often have split or double eyes with one-half looking up and the other half down (Land et al., 1979; Land, 1981). It would make a nice story if upper and lower lobes in the eyes of either group had different spectral sensitivities, one for examining bright bioluminescent sources against the dim depths and one for spotting dark spots against downwelling light. All indications so far, however, are that, while the optics are certainly different (Land et al., 1979; Land, 1981), the spectral sensitivities are essentially identical (Frank and Widder, 1999; T.W. Cronin, unpublished). In fact, the spectral distribution of light in both upwelling and downwelling light in the lower part of the mesopelagic realm, where many of these animals live, is very similar (Jerlov, 1976; Denton, 1990), so, in this sense, similar spectral sensitivity over the whole eye, despite its optical subdivisions, is not a surprise.

Several of the other deep-sea crustaceans known are likely dichromats. This includes the oplophorids and mysids, while the sergestids seem anatomically more like the euphausiids in that no functional R8 system has been found. *G. ingens* is the only mysid characterized and, being the only representative of its order, and with fascinatingly orange sensitivity, it and other mysids must remain a wonderful project for the future. With λ_{max} ranging between 490 and 520 nm (average 497 nm), R1–7 cell sensitivity in both the oplophorids and sergestids is longer than would be expected if they were trying to catch all photons from either downwelling light or bioluminescence.

Four possible explanations for this are as follows.

1. R1–7 sensitivity in oplophorids and sergestids is offset from the downwelling light maximum and bioluminescent sources (Fig. 18.3) in order to best *detect* these bright sources against the relatively dimmer background (see discussion above in relation to euphausiids and Lythgoe, 1966).

2. Many mesopelagic crustaceans undergo diurnal vertical migrations of several hundred meters. During these movements, the shrimps face the problem of knowing their depth accurately, and these migrations are critical both for finding food and avoiding predators (Frank and Widder, 1994a,b). One suggested way of doing this visually is by ratiometric comparison of light at different wavelengths, thus overcoming the problem of varying light due to both depth and daytime differences (Frank and Case, 1988a,b). While this may work in the top few hundred meters, below the euphotic zone, there is little change in spectral shape with time or depth (Frank and Widder, 1996). In this oceanic region, therefore, this hypothesis is replaced with the idea that the dichromatic system provides a method for discriminating bioluminescent spectra, as explained in item 3 below (Cronin and Frank, 1996).

3. The R1–7 spectral sensitivity (average 497 nm) and R8 cell sensitivity (usually close to 400 nm) of dichromatic mesopelagic crustaceans is ideal for *discrimination* of bioluminescent sources (Fig. 18.2). Most bioluminescent sources known have peak emissions between 440 nm and 515 nm (Latz et al., 1988). For *Systellaspis debilis*, a mesopelagic dichromat, this represents the region of maximum signal difference between R8 and R1–7 cells (Fig. 18.2). As a result, different bioluminescent emissions or indeed spectral differences between bioluminescence and background will be encoded by large R8/R1–7 cell signal differences. It is not known if such signal comparisons are made by

any deep-sea crustacean or indeed by any malacostracan. However, as bioluminescence is perhaps "the major visual stimulus in the deep-sea" (Frank and Widder, 1999), it is an attractive speculation that the spectral sensitivities of R8 and R1–7 cells have evolved in positions providing maximum interpretation of their meaning (Cronin and Frank, 1996).

4. The exact position of λ_{max} does not matter in deep-sea crustaceans, within limits, as the sensitivity of their R1–7 cells, set by the large dimensions and high visual pigment density, is such that they have effectively equal sensitivity over a broad range (Crescitelli et al., 1985; Hiller-Adams et al., 1988). The R1–7 cell sensitivity for *S. debilis* plotted in Figure 18.2, for example, is calculated according to these parameters (Marshall et al., 1999b) and is *almost* equally sensitive from 470 to 520 nm. Whether *almost* is good enough in the photon-starved depths is by no means certain.

An intriguing idea for the relatively long-wavelength sensitivity in the vent shrimp *Rimicaris exoculata*, and its close relatives, is worth mentioning. It has been suggested that these animals are straining to see light produced from the heat of the deep-water hot vents they inhabit rather than bioluminescence (most vents are below the photic zone—van Dover et al., 1989; Pelli and Chamberlain, 1989). While there may be just enough sensitivity in their 500 nm visual pigment to see the light emitted from the superheated water, this idea has yet to be satisfactorily proven (Land, 1989).

3.3. Freshwater Reexamined: Season, Temperature, and Color Dances

Two unrelated oddities are described here, the tetrachromatic water-flea and seasonal changes in spectral sensitivity in crayfish.

As described above, all visual pigments are constructed from two parts, a chromophore and surrounding opsin or protein part. In crayfish, two different chromophores have been found, retinal (producing A_1 visual pigment) and 3-dehydroretinal (producing A_2 visual pigment). A_2 based visual pigments absorb at longer wavelengths than A_1 equivalents, were first described in the invertebrates in crayfish (Suzuki et al., 1984), and are known in many freshwater vertebrates (Bridges, 1972; Knowles and Dartnall, 1977). A_2 based visual pigments are common in freshwater, evidently to shift spectral sensitivities toward the longer wavelengths of light that characterize such habitats (Lythgoe, 1979). Aquatic animals that migrate from freshwater to seawater and back (such as salmonids or anguilliforms), often switch between the A_1/A_2 systems for this reason (Lythgoe, 1979). Combinations of A_1 and A_2 are known within the same cells of vertebrates and indeed crustaceans (Sakamoto et al., 1996).

