

CREPUSCULAR AND NOCTURNAL ACTIVITIES OF
CALIFORNIAN NEARSHORE FISHES, WITH CONSIDERATION OF
THEIR SCOTOPIC VISUAL PIGMENTS AND THE PHOTIC ENVIRONMENT¹

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ABSTRACT

Activities in 27 of the major southern Californian nearshore fish species, with emphasis on trophic relationships, were studied between 1972 and 1975 at Santa Catalina Island. Because these fishes orient primarily by vision, they are strongly influenced by the underwater photic environment, which we define with representative spectra. We center on crepuscular and nocturnal events, but also describe daytime events for comparison.

The species that feed mostly by day include *Atherinops affinis*, *Paralabrax clathratus*, *Girella nigricans*, *Medialuna californiensis*, *Brachyistius frenatus*, *Cymatogaster aggregata*, *Damalichthys vacca*, *Embiotoca jacksoni*, *Chromis punctipinnis*, *Hypsypops rubicunda*, *Halichoeres semicinctus*, *Oxyjulis californica*, *Semicossyphus pulcher*, *Alloclinus holderi*, *Gibbonsia elegans*, *Heterostichus rostratus*, and *Coryphopterus nicholsi*. Those that feed mostly at night include *Scorpaena guttata*, *Sebastes atrovirens*, *S. serranoides* (subadult), *S. serriceps*, *Xenistius californiensis*, *Seriphus politus*, *Umbrina roncadior*, and *Hyperprosopon argenteum*. Those that show no clear diurnal or nocturnal mode include *Leiocottus hirundo* and *Pleuronichthys coenosus*.

Activity patterns tend to be defined less clearly in the warm-temperate fish communities of California than in fish communities of tropical reefs. Included are the twilight patterns of transition between diurnal and nocturnal modes, which are considered to be defined by predation pressures. The lesser definition of twilight patterns in California could mean reduced crepuscular predation there, but we believe that Californian fishes, too, have evolved under severe threats from crepuscular and nocturnal predators. We suggest this is evidenced in the spectral sensitivities of their scotopic visual pigments, which cluster around 500 nm—the best position for vision during twilight and at night in Californian coastal waters.

Although the scotopic system dominates vision in dim light, the spectral sensitivities of the scotopic pigments are poorly matched to the major forms of incident light at night—moonlight and starlight. Rather, they match twilight and bioluminescence, which favor similar spectral sensitivities. We believe this benefits these fishes most on defense. The match with twilight, when the low levels of incident light shift briefly to shorter wavelengths, enhances vision during the crepuscular periods of intensified threats from predators. And the match with bioluminescence permits fishes to react to threatening moves in nocturnal predators by responding to luminescing plankton that fire in the turbulence generated by these moves.

Most fishes that live in southern Californian coastal waters orient by vision, and so are strongly influenced by the characteristics of underwater light at different times of the diel cycle. Knowing that these variations in light are accompanied by differing behavior patterns in the fishes (Hobson and Chess 1976; Ebeling and Bray 1976), we consider here circumstances during twilight and at night, when light is reduced and the fishes'

scotopic (dim-light sensitive) visual systems are operating (McFarland and Munz 1975c). A later report will consider circumstances during daylight. We relate the crepuscular and nocturnal activities of the fishes and their scotopic visual pigments to the spectral composition of light in their warm-temperate habitat, and compare these relationships with the similar ties among activities, visual pigments, and light among fishes in tropical waters.

We stress trophic relationships, because we consider these the major forces shaping activity patterns and related sensory systems in these fishes. The species studied are among the more numerous and readily observed in the nearshore warm-temperate eastern Pacific Ocean. Our accounts of

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their activities cover observations over 15 yr in southern California—from San Diego north to Point Conception—but our more detailed observations, along with the light measurements and analysis of visual pigments, refer to Santa Catalina Island (lat. 33°28' N, long. 118°29' W), 35 km from the mainland (Figure 1). Here the water is consistently warmer and more transparent than on the adjacent mainland; during our study surface temperatures ranged between about 11° and 20° C, and underwater visibility generally exceeded 10 m. Thus, when related to comparable data collected earlier in the tropics (Hobson 1968a, 1972, 1974; Munz and McFarland 1973; McFarland and Munz 1975a), these results offer a conservative measure of differences between warm-temperate and tropical habitats.

METHODS

Determining the Spectral Composition of Submarine Sunlight

The spectral distribution of submarine light was measured with a Gamma 3000R spectroradiometer⁴ mounted in an underwater housing (Munz and McFarland 1973). The instrument, fitted with

⁴Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

a cosine receptor head and calibrated in photons per square centimeter per nanometer per second, draws a quantal irradiance spectrum. Radiance of the backlighting along a particular line of sight was measured by restricting the angle of view of the receptor head to a narrow cone (ca. 0.008 steradians). Usually radiance was determined along the zenith, horizontal, and nadir lines of sight.

Because we were interested in comparing the spectral distribution of submarine light for different water conditions and along different lines of sight, results have been normalized and are presented in terms of relative number of photons. The light levels that occur at twilight were beyond the spectroradiometer's sensitivity for measurement of spectral radiance. At twilight, therefore, spectral irradiance and not spectral radiance was measured. Irradiance data are reported in terms of absolute numbers of photons.

To facilitate comparisons, several of the spectral curves were indexed by calculating their λP_{50} values (Munz and McFarland 1973; McFarland and Munz 1975a). The λP_{50} value represents the wavelength within the visible spectrum (400-700 nm) that halves the total number of photons under a spectral curve. Because underwater light is usually homochromatic and fairly symmetrical in distribution, λP_{50} provides a useful single index to a spectrum.

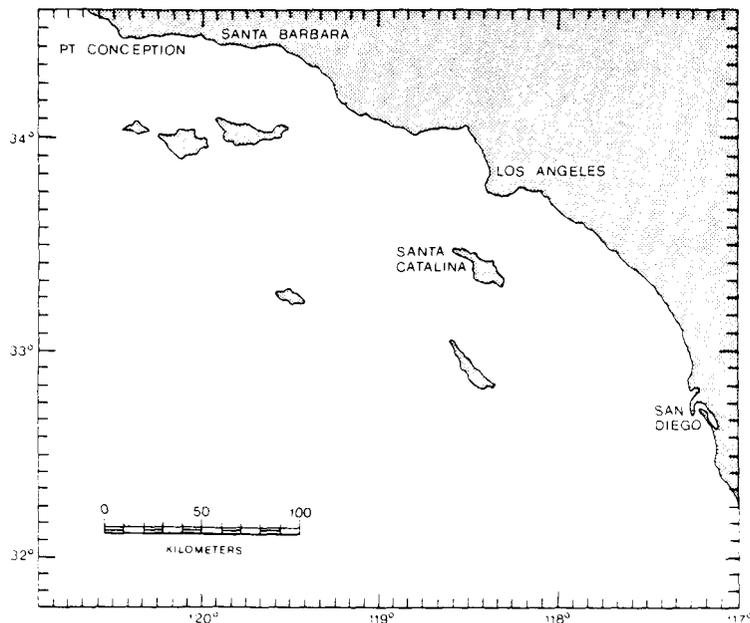


FIGURE 1.—The study area in southern California. Santa Catalina Island was the site of detailed observations, including light measurements and analysis of visual pigments in fishes.

Determining Activity Patterns in Fishes

Our accounts of activity patterns in the fishes stem from direct underwater observations and from study of gut contents. The underwater observations were made using scuba and by snorkeling during all hours of day and night. The gut contents were from fishes speared at all hours of day and night, but primarily during late afternoon and within 2 h before first morning light—times which best distinguish diurnal and nocturnal habits. To study the gut contents, the digestive tract of each fish specimen was removed immediately after collection and preserved in a 10% formaldehyde solution. Analysis under a binocular dissecting scope was performed later in the laboratory. We note in this report only major food items that we believe might add insight to our accounts of diel activity patterns. More detailed accounts of the food habits are given elsewhere (Hobson and Chess 1976; in prep.). All measurements of fish size are of standard length (SL). Although our accounts center on crepuscular and nocturnal events, we describe enough of what happens in daylight to consider these events in the context of diel patterns.