The crayfish, *Procambarus clarkii*, changes the 3-dehydroretinal content of its retina seasonally, apparently in response to both light environment and temperature and this has resulted in the variety of spectral sensitivities previously reported (Table 18.1). Recently, Cronin and Hariyama (2002) reported that summer crayfish eyes only contain A_1-based, visual pigment and a single R1–7 spectral sensitivity maximum at 600 nm. Winter crayfish eyes contain both A_1- and A_2-based visual pigments and four different spectral sensitivities at 560 nm (narrow), 600 nm (narrow), 600 nm (broad), and 640 nm (broad). The broad sensitivities are probably A_2-based and the narrow sensitivities A_1-based, and in order to explain the wintertime proliferation a second opsin must be expressed. Two opsins and two chromophore types will result in the four sensitivities seen.

Seasonal changes in mating behavior and water quality may underlie this change in the crayfish's visual world. Mating increases during the Japanese winter and the different spectral sensitivities may help discriminate between the differently colored males and females in muddy winter water (Cronin and Hariyama,

2002). Similar arguments are raised to explain seasonal variation in spectral sensitivity and color in stickleback (Cronly-Dillon and Sharma, 1968) and guppies (Houde and Endler, 1990).

The tiny freshwater water-flea *Daphnia magna* possesses small (22-ommatidia) compound eyes but has a surprising four spectral sensitivities located in its eight cell rhabdoms (Smith and Macagno, 1990). These peak at 348, 434, 525, and 608 nm, but instead of constructing a four-dimensional, tetrachromatic color space, it seems likely that each spectral sensitivity drives a certain behavior and these have been described as color dances by Smith and Baylor (1953). Blue light makes *D. magna* dance in an agitated manner and red light induces calm. How such behavior relates to cladoceran survival is unknown but such wavelength-specific behaviors are also described in lepidopteran insects (Scherer and Kolb, 1987; Kelber, 1996).

3.4. Polychromatic Vision: The Stomatopod Crustaceans

It is in the stomatopods (or mantis shrimps, a very ancient crustacean lineage) that spectral mechanisms reach their greatest complexity in crustaceans and perhaps in all animals. Some stomatopods in the superfamily Squilloidea are like most other crustaceans and have only one or two photoreceptor classes based on no more than a pair of visual pigment types (Cronin, 1985; Cronin et al., 1993). But species in the superfamilies Lysiosquilloidea and Gonodactyloidea express up to 16 different spectral types of photoreceptors in a single retina (Cronin and Marshall, 1989a,b; Cronin et al., 1993, 1994a,c, 1996; Marshall and Oberwinkler, 1999). Stomatopod vision is so different from that of other species that it will receive a rather extended discussion in this chapter.

3.4.1. Stomatopod Retinas, Visual Pigments, and Filter Pigments

To understand the nature of stomatopod vision, a brief discussion of their ocular anatomy is necessary, focusing on the eyes of lysiosquilloids and gonodactyloids (see Horridge, 1978; Manning et al., 1984; Schiff et al., 1986; Marshall et al., 1991a,b; Marshall and Land, 1993a,b; Cronin and Marshall, 2001). Stomatopod compound eyes are typically composed of three ommatidial regions. Two of these form the nearly symmetrical dorsal and ventral halves of the eye, while the third region separates them and forms an equatorial midband, usually with six parallel rows of ommatidia. The dorsal and ventral hemispheric ommatidial arrays resemble those of typical decapod crustaceans. Here, a main rhabdom, formed from a ring of seven retinular cells and containing a middle-wavelength visual pigment, is topped by an eighth retinular cell having an ultraviolet-sensitive rhodopsin (Cronin, 1994; Marshall and Oberwinkler, 1999). In any given species, visual pigments in all these ommatidia are identical, and thus provide, at best, dichromatic vision specialized for polarizational (Marshall et al., 1991a) and spatial (Horridge, 1978; Marshall and Land, 1993a) analysis.

The complex spectral system is confined to the four most dorsal ommatidial rows of the six-row midband. Here, rhabdoms are divided into a series of three to five tiers, depending on the particular retinal location and species being considered (Marshall, 1988; Cronin and Marshall, 1989a,b, 2001, 2002; Marshall et al., 1991a,b). In all lysiosquilloids and gonodactyloids, rhabdoms in Row 1 (the most dorsal) and Row 4 have three tiers: the R8 rhabdomere at the top followed by a main rhabdom that is subdivided into an upper tier formed from three retinular cells overlying a deeper one with rhabdomeres of the four remaining cells. Each tier of the main rhabdom contains a different visual pigment based on a retinal$_1$ chromophore (Goldsmith and Cronin, 1993). The pigment of the distal tier absorbs at shorter wavelengths than that of the proximal tier by about 25 to 50 nm (Cronin and Marshall, 1989a,b, 2001, 2002; Cronin et al., 1993, 1994a, 1996), thereby partially blocking its normal short-wavelength absorption and sharpening its spectral tuning (see Cronin, 1994). This effect can be seen in Figure 18.4 by comparing the panels labeled "Visual Pigments" with the cor-

responding panels for "Spectral Sensitivities"—the sensitivities are more sharply tuned and are slightly more separated than the absorption spectra of the visual pigments alone in Rows 1 and 4.

The other two "chromatic" midband rows take tuning and filtering further (see Cronin and Marshall, 2001). In Rows 2 and 3, the junctions between the rhabdomere of R8 and the topmost tier of the main rhabdom are separated by a section of photostable filter material, generally containing a carotenoid pigment that transmits medium to long wavelengths (Figs. 18.4 and 18.5). By removing light that would normally stimulate the main absorption bands of underlying visual pigments, these unique filters limit the photoreceptor's sensitivity to medium to long wavelengths (Fig. 18.1). In many species (and almost all gonodactyloids) a second filter, transmitting at yet-longer wavelengths, is located between the distal and proximal tiers of the main rhabdom, further tuning spectral sensitivity functions of the most proximal receptor tier. Due to all this filtering, photoreceptors in Rows 2 and 3 of the midband are spectrally specialized to detect light of longer wavelengths (Fig. 18.4), sometimes out to nearly 700 nm.

Together, main rhabdoms of the dorsal four midband rows smother the spectrum from near 400 nm to about 600 or 700 nm with eight narrow, closely spaced receptor classes. Each row specializes in the analysis of a particular region within this range. The pattern illustrated in Figure 18.4 is found in all 16 stomatopod species with six ommatidial rows in the midband region that have been described. In order of increasing wavelength, spectral coverage of each row is as follows: Row 1, Row 4, Row 2, and Row 3. The remaining two rows, the most ventral, are specialized not for spectral analysis of light but for its polarizational analysis (Marshall, 1988; Marshall et al., 1991a, 1999a,b).

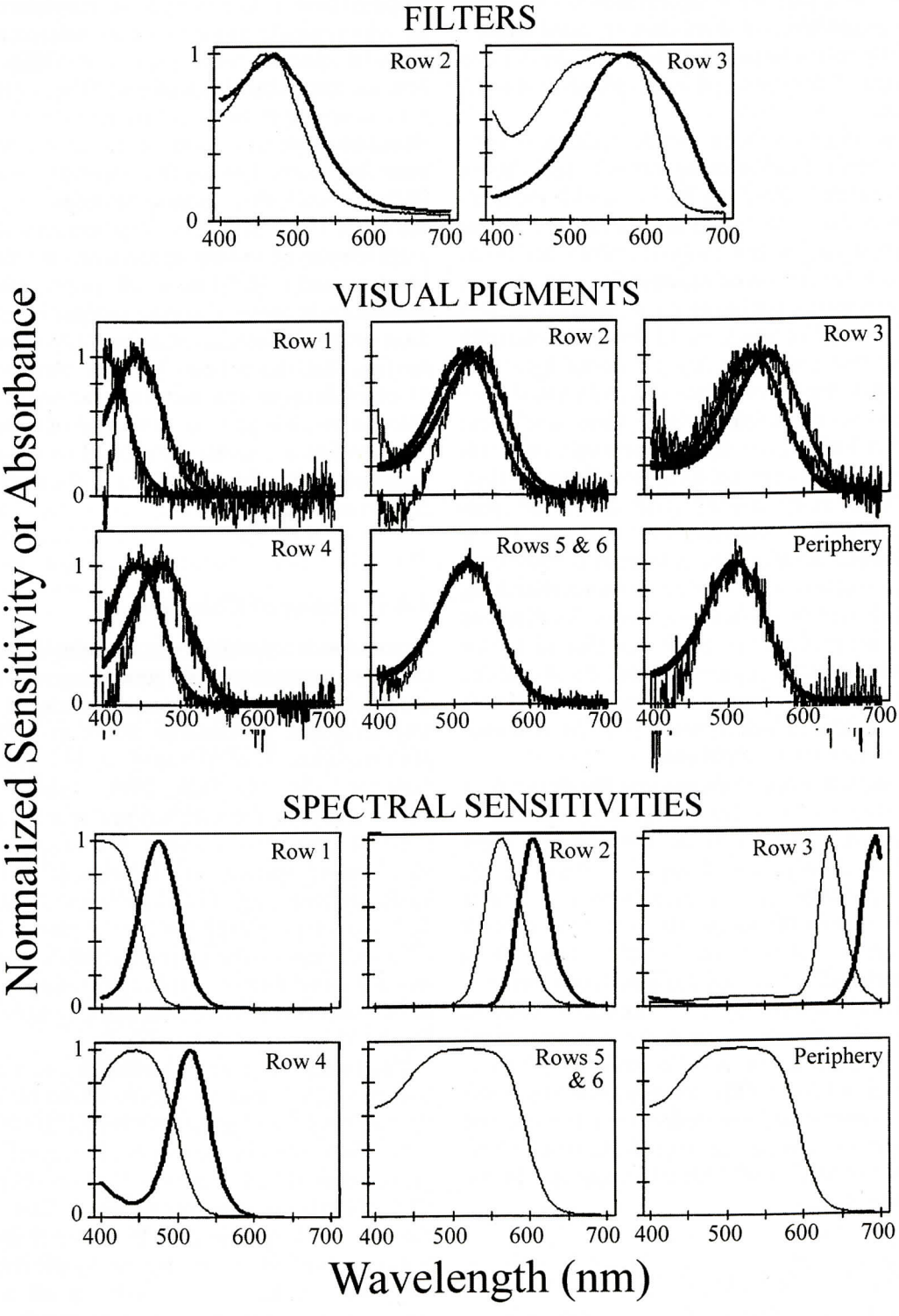
3.4.2. *Color Vision in Stomatopods*

With their complex retinas, visual pigment arrays, and diversity of spectral sensitivity mechanisms, it is no surprise that the stomatopods have true color vision; they can visually discriminate among objects solely on the basis of spectral reflectance. This ability was first suspected by Caldwell and Dingle (1975), who noted that body colors associated with visual displays tend to be more intense in the most aggressive species. Subsequently, Hazlett (1979) found that mantis shrimps evaluate colors of the meral spot, a prominent signal mark displayed during aggressive encounters. Most recently, Marshall et al. (1996) trained stomatopods to discriminate stimuli based on their spectral reflectances, a conclusive demonstration that the animals possess color vision. Mantis shrimps themselves are beautifully colored, and it is possible that some of their signaling colors are spectrally shaped for easy discrimination by other members of their species (Chiao et al., 2000).