Determining Spectral Photosensitivity of Fishes

Two techniques were used to obtain both fresh, and dark-adapted retinæ from the fishes. Some of the specimens were captured alive and dark-adapted under laboratory conditions, whereas others were speared at night and immediately placed in dark containers before being returned to the laboratory for additional treatment. Spectral absorbance characteristics of the visual pigments from these retinæ were determined by standard procedures. After each fish was dark-adapted, its eyes were enucleated, the retinæ were removed under deep red light (Wratten #2 filter), and then frozen in 4% alum. Later the retinæ were thawed, washed in triplicate, centrifuged, and the pellet extracted in 2% digitonin. Sonication of the pellet at 0° C for 1 min assisted solubilization of the visual pigment. After centrifugation, 10% by volume of saturated sodium borate and 10% by volume of 0.2 M hydroxylamine were added to the supernatant and the spectral absorbance of the extracted visual pigment recorded with a Cary 14 spectrophotometer. The method of partial bleaching (Dartnall 1952) was applied to test whether

each retinal extract was homogeneous or contained more than one visual pigment. Pigment analysis was assisted by a computer program (Munz and Allen 1968) designed to test for homogeneity and also to characterize each visual pigment by estimation of the wavelength of peak absorbance (λ_{max}). Generally, the major photolabile component in a vertebrate retinal extract is the rod visual pigment, and the minor component(s) is the cone visual pigment(s) (Munz and McFarland 1975; McFarland and Munz 1975b). Thus, in each retinal extract from the Catalina samples the dominant pigment is considered the scotopic (or rod) visual pigment.

UNDERWATER PHOTIC ENVIRONMENT

Coastal waters characteristically absorb light of shorter wavelengths than do oceanic waters because they contain more dissolved organic matter. They also scatter more light due to higher concentrations of suspended particulate matter. As a result, they transmit light of longer wavelengths, and, therefore, under a midday sun appear blue-green, rather than blue like the open sea (see Jerlov 1968 for classification of water types). Starting with these well-established facts, we attempted to characterize the underwater photic environment at Santa Catalina Island.

Submarine Daylight

Midday Spectra

Essentially all submarine daylight meaningful to fishes is produced by the sun. Although photic conditions during midday are not our concern in this paper (they will be considered in a later report), midday spectra effectively illustrate some fundamental aspects of the photic environment that are needed to understand scotopic vision in fishes. In particular, midday spectra can be used to define the spectral transmission characteristics of a given water mass, and so provide means to compare the photic environment in Californian coastal waters with the photic conditions elsewhere, including comparisons of crepuscular and nocturnal circumstances between different habitats.

Californian coastal waters vary greatly in the way they transmit light, and while some of this variation is seasonal, much is shorter term and irregular. At times during our study at Santa Catalina very little suspended material was pres-

ent, and underwater visibility exceeded 20 m, but at other times heavy phytoplankton blooms reduced visibility to <3 m. (We define underwater visibility as the horizontal distance over which we could see major environmental features in daylight.) Most of the time, however, conditions were intermediate between these extremes. Although our irregular observations of visibility do not permit a precise figure, we estimate that at least 70% of the time horizontal visibility in daylight was between 8 and 12 m. The images that we saw in these more typical conditions were relatively sharp—more like images seen in clear water than the relatively fuzzy images seen in turbid water.

So in characterizing the photic environment in the surface waters, we recognize three sets of conditions: 1) clear—when visibility exceeded about 15 m amid relatively small amounts of visible suspended or dissolved materials, 2) bloom—when visibility was less than about 5 m owing to dense phytoplankton, and 3) typical—the more usual condition, when circumstances were intermediate to the above. Thus, when visibility was about 20 m in July 1976, the spectral radiance showed the essential blue-greenness of the water (Figure 2: clear curve), whereas when visibility was about 3 m during a phytoplankton bloom in May 1974, the spectra showed a shift toward the yellow-green

wavelengths (with >50% of the photons in the visible spectrum located between 500 and 600 nm; Figure 2: bloom curve). Under bloom conditions, therefore, the radiance was similar to that of lakes rich in plants (McFarland and Munz 1975c). The more usual intermediate condition, however, was closer to the clear than to the bloom condition (Figure 2: typical curve). Nevertheless, even under the clearest conditions encountered at Santa Catalina, the water was greener than it was under similar circumstances in a tropical lagoon (Figure 2: tropical-sea curve).

The spectra depicted in Figure 2 represent a horizontal view, which effectively measures the background spacelight (or horizontal backlighting) against which the fishes studied here see most objects. At the same time we also measured downwelling and upwelling spectra, but they add nothing to the topics considered in this paper that is not illustrated by the horizontal readings. So they will be included in our later paper on photic conditions during midday.

Twilight Spectra

The broad spectrum of downwelling light in near-surface waters at Santa Catalina shifted toward the blue during twilight (Figures 3, 4), even though skylight acquires relatively more red photons at this time. Fading daylight characteristically loses photons between 550 and 700 nm more rapidly than it loses photons below 550 nm, so that as twilight progresses the proportion of photons at the shorter wavelengths steadily increases (McFarland and Munz 1975c; McFarland et al. 1979). The pattern varies in response to changing local conditions, however. For example, on 21 November 1974, events at day's end proceeded typically under a clear sky until shortly after sunset (Figure 3, top and middle panels). At this time, the sky suddenly was covered by a layer of cirrostratus clouds and immediately acquired a red-orange hue (through refraction of the sun's rays). Although we did not record atmospheric spectra at this time, an underwater spectrum recorded 10 min after sunset (Figure 3, bottom panel) was essentially flattened across the visible wavelengths. Other variations in the twilight shift to shorter wavelengths occur under differing water conditions, as exemplified by a weakening of the phenomenon during phytoplankton blooms (Figure 4). The extent of the blue shift during underwater twilight can be measured by the

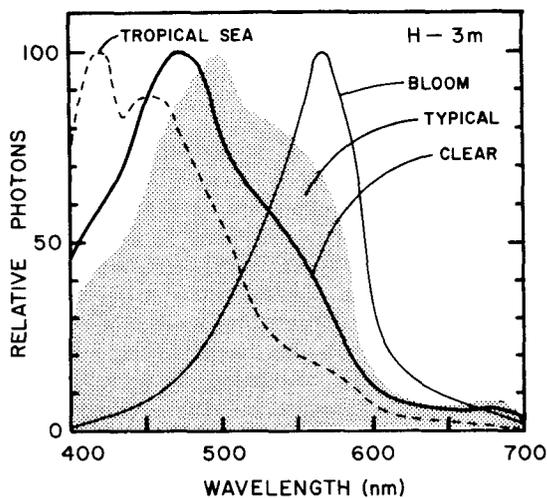


FIGURE 2.—Horizontal spectral radiance in warm-temperate coastal waters (Santa Catalina Island) under typical, bloom, and clear conditions, and in a tropical sea (Enewetak Atoll) under clear conditions. Cosine detector was 3 m below surface oriented horizontally (90° from the zenith). All values normalized, with typical condition at Santa Catalina stippled for emphasis.

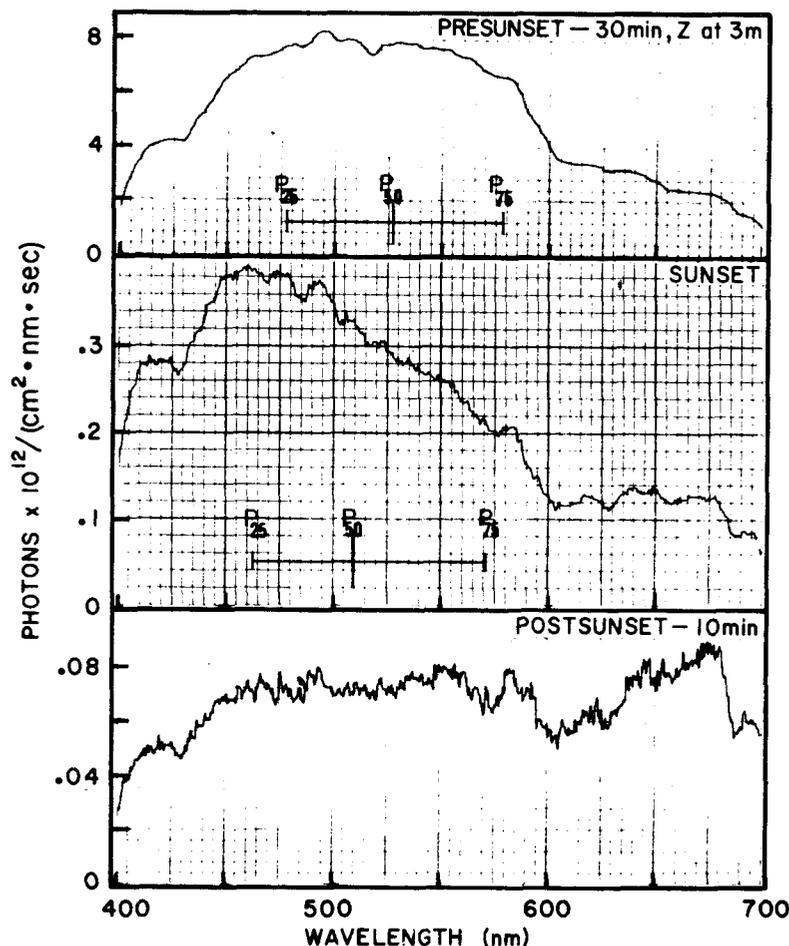


FIGURE 3.—Changes in downwelling submarine spectral irradiance through sunset near the surface at Santa Catalina Island under typical conditions. The shift toward the shorter wavelengths typical of surface waters at sunset (McFarland and Munz 1975c) is apparent in the upper and center graphs, where those wavelengths that divide the number of visible photons into equal quarters are identified by P_{25} , P_{50} , and P_{75} . The bottom graph represents the underwater spectrum when a thin-layer of clouds moved over the sky at about 300 m altitude and demonstrates some of the variability that can stem from meteorological events.

changes in λP_{50} . Thus, during our observations under typical conditions, λP_{50} shifted from a pre-sunset value of 527 to 509 nm (Figure 3), and during bloom conditions from 540 to 528 nm (Figure 4). Presumably the λP_{50} would have been closer to 500 nm had we made comparable measurements during twilight when the water was exceptionally clear.

Submarine Nightlight

Moonlight, starlight, and bioluminescence are the major forms of submarine nightlight meaningful to fishes. We did not measure these during the

present study, but data available in the literature permit a comparison of the spectra each would be expected to produce in water like that typical of Santa Catalina (Figure 5). The influence of moonlight and starlight on activities in fishes and other aquatic predators has been discussed (e.g., Hobson 1965, 1966). This report considers the role of bioluminescent emissions of epipelagic plankton in predator-prey relationships.

Epipelagic bioluminescent plankton, especially dinoflagellates, are widespread in most neritic and oceanic seas (Tett and Kelley 1973). Sailing narratives and logbooks of open water mariners are replete with descriptions of the "phosphorescent

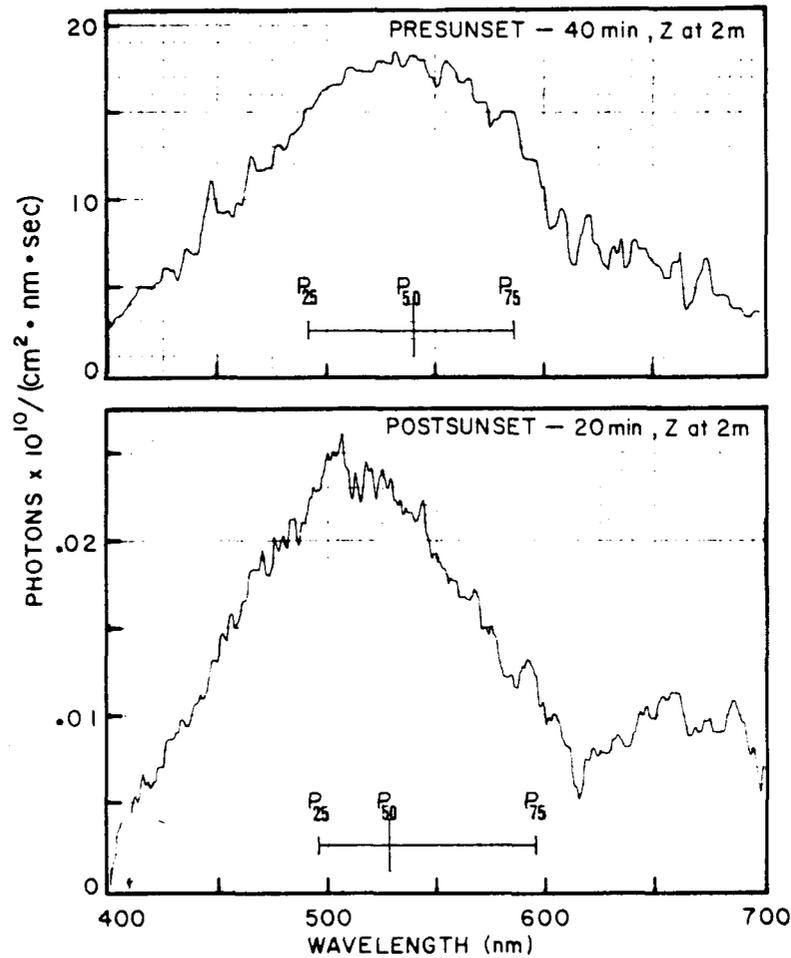


FIGURE 4.—Changes in downwelling submarine light through sunset near the surface at Santa Catalina Island during a phytoplankton bloom. Although there is relatively less blue light under these conditions, a blue shift at and following sunset is nonetheless evident when compared with daylight under bloom conditions (Figure 2). P_{25} , P_{50} , and P_{75} identify those wavelengths that divide the number of visible photons into equal quarters.

fire" of the ship's wake, the luminescent shroud about porpoises running before the bow, and the showers of sparks that trail fishes dashing below the hull. At Santa Catalina Island, bioluminescence from plankton was visible in the water at all times of the year, more so at some times than at others.

Most marine bioluminescent plankton emit light in the blue region of the spectrum (Tett and Kelley 1973). For example, light from *Gonyaulax polyedra* and *Noctiluca miliaris* (which is representative of most dinoflagellates) peaks near 475 nm, and more than half of the photons are emitted below 500 nm (Hastings and Sweeney 1957; Nicol

1958). Because of the skewed emission spectra from these organisms (Figure 6), however, fishes close to the luminescent source would absorb more photons with visual pigments that have λ_{max} values nearer 490 nm than 475 nm.

In any event, the spectral quality of bioluminescence received by the fishes is modified by two variables—distance the fishes are from the light's source, and clarity of the intervening water. Because the water more effectively absorbs the longer than the shorter wavelengths, a fish farther from a target in clear water will receive relatively more photons at the shorter wavelengths (Figure 6, upper panel). Water clarity, however, has an

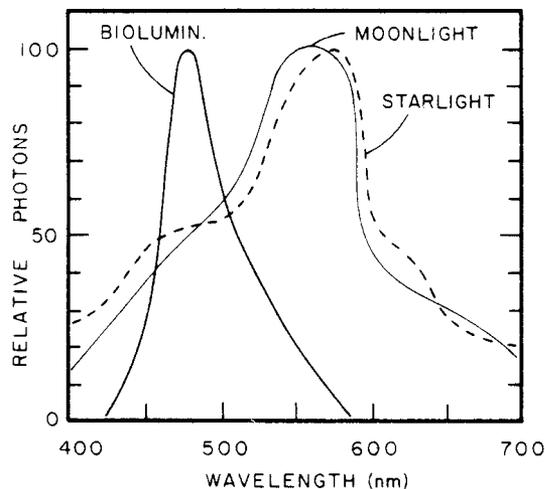


FIGURE 5.—Underwater spectral distributions of moonlight, starlight, and bioluminescence. Values for bioluminescence are for *Noctiluca miliaris*, as given by Nicol (1958), at zero range. Values for moonlight and starlight, based on measurements in Munz and McFarland (1977), are for downwelling light at zero range from a flat spectral reflector at a depth of 3 m in water equivalent to typical conditions at Santa Catalina Island (Jerlov 1968, Coastal Type 1).

even greater effect than distance on the attenuation and spectral modification of submarine light. In the typical water we encountered at Santa Catalina, for example, there was a fairly high transmission of light between 425 and 575 nm. As light travels from a source like *N. miliaris* under these conditions its radiance attenuates slowly and its spectrum shifts only slightly (Figure 6, middle panel). On the other hand, as the same light travels through water heavily loaded with phytoplankton it attenuates rapidly and there is a marked and continuous spectral shift toward the green (Figure 6, lower panel).