3.4.3. *Tuning of Color Vision*

Stomatopods are unique among animals (not to mention crustaceans) in producing narrowly tuned photoreceptor classes by means of serially arranged, photostable filters in a single photoreceptor unit (Cronin et al., 1994a,d; Douglas and Marshall, 1999; Cronin and Marshall, 2001). The numbers and spectral positions of filter classes found in a single retina vary among species and habitats (Fig. 18.5). Lysiosquilloids (e.g., *Lysiosquilla maculata*, Fig. 18.5, top left) typically have fewer classes (two or three) than do the gonodacytyloids, most of which possess four filter types per retina, two in Row 2 and two in Row 3 (remaining panels of Fig. 18.5).

The benefit of narrow tuning is easily realized in shallow marine waters, where incident light is bright and spectrally broad. Here, the very high photon densities overcome the greatly diminished sensitivity that results from all the filtering (Cronin et al., 1994a). This is not the case with species that live deeper in the water column, where absorption by the overlying water diminishes intensities at all wavelengths. Long wavelengths in particular, beyond 550 nm, are severely attenuated even in the clearest marine waters. Therefore, receptors


FILTERS
Row 2
Row 3
VISUAL PIGMENTS
Row 1
Row 2
Row 3
Row 4
Rows 5 & 6
Periphery
SPECTRAL SENSITIVITIES
Row 1
Row 2
Row 3
Row 4
Rows 5 & 6
Periphery
Normalized Sensitivity or Absorbance
Wavelength (nm)
0
1
400
500
600
700

like those of Row 3 in Figure 18.4 would probably be nonfunctional at depths exceeding a few meters.

Nevertheless, many stomatopod species live in deeper water, or are active at night. Their retinas include filter sets that are blue-shifted relative to those of shallower species (Cronin et al., 1994a). This shift in filtering greatly enhances sensitivities of the deeper receptors, because the longest-wavelength receptors (Figs. 18.4 and 18.6) are based on visual pigments that absorb maximally near 550 nm. The peak sensitivities at much longer wavelengths (>650 nm) therefore rely on the merest absorption by the long-wavelength tails of these pigments. Even a small shift to shorter wavelengths in the filter's transmission can produce a huge increase in photon capture, and thus absolute sensitivity, in the underlying photoreceptors.

Filters of *Gonodactyaceus mutatus* (Fig. 18.4) or *Gonodactylus smithii* (Fig. 18.5, middle left panel) typify those of shallow-water gonodactyloids, while those of *Pseudosquilla ciliata* or *Gonodactylellus affinis* (Fig. 18.5, top and middle right) characterize related species from deep water. Note that the filters of Row 3 in the species that live deeper are blue-shifted by 50 nm or more, compared to the corresponding classes in shallow-water retinas. This level of change in the transmission spectra of the filters profoundly affects spectral sensitivities of long-wavelength receptors.

Somewhat surprisingly, the visual pigments of deeper-living species do not show indications of tuning to the photic environment (Fig. 18.6, top). Within each retinal region, the spectral placement of visual pigment λ_{max} certainly varies, but the pattern of this change is not related in any simple way to depth. In the top part of Figure 18.6, λ_{max} positions of visual pigments in main rhabdoms of corresponding retinal regions of all lysiosquilloid and gonodactyloid species characterized to date (16 species) are plotted. The data have been placed into four classes according to the depths at which each species normally lives, from intertidal to deep. In the midband rows devoted to color vision (Rows 1–4), there is a general pattern of increasing λ_{max} in the order of Row 1, 4, 2, and 3, and the proximal tier's pigment visual pigment is always sensitive to longer wavelengths than the distal tier's. While λ_{max} may vary by 15 to 50 nm in any given region across species, there is no particular pattern of change with habitat depth; the ranges tend to overlap nearly completely in species from different habitats. For contrast, note that the visual pigments of the peripheral retina (i.e., the retinal hemispheres) do show the typical

FIGURE 18.4. Filter pigments, visual pigments, and spectral sensitivities of photoreceptors in the retina of the stomatopod crustacean, *Gonodactylaceus mutatus*. *Top:* Normalized absorbance spectra of intrarhabdomal filters in Rows 2 and 3 of midbands of compound eyes. Each panel illustrates filters from one row (light trace, distal filter; dark trace, proximal filter). *Middle:* Normalized absorbance spectra (light, jagged traces) and best-fit templates (dark, smooth traces) of visual pigments in main rhabdoms of each retinal region of compound eyes. Rows 1 through 6 refer to the midband region (Rows 5 and 6 contain the same visual pigment); "periphery" refers to the peripheral retina. Main rhabdoms in Rows 1 through 4 have two tiers, each with a different visual pigment; the visual pigment of the proximal tier always absorbs at longer wavelengths than that of the distal tier. Best-fit template spectra have the following maxima: Row 1 distal tier, 400 nm; Row 1 proximal tier, 443 nm; Row 2 distal tier, 513 nm; Row 2 proximal tier, 527 nm; Row 3 distal tier, 532 nm; Row 3 proximal tier, 553 nm; Row 4 distal tier, 443 nm; Row 4 proximal tier, 475 nm; Rows 5 and 6, 518 nm; peripheral retina, 510 nm. *Bottom:* Computed spectral sensitivities of all main rhabdoms or tiers. Each panel shows the sensitivity of one retinal region, as for visual pigments (above). In panels for Rows 1 through 4, light traces illustrate sensitivities of distal tiers; dark traces illustrate proximal tiers. Sensitivity maxima (rounded to the nearest 5 nm) are as follows: Row 1 distal tier, 400 nm; Row 1 proximal tier, 465 nm; Row 2 distal tier, 560 nm; Row 2 proximal tier, 605 nm; Row 3 distal tier, 635 nm; Row 3 proximal tier, 695 nm; Row 4 distal tier, 445 nm; Row 4 proximal tier, 515 nm; Rows 5 and 6, 520 nm; peripheral retina, 510 nm.