ACTIVITY PATTERNS AND VISUAL PIGMENTS IN FISHES

Because the photic environment contrasts sharply between day and night, those visually orienting fishes that are adapted to diurnal conditions should be less suited to feed after dark, while those adapted to nocturnal conditions should be less suited to feed by day. This expectation has been supported in studies of temperate species, both marine (Hobson and Chess 1976; Ebeling and Bray 1976) and freshwater (Emery 1973; Helfman 1979), just as it has in studies of marine fishes in

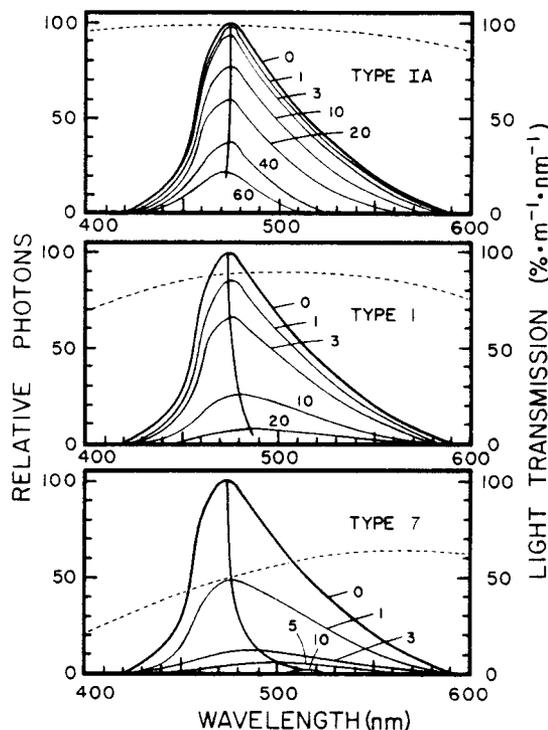


FIGURE 6.—Attenuation and spectral distribution of light emitted by *Noctiluca miliaris* over distance in water of differing clarities. The three panels of the figure each represent a different water type (clarity), as defined by Jerlov (1968): Type IA (upper) is equivalent to clear tropical seas; Coastal Type 1 (middle) is equivalent to typical conditions at Santa Catalina Island; and Coastal Type 7 (lower) is equivalent to conditions of heavy phytoplankton bloom at Santa Catalina. The heavy outer curve in each panel represents the light emitted by *N. miliaris* (left axes) at zero range, and so is the same in each water type. The inner curves in each panel represent relative attenuation of light at distances (in meters) indicated by the accompanying numbers. The broken line in each panel represents the transmission values/meter (right axes) for that water type, as given by Jerlov (1968).

the tropics (Hobson 1965, 1968a, 1972, 1974, 1975; Starck and Davis 1966; Collette and Talbot 1972; Smith and Tyler 1972; Vivien 1973). Thus, in considering the impact of diel variations in the photic environment it is meaningful to distinguish diurnal and nocturnal species, even though some near-shore fishes feed at all hours—many by changing their food or tactics between day and night, e.g., the serranids *Epinephelus labriformis* in the Gulf of California (Hobson 1968a) and *E. merra* in the Indian Ocean (Harmelin-Vivien and Bouchon 1976) and the mullid *Parupeneus bifasciatus* in Hawaii (Hobson 1974).

We consider 27 of the most abundant fish species in the nearshore waters at Santa Catalina Island, describing what each does during twilight and at night, and noting the wavelengths of light to which the scotopic system of each is most sensitive (λ_{\max}). In examining the retinae from the fishes, we noted whether the visual pigments were homogeneous. Significantly, there were no secondary pigments in 12 species and only a trace in 5. Secondary pigments, which presumably are cone pigments (Munz and McFarland 1975), were present in 10 species and abundant in only 3. The data are given below, grouped according to that segment of the diel cycle when the species obtains most of its food. It is important that we observed only slight variation in the λ_{\max} of any one species.

Fishes That Feed Primarily by Day

Some of the fishes that feed primarily by day are known to be inactive at night, but evidence of nocturnal inactivity remains lacking for others, and still others are known to feed routinely after dark. The predominantly diurnal Californian fishes considered in this paper, along with certain of their visual characteristics, are listed in Table 1. The following accounts of diel activities emphasize crepuscular and nocturnal habits.

Atherinidae: *Atherinops affinis*

The topsmelt aggregates by day in the surface waters close to kelp forests, but at night most larger individuals move away from the kelp and disperse close beneath the water's surface over adjacent deeper water. At first we suspected these larger individuals might feed after dark. Their movements are similar to those of tropical Pacific atherinids of the genus *Pranesus*, which are known to be nocturnal feeders (Hobson and Chess 1973; Hobson 1974; Major 1977), and nocturnal habits are widespread in other planktivorous atherinids, including *Allanetta harringtonensis* in the tropical Atlantic Ocean (Starck and Davis 1966). Furthermore, we have often seen *Atherinops affinis* feed at night next to illuminated piers, although we consider this an artificial situation.

Despite the evidence of nocturnal feeding in other atherinids, however, our suspicions concerning *A. affinis* were contradicted by examination of gut contents. Of 22 individuals (129-219 mm SL, \bar{x}

TABLE 1.—Some southern Californian marine fishes that feed primarily by day, with the spectral absorbance maximum (λ_{\max}) of pigments extracted from their retinae.

Family and species	λ_{\max} \pm 95% C.I.	N	Other pigments ¹
Atherinidae:			
<i>Atherinops affinis</i> ²	505.8	2	0
Serranidae:			
<i>Paralabrax clathratus</i> ²	498.8 \pm 2.0	4	+
Kyphosidae:			
<i>Girella nigricans</i>	498.3 \pm 1.0	3	0
<i>Medialuna californiensis</i>	496.9	2	+
Embiotocidae:			
<i>Brachyistius frenatus</i>	500.9 \pm 0.5	3	0
<i>Cymatogaster aggregata</i>	500.4 \pm 4.0	3	+
<i>Damalichthys vacca</i>	500.9	2	+
<i>Embiotoca jacksoni</i> ²	500.8	2	+
Pomacentridae:			
<i>Chromis punctipinnis</i> ²	496.1	1	+
<i>Hypsypops rubicunda</i>	496.3 \pm 0.1	3	0
Labridae:			
<i>Halichoeres semicinctus</i> ³	513.2 \pm 7.4	3	++
<i>Oxyulis californica</i> ³	511.8	1	++
<i>Semicossyphus pulcher</i> ²	496.7 \pm 3.5	3	++
Clindae:			
<i>Alloclinus holderi</i>	496.5	2	0
<i>Gibbonsia elegans</i>	499.7 \pm 8.9	3	+
<i>Heterostichus rostratus</i>	499.7 \pm 2.0	4	T
Gobiidae:			
<i>Coryphopterus nicholsi</i> ²	497.9	1	0
Mean ⁴	499.1		
Range ⁴	496.1-505.8		

¹Other than the primary pigment: 0 = none; T = trace; + = <10%; ++ = >10%.

²Visual pigments for these species were also studied by Munz (1957, 1958b, c, 1964). He reported similar λ_{\max} values for all but *E. jacksoni*, which he listed (Munz 1958b) as 506 nm. The difference can be attributed to varying amounts of secondary pigments in his extracts, which can bias the λ_{\max} estimates if not taken into account.

³Visual pigments in these species are porphyropsins, which are based on the aldehyde of Vitamin A₂. Pigments in all other species are rhodopsins, which are based on the aldehyde of Vitamin A₁.

⁴*Halichoeres semicinctus* and *O. californica* excluded owing to basic differences in their pigments (see footnote 3, above).

= 168.8) collected at dawn as they reassembled in schools along the outer edge of kelp forests, 19 were empty, 2 contained just a few fish scales, and 1 contained calanoids and cyphonautes larvae that appeared recently ingested—probably since sunrise that morning. At least some of the smaller *A. affinis* remain close to the kelp at night, but there is little evidence that they feed during that period. Of 10 (82-160 mm SL, \bar{x} = 102.4) collected close to kelp during the hour before dawn, 9 were empty. The one with food, however, contained three gammarids and one isopod that obviously had been taken at night. In contrast, there is ample evidence that *A. affinis* feeds intensively during the day. We routinely observed this species feeding in the surface waters during all daylight hours, and only 1 of 10 (126-190 mm SL, \bar{x} = 158.6) collected from a large aggregation during midafternoon lacked food in its gut; the other 9 contained \bar{x} = 1,325 prey items, mostly cladocerans and copepods.

Serranidae: *Paralabrax clathratus*

The kelp bass progresses through three major ontogenetic phases based on trophic relationships. The first phase includes juveniles up to about 65 mm SL that feed primarily on zooplankton during the day and pass the night sheltered amid vegetation. The third phase includes the largest individuals—those exceeding about 165 mm SL—which are increasingly piscivorous with growth and may be primarily crepuscular (although limitations in our data leave the feeding chronology at this larger size in question).

In this paper we consider individuals representing the second phase—subadult fish between 65 and 165 mm SL. Individuals of this size feed mostly on crustaceans that live on or close to a substrate by day and swim in the water column after dark, including certain gammarid and caprellid amphipods, isopods, cumaceans, mysids, and carideans. The subadult *P. clathratus* capture these crustaceans mainly by day close to benthic cover. Most subadult *P. clathratus* do not feed at night. Only 42% (13 of 31, 72-163 mm SL, $\bar{x} = 110.3$) of those collected during the hour before sunrise contained prey, whereas there was prey in 96% (51 of 53, 68-153 mm SL, $\bar{x} = 107.9$) of those collected during the afternoon.

Whether or not the subadult *P. clathratus* feeds at night, however, seems related to their location. Most of them are amid rocks and vegetation at night, just as during the day, and here they seem to feed little, if at all. Of 16 (95-146 mm SL, $\bar{x} = 108.6$) collected in these surroundings during the hour before dawn, only 1 (6%) had food in its stomach (a moderately digested caridean). Nocturnal feeding in subadult *P. clathratus* seems to occur mostly in those individuals that move after dark out over open sand (Figure 7)—a habitat only infrequently occupied by them during the day. Of the 16 (72-148 mm SL, $\bar{x} = 97.4$) collected in such places during the hour before dawn 12 (75%) contained food, much of it fresh. Major prey were the cumacean *Cyclaspis nubila* (4 mm), the gammarids *Ampelisca cristata* (3-4 mm) and *Amphideutopus oculatus* (2-3 mm), and the caprellid *Caprella californica* (6-8 mm)—all species that are active on or close above the sand at night. Clearly, the nocturnal move over the sand is a well established feeding pattern in subadult *P. clathratus*. Nevertheless, even under these special circumstances predatory success after dark seems limited. Among specimens from open sand at night the stomachs containing food averaged only 30% full, compared with 66% full for specimens from a wide range of diurnal circumstances.

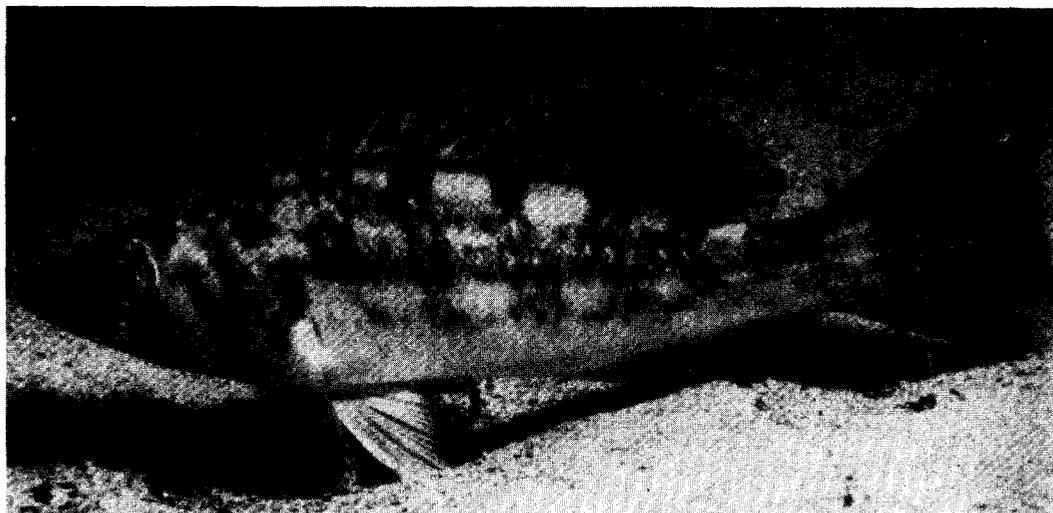


FIGURE 7.—A subadult *Paralabrax clathratus*, about 150 mm SL, alert on open sand at night. Some individuals of this size feed under these circumstances even while larger and smaller conspecifics are inactive close to rocks and algae. Apparently the sand reflects enough moonlight and starlight to permit some predominantly diurnal fishes to feed in these surroundings at night.

Kyphosidae: *Girella nigricans*

The opaleye does not seem to feed extensively at night, although our limited observations on this point are somewhat ambiguous. This rather tenuous opinion rests heavily on two points. First, the species feeds largely on algae, and various organisms that live on algae—a diet generally indicative of diurnal feeding (Hobson 1965, 1974; Vivien 1973). Second, kyphosids generally have been found to feed by day (e.g., Randall 1967). On the other hand, observations of kyphosids at night have indicated a variable condition. *Kyphosus incisor* reportedly rests "...in sheltered, though not confined, locations on the reef-top" in the Florida Keys (Starck and Davis 1966), and *K. elegans* has been noted to behave similarly in the Gulf of California (E. S. Hobson unpubl. obs.). But *K. elegans*, at least, is alert in these shelters, and *K. cinerascens* in Hawaii not only swims above the reef at night, but may feed at this time as well (Hobson 1974). The presence of *G. nigricans* "...in holes or on the bottom..." at night led Ebeling and Bray (1976) to consider it diurnal. We agree with them even though we frequently saw this species swimming in the water column after dark, especially in the kelp forest.

Limited study of gut contents suggest reduced feeding in some *G. nigricans* at night. One (201 mm) sampled among the rocks during the hour before sunrise had an empty stomach, but the stomach of another (264 mm) that was swimming above the bottom at this time was 20% full. Sixty-seven percent of the gut contents in this second individual consisted of motile animals, including gammarids, caprellids, carideans, and the gastropod *Tricolia* sp., whereas only 10% consisted of algae. This material, much of it fresh, differed sharply from that in gut contents of individuals that had been feeding by day. Benthic algae constituted 81% of the material in all 11 individuals (173-255 mm SL, \bar{x} = 206) that were collected during the afternoon, and whose stomachs averaged 75% full; essentially all other items in these individuals were sessile organisms that encrust, or live attached to, algae—principally bryozoans and hydroids.

Kyphosidae: *Medialuna californiensis*

We consider the halfmoon primarily diurnal for essentially the same tenuous reasons that led us to this conclusion for *G. nigricans*: many of its close

relatives reportedly are diurnal, as documented above, and it feeds heavily on plants (Limbaugh 1955; Quast 1968), a diet widely associated with diurnal foraging. Furthermore, we saw *M. californiensis*, like *G. nigricans*, in the water column in far fewer numbers at night than during the day. But although we saw *G. nigricans* in larger numbers close to rocky substrata at night, we saw *M. californiensis*, which was exceptionally numerous in the kelp forests by day, only in sharply reduced numbers there after dark. Reporting a similar situation in a kelp forest at Santa Barbara, Ebeling and Bray (1976) observed about half as many *M. californiensis* on their transect line at night as during the day. They summarized their nocturnal observations by stating that this species "...often appeared to be more sensitive to our presence than were individuals of other species near the bottom, and we cannot deny the possibility that *Medialuna* feeds at night." Leading to much the same position, our study of gut contents from 14 specimens (146-243 mm SL, \bar{x} = 196) collected during the afternoon (Hobson and Chess in prep.) shows that this largely herbivorous species unquestionably feeds by day, but leaves unanswered whether or not it also feeds at night.