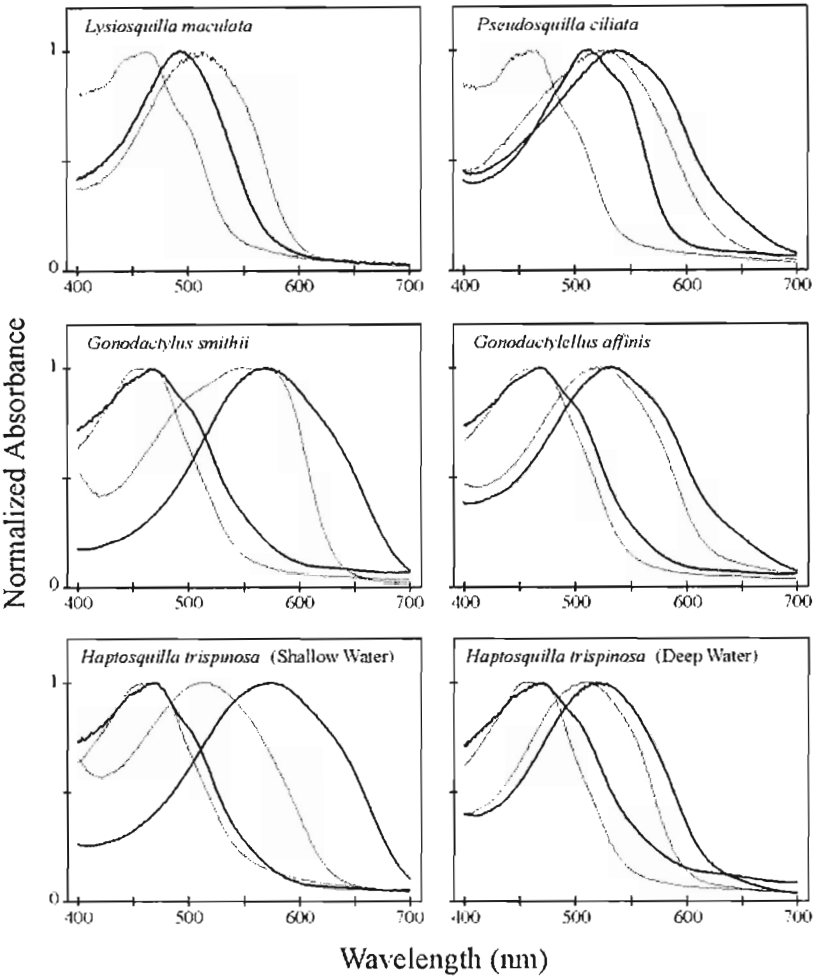


FIGURE 18.5. Normalized absorbance spectra of all filter classes in retinas of selected lysiosquilloid and gonodactyloid stomatopods. The species name is given in each panel. The lysiosquilloid *L. maculata* has only three filter types, while the gonodactyloids (*P. ciliata*, *G. smithii*, *G. affinis*, and *H. trispinosa*) have four types. Distal filters are plotted as thin traces, proximal filters as thick traces. In each panel, the wavelength of maximum absorption proceeds from left to right in the following sequence: Distal filter, Row 2; proximal filter, Row 2; distal filter, Row 3; proximal filter, Row 3. The "shallow-water" filter set was used to compute the sensitivity maxima plotted for *H. trispinosa* in Figure 18.3. See text for further details.

pattern of decreasing λ_{max} with increasing depth (see also Cronin and Marshall, 2002).

The lower half of Figure 18.6 shows how filtering, by visual pigments alone (proximal tiers of Rows 1 and 4) or by the combined effects of visual pigments and filters (Rows 2 and 3), affects peak spectral sensitivity. The effect is by far the greatest in Row 3, where peak spectral sensitivity can be shifted by over 100 nm to longer wavelengths than the visual pigment's λ_{max}. Also, the very-long-wavelength receptors of Row 3 (particularly in the proximal tier), which arise from the use of very long-wavelength-transmissive filters, exist only in gonodactyloid stomatopods that occupy very shallow water. Filtering is much less extreme in gonodactyloids living in deeper water and all lysiosquilloid species (Figs. 18.5 and 18.6).