Embiotocidae: *Brachyistius frenatus*

Although the kelp perch is basically diurnal throughout life, this characteristic can be somewhat variable. When less than about 100 mm SL it feeds primarily on zooplankters in the water column, and as it grows larger it increasingly turns to tiny prey—mostly crustaceans—that it picks from vegetation (Hobson and Chess 1976). At night it occurs in most of the same places that it occupies by day, but is more numerous in midwater aggregations fully exposed along the outer edges of the kelp forests (Hobson and Chess 1976). Describing the nocturnal condition of this species, Bray and Ebeling (1975) noticed that it "...tended to hang motionlessly along the kelp stipes or even in open water" and added that it was "...quiescent at night and easily caught with a small hand net..." They concluded that *B. frenatus* feeds "...mostly, if not exclusively, during the day"—an opinion based on study of gut contents from specimens collected every 2 h throughout the night. But Hobson and Chess (1976) reported that while *B. frenatus* is primarily diurnal, larger individuals also feed to a limited extent at night. In addition to the data presented in that paper, all of which involved

specimens <100 mm long, 6 of 14 (102-114 mm SL, \bar{x} = 106.8) collected during the hour before dawn contained prey, many of them fresh. The major nocturnal prey, which included the gammarid *Batea transversa* (2-4 mm), the caprellid *Caprella californica* (8-14 mm), and the isopod *Paracercius cordata* (1-6 mm), were organisms that rise into the water column at night. We believe these prey were captured in the water column because most were in fish that had been aggregated in midwater outside the seaward edge of a kelp forest. Perhaps Bray and Ebeling (1975) found no evidence of nocturnal feeding because their sample comprised mostly smaller fish. Significantly, the major organisms apparently taken in the water column at night include the same species picked from the surface of algae by day.

Embiotocidae: *Cymatogaster aggregata*

The shiner perch, which is even more variable in its diel behavior than *Brachyistius frenatus*, has two basic feeding modes: it captures zooplankton, mostly crustaceans, in the water column, and it captures organisms, again mostly crustaceans, that are in, on, or close above a sandy bottom. The planktivorous habit predominates among individuals smaller than about 65 mm SL and continues to be important throughout life, whereas feeding on sand-dwelling forms becomes increasingly important to individuals >65 mm SL until it predominates among the largest individuals. The planktivorous habit is diurnal, whereas feeding on or close to a sandy bottom occurs during both day and night, but mostly at night.

Thus, the small juveniles are primarily day feeders: of 23 (53-64 mm SL, \bar{x} = 58.2) collected during the afternoon, 12 (53%) contained food, the major items being zooplankters (mostly copepods). Only two (12%) also included prey that may have been taken from the seafloor (gammarid fragments). In comparison, only 2 of 17 (37-64 mm SL, \bar{x} = 46.5) collected during the hour before dawn contained food: one (58 mm) contained just a few cumacean fragments, but the other (54 mm) contained a variety of sand-dwelling crustaceans, some fresh, including the cumacean *Cyclaspis nubila* (2-4 mm), the gammarid *Acuminodeutopus heteruopus* (1-2 mm), and the tanaid *Leptochelia dubia* (2-4 mm), along with sand.

The changes in food habits that appear among individuals >65 mm SL were similarly defined. Of 34 (67-110 mm SL, \bar{x} = 91.8) collected during the

afternoon, 27 (79%) contained food presumably taken by day: 19 (70%) of these had fed exclusively on zooplankton (primarily calanoid and cyclopoid copepods and cladocerans), 4 (15%) had taken only sand-dwellers (primarily tanaids and gammarids), and 4 (15%) had fed on both zooplankton and sand-dwellers in large numbers (combinations of the above forms, with the two types sharply separated in the guts). In comparison, of 46 (66-120 mm SL, \bar{x} = 85.9) collected during the hour before dawn, 37 (80%) contained prey, many fresh, that appeared for the most part to have been taken at night. Significantly, all these prey were sand-dwellers, the major forms being the cumacean *Cyclaspis nubila* (2-4 mm), the gammarids *Acuminodeutopus heteruopus* (1-2 mm) and *Ampelisca christata* (2-4 mm), the tanaid *Leptochelia dubia* (3-4 mm), and the ostracod *Euphilomedes carcharondonta* (1-2 mm), along with sand.

Embiotocidae: *Damalichthys vacca* and *Embiotoca jacksoni*

Damalichthys vacca, the pile perch, and *E. jacksoni*, the black perch, both appear to be strictly diurnal feeders. During daytime, adults of *D. vacca* feed primarily on mollusks and other heavily shelled prey, whereas adults of *E. jacksoni* take an exceptionally wide variety of benthic organisms, including polychaetes, mollusks, gammarids, caprellids, isopods, and mysids (Limbaugh 1955; Quast 1968). At night we observed both species hovering close to the seafloor, generally in exposed positions. On the other hand, Ebeling and Bray (1976) reported *D. vacca* "... scattered in the water column at night." That neither species feeds after dark is evidenced by the absence of fresh food in their guts at that time (Ebeling and Bray 1976).

Pomacentridae: *Hypsypops rubicunda* and *Chromis punctipinnis*

Although the Californian pomacentrids—*H. rubicunda*, the garibaldi, and *C. punctipinnis*, the blacksmith—are strictly diurnal fishes that remain relatively inactive in their nocturnal shelters, they nevertheless remain alert throughout the night. *Hypsypops rubicunda*, in fact, often appears restless as it moves in its shelter place. This species is solitary during both day and night, and its nocturnal shelter is a specific hole or crevice in the well-defined territory that also includes its

diurnal foraging area (Clarke 1970). In contrast, *C. punctipinnis* is highly gregarious during both day and night, and often individuals crowd nocturnal shelters among the rocks. When its nocturnal resting places are far from its diurnal feeding grounds, *C. punctipinnis* migrates between the two locations during twilight in prominent processions (Hobson and Chess 1976). These migrations tend to be better defined in the evening than in the morning. At times evening migrations began up to 30 min or more before sunset, while at other times they were not evident until about sunset. Generally, however, the migrations peaked from shortly before sunset until about 15 min after, and then continued at greatly reduced levels for another 10 min or so before ending.

Chromis punctipinnis is among the most numerous species on many nearshore reefs in southern California (Limbaugh 1955; Quast 1968), and in some places apparently there is insufficient rocky shelter to accommodate at night the vast numbers that forage in the water column by day. In such places excess individuals sometimes cluster after dark in dense numbers on the sand next to the reef. Occasionally *C. punctipinnis* is in the water column at night, but does not seem to feed at this time. This is attested by the empty stomachs of all 11 specimens examined from predawn collections by Hobson and Chess (1976).