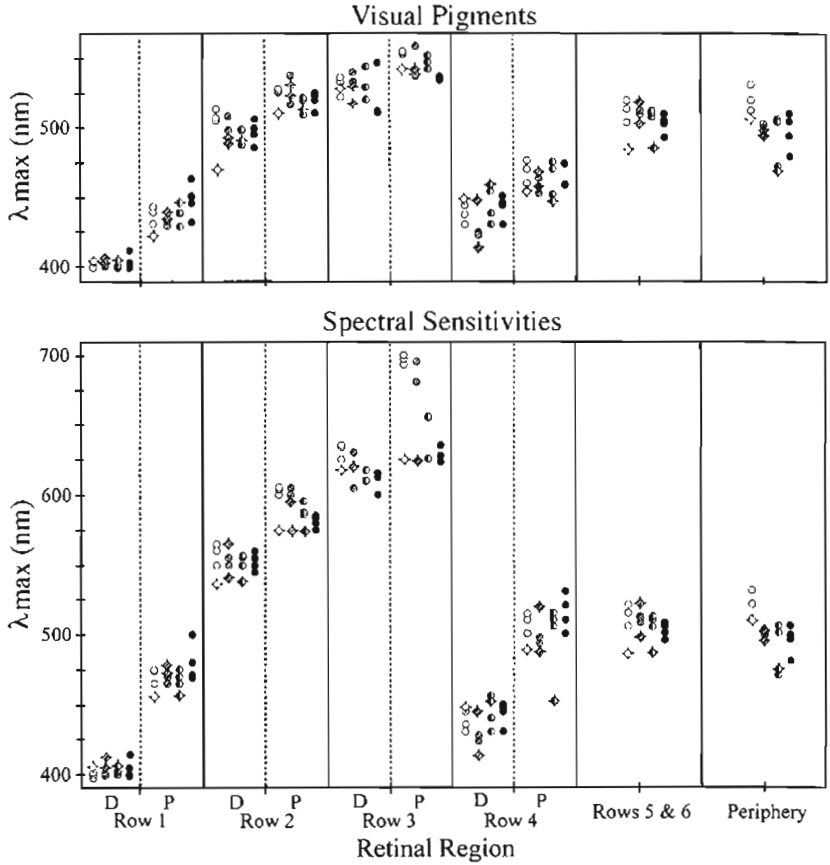


FIGURE 18.6. Spectral maxima of visual pigment absorbances (*top*) and spectral sensitivities (*bottom*) in 4 lysiosquilloid and 12 gonodactyloid species of stomatopod crustaceans from four classes of photic environments. Each panel of the figure includes data from main rhabdoms of all retinal regions, with each plotted point representing data from one receptor class of one species. Each retinal region is plotted in an enclosed rectangle; in the tiered Rows 1 to 4, this area is subdivided by a dashed vertical line so each tier is plotted separately (D, distal tier; P, proximal tier). Species have been assigned to four photic environmental classes, based on their most common depths of occurrence: open circles, intertidal; hatched circles, shallow subtidal (<5 m); half-filled circles, inhabiting a depth range from shallow to deep; filled circles, deep (5–50 m). Gonodactyloid species and their environmental class assignments are as follows: *Gonodactylellus affinis* (range of depths), *Gonodactylaceous mutatus* (intertidal), *Gonodactylus smithii* (intertidal), *Gonodactylopsis spongicola* (range of depths), *Haptosquilla trispinosa* (shallow subtidal), *Hemisquilla ensigera* (deep), *Neogonodactylus curacaoensis* (range of depths), *N. oerstedii* (intertidal), *Odontodactylus brevirostris* (deep), *O. havanensis* (deep), *O. scyllarus* (range of depths), and *Pseudosquilla ciliata* (shallow subtidal). Symbols for lysiosquilloid species are marked with a cross, and are as follows: *Coronis scolopendra* (shallow subtidal), *Lysiosquilla sulcata* (shallow subtidal), *Pullosquilla litoralis* (intertidal), and *P. thomassini* (range of depths).

Among gonodactyloids, there is a clear progression to shorter sensitivity maxima in Row 3 receptors of successively deeper-living species, despite the overall similarities in their visual pigments in this retinal region (Fig. 18.6).

A recent, unexpected finding is that individuals *within* a single stomatopod species have

retinas that are tuned to specific habitats in their overall range of photic environments (Cronin et al., 2001, 2002; Cronin and Caldwell, 2002). In *Haptosquilla trispinosa*, for instance, filters of Row 3 vary among individuals, depending on where each lives (Cronin et al., 2001). This is illustrated in the bottom row of panels in Figure 18.5; note that the filters of deep-water *H. trispinosa* (bottom right) are severely blue-shifted compared to those of the shallow-water individuals (bottom left). The specific tuning to habitat occurs during development, and can be induced in the laboratory by raising young *H. trispinosa* in lighting that mimics illumination in shallow or deep water (Cronin et al., 2001). Recent results suggest that the filters can be altered at any time throughout the life of an individual, illustrating just how flexible the tuning of spectral sensitivity can be.

3.4.4. The Ultraviolet System

Ultraviolet (UV) sensitivity is common among arthropods in general, and crustaceans in particular, but stomatopods sample this spectral range most thoroughly (Cronin et al., 1994b; Marshall and Oberwinkler, 1999). At least four UV receptor types, with λ_{max} from 315 to 380 nm, can be present. Here again, the theme of spectral tuning by filtering recurs. The UV classes all have sensitivity functions that are too narrow for visual pigments alone, and they instead seem to be formed by filtering various UV visual pigments, with λ_{max} ranging from 300 to 370 nm, with nonvisual pigments probably located in the cornea or crystalline cone (Marshall and Oberwinkler, 1999).

While there is as yet no behavioral evidence that stomatopods can discriminate among stimuli based solely on their ultraviolet reflectances, it is likely that their color vision operates throughout a 400-nm spectral range, from ~300 nm to beyond 700 nm, the broadest coverage of any group of animals. Throughout the entire span, receptors remain narrowly tuned by the judicious combination of visual pigments with appropriate filters, matching the series of λ_{max} functions steadily from shortest to longest wavelengths while preserving discrimination at every point. The design promotes outstanding color constancy (Osorio et al., 1997), and may lead to a color vision sense that is defined by a series of wavebands rather than broad opponencies, much as the auditory system samples frequency space.

4. Development of Crustacean Spectral Sensitivity Mechanisms

Many marine crustacean species pass through larval stages, metamorphosing to the adult form. Not only is the sensory equipment of larvae and adults likely to be different, but they often inhabit different sensory worlds with divergent sensory requirements. For instance, almost all marine crustaceans are planktonic as larvae, but the adults are often nektonic or benthic. Therefore, changes in eye size, and frequently optical design as well (Nilsson, 1983; Nilsson et al., 1986), are often accompanied by metamorphosis of spectral mechanisms. Crustacean eye development has been recently reviewed (Cronin and Hariyama, 2002; Cronin and Jinks, 2002), and only a very brief account is provided here.

Larval crustaceans probably have the typical dichromatic spectral sensitivity design, with a short-wavelength visual pigment housed in R8 overlying a main rhabdom of 7 retinular cells packed with a middle-wavelength pigment. This is conjectural, however, since all larval visual pigments described to date are from the main rhabdoms (Cronin et al., 1995; Jutte et al., 1998; Cronin and Jinks, 2002), with spectral maxima ranging from 447 to 509 nm.

While data concerning changes in visual pigments are sparse, it appears that many species retain the larval pigment as adults; this is the case with the crab *Callinectes sapidus* (Cronin et al., 1995) or the squilloid stomatopod *Squilla empusa* (Cronin and Jinks, 2002). However, in polychromatic stomatopod species the retina completely turns over at metamorphosis; the larval retina is rejected, and an entirely new adult-type retina appears (Williams et al., 1985; Cronin et al., 1995). In these cases, the larval visual pigments apparently do not survive metamorphosis, and the adult retina

not only introduces the photostable retinal filters but also expresses a new set of visual pigments. As in other aspects of their visual physiology, compound eye development in gonodactyloid and lysiosquilloid stomatopods is unusual.

5. Temporal Aspects of Crustacean Vision

Animals are challenged with the task of detecting movement and predator/prey locations under a wide range of light intensities. This requires balancing high sensitivity against the competing demand of high resolution in order to obtain the most comprehensive picture under each lighting condition.

One mechanism for dramatically improving photon capture is to increase the integration time of the photoreceptor (Pirenne and Denton, 1952; Pirenne, 1967; Lythgoe, 1979; Snyder, 1979), that is, increasing the temporal summation. This would have the same effect as leaving the shutter open longer on a camera in dim light (Lythgoe, 1979), and comes at the cost of temporal resolution. However, an analysis by Warrant (1999) demonstrated that, in the absence of summation (both spatial and temporal), the ability to resolve detail is lost at much higher intensities than when summation is occurring. Therefore, he concluded that the improvement in photon capture in dim light due to summation far outweighs losses in spatial and temporal resolution. In addition, his model predicts that animals trying to see small, slowly moving objects are better off if temporal summation is employed as a strategy for improving photon capture rather than spatial summation, and that for the detection of point sources (which are common sources of light in the marine environment where bioluminescence is so prevalent), spatial summation is not very effective (Chapter 16). Srinivasan and Bernard (1975) determined that the spatial resolution of objects moving at angular velocities above a critical value is also dependent on photoreceptor dynamics in the compound eye. These last two points are of particular importance for crustaceans: The vast majority of crustacean species are aquatic, so either they or their prey must be constantly moving, and for deep-living marine species, bioluminescent point sources are the prevailing light stimuli. Therefore, any comprehensive analysis of the visual systems of crustaceans should include the temporal characteristics of the photoreceptor.

Classic studies by Autrum (1950, 1958) on intact eyes of terrestrial arthropods gave rise to the idea that the temporal response characteristics of photoreceptors match the habitat and lifestyle of the organism. More recent studies on the intracellular responses of single cells (Howard et al., 1984; de Souza and Ventura, 1989; Laughlin and Weckstrom, 1993) support this idea in that the response characteristics of photoreceptor cells from slow-moving nocturnal species are considerably slower than those of fast-moving, diurnal species. One would predict the same type of match for crustaceans, with the photoreceptors of those species inhabiting dim-light environments showing slower response dynamics than those inhabiting bright-light environments.

Determination of the maximum flicker fusion frequency (FFF), which is the maximum flicker rate the eye is capable of following at any light intensity, has been used most often in comparative studies of temporal resolution in crustaceans. Comparing results from these studies (Fig. 18.7 and Table 18.3) shows that, in general, the trend observed for insects is also present for crustaceans. For terrestrial crustaceans, those species that inhabit a bright environment during the day (the day-active terrestrial isopods *Ligia occidentalis* and *L. italica* and the hermit crab *Pagurus*) have considerably higher flicker fusion frequencies (50–120 Hz) than the wood lice (*Porcellio* and *Armadillo*), which are nocturnal and hide beneath stones during the day (24–32 Hz). For aquatic species, the shallow-living species (water louse *Asellus*, rock lobster *Jasus edwarsii*, and crayfish *Cambarus*) have considerably higher flicker fusion frequencies (50–60 Hz) than the deeper-living marine species (17–32 Hz), as one would anticipate due to differences in their ambient daytime light fields.