Labridae: *Oxyjulis californica*, *Halichoeres semicinctus*, and *Semicossyphus pulcher*

The Californian labrids are so obviously quiescent at night that we have no doubt that, like tropical labrids (Hobson 1965, 1974), they do not feed at this time. Also, like their tropical relatives, they follow precise patterns when shifting between diurnal and nocturnal modes (Hobson 1972; Domm and Domm 1973). *Oxyjulis californica*, the señorita, buries in the sand at nightfall (Herald 1961), a habit also attributed to *H. semicinctus*, the rock wrasse, by Limbaugh (1955), who noted that this species "sleeps buried with head protruding." Feder et al. (1974) repeated this statement, as did Fitch and Lavenberg (1975), who reported that it also "burrows between or under rocks to escape predators or to sleep." We found that *H. semicinctus* consistently took nocturnal shelter amid low benthic algae (from which it often was unintentionally flushed by our nocturnal activities). Both *O. californica* and *H. semicinctus*

were consistent in timing their descent to shelter in the evening, and their rise into the water the next morning. Data on the timing of these events were collected during 1973 and 1974 at Fisher-man's Cove, Santa Catalina Island, in a sand-bottomed habitat dominated by the low brown alga *Dictyopteris zonaroides*. The last *O. californica* seen entering the sand on four evenings at this site slipped from view 11-22, $\bar{x} = 16.8$, min after sunset, which agrees with Bray and Ebeling (1975), who on three occasions observed this species entering sand and rubble "About 15 min after sunset...." The first *O. californica* seen here on 11 mornings appeared 11-22, $\bar{x} = 15.8$, min before sunrise. During the same period at this site the last *H. semicinctus* seen taking cover on six evenings disappeared 20-24, $\bar{x} = 22.0$, min after sunset, and the first to appear on 10 mornings emerged 18-25, $\bar{x} = 22.8$, min before sunrise. It may be significant that *H. semicinctus*, which grows to a larger size, tended to be active later in the evening and earlier in the morning. Among diurnal fishes on tropical reefs, the larger individuals tend to retire later and rise earlier (Hobson 1972). Comparable data are lacking for *S. pulcher*, the sheephead (the largest of the three Californian labrids), even though this species was numerous at the observation site during the day. *Semicossyphus pulcher* shelters among rocks at night (Hobson 1968b), and probably because the observation site lacked rocks, this species left the area sometime before going under cover. On 4 evenings the last *S. pulcher* departed the observation site 10-21, $\bar{x} = 18.0$, min after sunset, and on 11 mornings the first to return arrived 11-24, $\bar{x} = 17.0$, min before sunrise. On just one evening, in a nearby rocky area where the species found shelter, the last active *S. pulcher* was seen 30 min after sunset.

Because *S. pulcher* rested in distinctive shelters and was visible throughout the night (Figure 8), it offered the best opportunity to investigate consistency in resting places among individuals. Reportedly, at least some tropical wrasses return each evening to specific resting sites (Winn and Bardach 1960; Starck and Davis 1966; Hobson 1972). So the resting places of nine *S. pulcher* were located at midnight during November 1973, and then revisited at the same hour once each week for 3 wk. On the first return only two of the nine positions were occupied, No. 3 and No. 5—both by what appeared to be the same individuals that had been there before. On the second return, again only two positions were occupied: No. 5 seemed to



FIGURE 8.—A female *Semicossyphus pulcher* at rest on the seafloor at night, showing the typical pattern of its nocturnal hues. Its exposed position is common in this and many other nocturnally resting diurnal fishes in California.

harbor the same fish as before, but this time position No. 1 contained a small individual not seen before. On the final return, position No. 5 once more was occupied by what seemed to be the same fish. Again, just one other position was filled—No. 6, which harbored the fish seen in position No. 9 on the first night (recognized by a notch in its dorsal fin), but which had gone unseen since then. Thus, only one position, No. 5, sheltered a fish each time. And contrary to what one might expect, of the nine positions, No. 5 offered the least cover. It was simply a shallow depression on the reeftop where the resting fish was largely exposed, and certainly would not seem an effective shelter.

Clinidae: *Alloclinus holderi*, *Gibbonsia elegans*, and *Heterostichus rostratus*

The three Californian clinids studied here—A.

holderi, the island kelpfish; *G. elegans*, the spotted kelpfish; and *H. rostratus*, the giant kelpfish—are known to feed regularly by day, based on fresh food in specimens collected during the afternoon (Hobson and Chess in prep.). But it is difficult to determine relative activity in these highly cryptic fishes because they move so infrequently and, therefore, often go unnoticed even when fully exposed. Both *A. holderi*, which sits on rocks, and *G. elegans*, which sits amid benthic algae, retire to shelter at nightfall, as do various tropical clinids (Starck and Davis 1966; Smith and Tyler 1972). *Heterostichus rostratus*, on the other hand, often hovers among columns of giant kelp during both day and night (Figure 9). Our data comparing relative feeding activity in *H. rostratus* between day and night are limited, but indicate that daytime feeding predominates. The one individual (184 mm) collected during the hour before sunrise

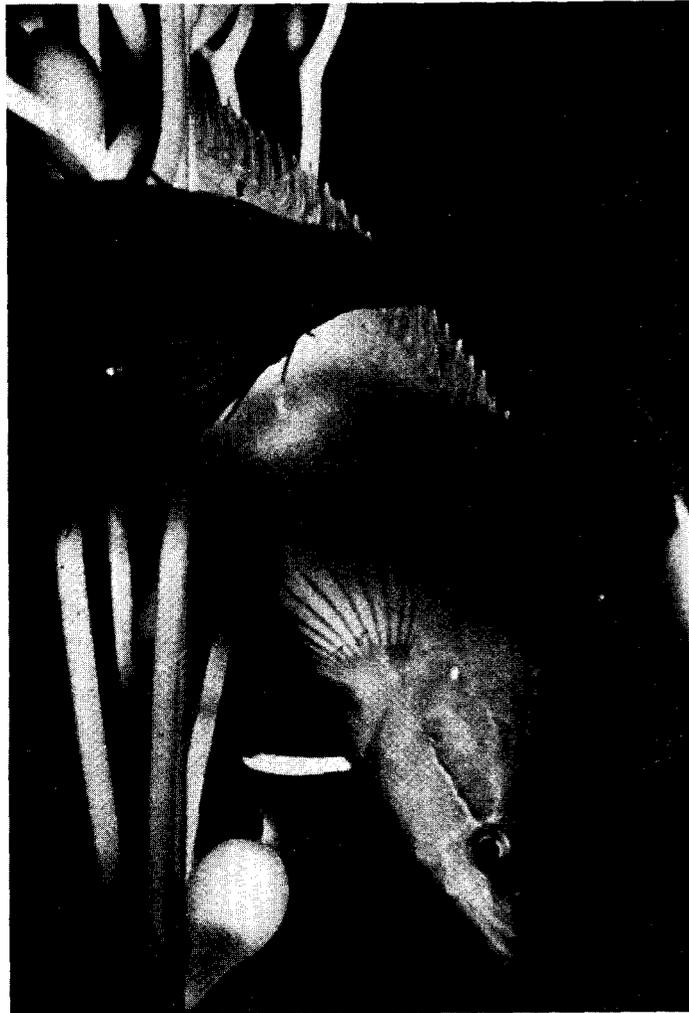


FIGURE 9.—While most of its smaller blennioid relatives go under cover at nightfall, the large clinid *Heterostichus rostratus*, here amid rising kelp stipes at night, shows a similar attitude at all hours, even though it seems to feed primarily by day.

was empty, and the two (163 and 207 mm) collected at midnight contained only well digested fragments. In comparison, among eight individuals (234-385 mm SL, \bar{x} = 280) collected during midafternoon, four contained fresh food, one contained only well digested fragments, and three were empty.

Gobiidae: Coryphopterus nicholsi

Large numbers of the blackeye goby rested in exposed positions on sand bottoms in and around rocks throughout the day, when intermittently,

they darted forward, or a short distance into the water column, and snapped at tiny prey. Few, however, were visible at night. Presumably most sheltered in the reef after dark—a pattern reportedly followed by four species of *Coryphopterus* in the tropical Atlantic Ocean (Smith and Tyler 1972). Gut contents indicate this species feeds little, if at all, after dark. Among the few individuals seen at night, seven (43-83 mm SL, \bar{x} = 59.3) were collected during the hour before the first morning light; the gut of one was empty, and the other six contained only well digested items. In comparison, all 69 specimens (36-90 mm SL, \bar{x} = 64.1) collected

during the afternoon had food in their guts, with 61 of these (88%) containing recently ingested material.

Fishes That Feed Primarily at Night

The fishes that feed primarily at night clearly are specialized to detect and capture prey in the dark; nevertheless, under appropriate circumstances some also take prey during the day. The predominantly nocturnal species considered in this paper, with certain of their visual characteristics, are listed in Table 2. The following accounts of diel activities highlights major features of their crepuscular and nocturnal habits.

Scorpaenidae: *Scorpaena guttata*

The sculpin rests immobile among rocks during the day (Figure 10) and generally is difficult to discern owing to its cryptic features. Although

TABLE 2.—Some southern Californian fishes that feed primarily at night, with the spectral absorbance maximum (λ_{\max}) of pigments extracted from their retinæ.