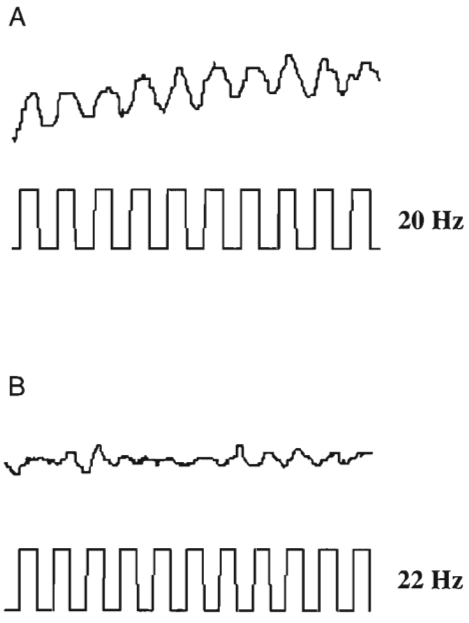


FIGURE 18.7. Representative example of flicker fusion frequency. Top trace is the electroretinogram (ERG) response recorded from the eye of the penaeid shrimp, *Funchalia villosa*. Lower trace is the flickering light stimulus. Data shown are 0.5 s of a 2-s stimulus pulse. (A) The eye was able to follow the stimulus light at 20 Hz. (B) The eye was not able to follow the stimulus light at 22 Hz. The critical flicker fusion frequency for the specimen is 20 Hz, as this was the highest frequency, at any irradiance, at which the ERG of this specimen was able accurately to match the phase of the stimulus light.

The ambient light field in the marine environment at a depth of 400 m in Jerlov's Type 1 or 1A water (the clearest ocean water; Jerlov, 1976) is equivalent to that provided by moonlight for nocturnal terrestrial species (Munz and McFarland, 1973; Land, 1981a,b), and therefore one might anticipate that the maximum FFF of these deeper-living marine species would be equivalent to that of the two terrestrial nocturnal species that have been studied. This is indeed the case, with some rather notable exceptions. The euphausiid crustaceans (*Stylocheiron* and *Nematobrachion*), which all have daytime depths below 250 m, have flicker fusion frequencies (40–50 Hz) approaching those of the shallow-living species. This brings up the issue that for coastal and open-ocean crustacean species, matching temporal resolution to the ambient light field takes on added complexity due to the prevalence of bioluminescence in the marine environment. The euphausiids, which appear to possess photoreceptors with flicker fusion frequencies too fast for their dim ambient light environment, feed primarily on rapidly moving, bioluminescent copepods. Since their prey might be visible as a rapidly moving bright light against a dark background, the advantages of higher temporal resolution might outweigh the disadvantages of lower sensitivity.

Two other studies have been conducted on the temporal characteristics of crustacean photoreceptors, utilizing intermediate light levels to look at flicker fusion frequencies (Moeller and Case, 1995) and frequency responses to sinusoidal light stimuli (Johnson et al., 2000). Because temporal resolution is so strongly dependent on light intensity (Bröcker, 1935; Crozier and Wolf, 1939; Crozier et al., 1939; Frank, 2000), results from these studies cannot be directly compared with results from the studies utilizing the invariant maximum flicker fusion frequency. However, the same general trends are apparent in these two studies, in that the deeper-living and/or slower-moving species from dimmer light environments have slower-responding eyes than the shallower-living and/or more active species from brighter habitats.

6. Conclusion

Crustaceans have long served as model organisms for the study of visual function. Often this has been with the primary concern focused on basic aspects of visual pigment photochemistry or visual processing, or on the applicability of their modular eyes to artificial imaging designs or autonomous systems. While retaining much of this traditional significance, today they are studied mainly either for their own sakes or for their ability to contribute to our understanding of how the visual systems of organisms are specialized for function in challenging environments or for unusual and exotic visual tasks. With their huge diversity of optical designs,

TABLE 18.3. Maximum flicker fusion frequencies and habitat/depth distributions.

Species	Temporal	Habitat/daytime depth
Order Isopoda		
Ligia occidentalis[1]	120	terrestrial, rocky shores
Ligia italica[2]	78	terrestrial, rocky shores
Asellus communis[3]	52	shallow freshwater
Armadillo officinalis[2]	24	terrestrial, nocturnal
Porcellio loewis[2]	32	terrestrial, nocturnal
Order Decapoda		
Pagurus bernhardus[4]	56	terrestrial, rocky shores
Cambarus bartoni[5]	50	shallow freshwater
Jasus edwarsii[6]	60	coastal, sublittoral to 50 m
Funchalia villosa[7,8]	21	open ocean, 300–550 m
Janicella spinacauda[7]	31	open ocean, 500–600 m
Oplophorus gracilirostris[7]	32	open ocean, 500–650 m
Systellaspis debilis[7]	21	open ocean, 600–900 m
Pasiphaea multidentata[8]	17	open ocean, 600–960 m
Sergestes arcticus[8]	24	open ocean, 600–960 m
Sergia filictum[7]	24	open ocean, 600–900 m
Sergia grandis[8]	22	open ocean, 600–900 m
Order Amphipoda		
Phronima sedenteria[8]	27	open ocean, 120–600 m
Order Euphausiacea		
Stylocheiron maximum[7,8]	40	open ocean, 250–500 m
Nematobrachion sexspinosus[7]	50	open ocean, 400–600 m
Nematobrachion flexipes[7]	44	open ocean, 450–600 m

[1] Ruck and Jahn (1954).
[2] Benguerrah and Carricaburu (1976).
[3] Crozier and Zerrahan-Wolf (1939).
[4] Bröcker (1935).
[5] Crozier and Wolf (1939).
[6] Meyer-Rochow and Tiang (1984).
[7] Frank (1999).
[8] Frank (2000).

body plans, habitats, and ecological niches, the crustaceans continue to fascinate students of visual or sensory physiology. They have much to teach us about the evolution, function, and design of sensory systems.

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