Family and species	λ_{\max} = 95% C.I.	N	Other pigments ¹
Scorpaenidae:			
<i>Scorpaena guttata</i> ²	496.7	2	0
<i>Sebastes atrovirens</i>	497.5	2	+
<i>S. serranoides</i> (subadult)	501.3	2	+
<i>S. serriceps</i>	496.4±1.0	3	0
Haemulidae:			
<i>Xenistius californiensis</i>	501.8±0.4	2	T
Sciaenidae:			
<i>Seriphus politus</i> ²	502.2±1.5	3	0
<i>Umbrina roncadore</i>	503.1±0.4	3	0
Embiotocidae:			
<i>Hyperprosopon argenteum</i> ²	505.1±0.9	7	0
Mean	501.0		
Range	496.4-505.1		

¹See Table 1, footnote 1.

²See Table 1, footnote 2.

Limbaugh (1955) noted *S. guttata* on open sandy bottoms in deeper (to 60 m) water during the day, at our study sites it generally occurred among rocks. This fish seems well suited by its cryptic and immobile attitude to ambush prey that have come

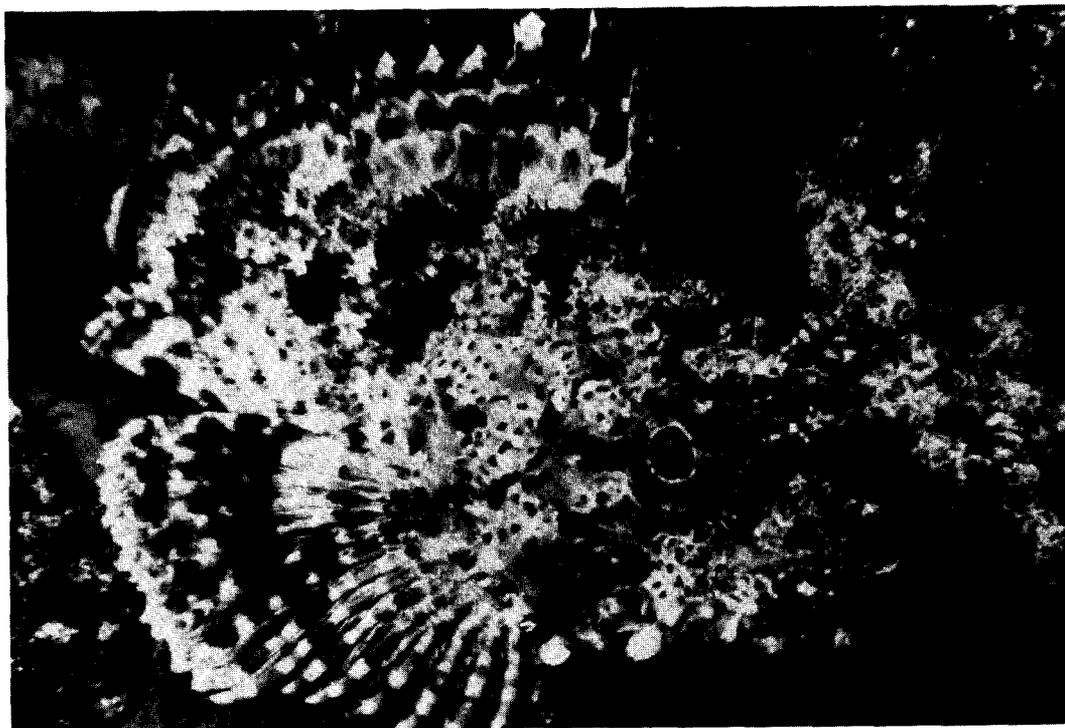


FIGURE 10.—The morphology, coloration, and sedentary behavior of *Scorpaena guttata* render it virtually invisible on the seafloor. Although many tropical scorpaenids use these features to advantage in ambushing prey during the day, *S. guttata* is primarily nocturnal.

within range of a short, explosive rush—a tactic used during the day by the Hawaiian scorpaenid, *Scorpaenopsis cacopsis*, which is similarly cryptic (Hobson 1974). Based on gut contents, however, *Scorpaena guttata* seems to capture most of its prey at night. All seven specimens (140-270 mm SL, \bar{x} = 213) collected during the hour before dawn contained prey, many of them fresh. Major items were the crab *Podocheilia* sp. (7 mm), the shrimps *Lysmata californica* (50 mm) and *Spirontocaris* sp. (15 mm), and the squid *Loligo opalescens* (120-190 mm), a species that was spawning in the area at the time. One *Scorpaena guttata* had captured a 108 mm *Chromis punctipinnis*, a species that shelters among the rocks at night (see above). In comparison, of seven individuals (164-237 mm SL, \bar{x} = 208.3) collected among the rocks during mid-afternoon, the stomachs of four were empty, two contained only well digested octopuses, and one contained recently ingested prey (a crab, *Paraxanthias taylori*, 17 mm wide, and a shrimp, *Alpheus clamator*, 20 mm long). Crabs, shrimps, octopuses,

squids, and fishes are recognized prey of this species (Limbaugh 1955; Quast 1968).

Scorpaenidae: *Sebastes atrovirens*

The kelp rockfish feeds at night while hovering solitarily in the water column close among the giant kelp plants (Figure 11). It is relatively inactive by day—often at rest on rocky substrata or hanging motionless close beneath the kelp canopy. This was the conclusion of Hobson and Chess (1976), who presented details of its diel feeding habits. Of 23 individuals (89-225 mm SL, \bar{x} = 177.5) collected at night, more than 4 h after sunset, 20 (87%) contained prey, many recently ingested. Major prey were mysids (*Siriella pacifica*, 4-10 mm, and *Acanthomysis sculpta*, 4-10 mm), carideans (*Hippolyte clarki*, 7-14 mm, and *Eualus herdmani*, 5-10 mm), a gammarid (*Batea transversa*, 3-4 mm), and an isopod (*Paracercies crodata*, 2-9 mm).



FIGURE 11.—In hovering tail-down close beneath the canopy of a kelp forest, this *Sebastes atrovirens* illustrates an attitude typical of many nocturnal predators that hunt in the water column. From this position they may use the relatively light water's surface as a contrasting background against which prey are visible.

Scorpaenidae: *Sebastes serranoides*

The olive rockfish progresses through stages characterized by distinctive trophic relationships (as described by Hobson and Chess 1976). These stages parallel those described above for the seranid *Paralabrax clathratus*, although the nocturnal element in the subadults is much stronger in *S. serranoides*.

Juveniles appear inshore when they are about 30 mm SL, and feed by day on zooplankton until they have grown to about 55-65 mm. When about 55 mm SL they begin to feed at night, a transition most of them complete by the time they are 65 mm SL. These nocturnal feeders, which are our major concern here, have assumed a pattern of activity that will characterize them until they are about 120-150 mm SL. By day they hover in relatively inactive schools, often at the edge of kelp forests, and during evening twilight they disperse over the surrounding area, where they forage in the water column. Many of them move away from the sheltering kelp to hover solitarily in open water. On the five evenings that the event was noted, the first one seen in a nocturnal mode away from cover was noted 16-30, $\bar{x} = 25.8$, min after sunset. They remain in these positions throughout the night, often assuming a tail-down attitude, now and then darting a few centimeters forward and snapping at objects in the dark water.

When these fish shift to nocturnal foraging they also change their diet. From the copepods and other small zooplankton (about 1-2 mm long) they had taken during their earlier diurnal phase, they now capture larger organisms that swim in the nearshore water column only after dark (Hobson and Chess 1976). These nocturnal food habits were defined by study of gut contents. Of 72 individuals (65-157 mm SL, $\bar{x} = 85$) collected more than 4 h after sunset, 70 (97%) were full of prey, many of them fresh. Major prey were the gammarid *Batea transversa* (2-5 mm), the mysid *Siriella pacifica* (3-9 mm), the cumacean *Cyclaspis nubila* (4-6 mm), the caprellid *Caprella pilidigita* (5-11 mm), and the isopod *Paracercis cordata* (3-6 mm).

Scorpaenidae: *Sebastes serriceps*

The treefish rests in rocky crevices at all hours of day and night, and evidence of specific feeding times is limited; nevertheless, it appears to be predominantly nocturnal or crepuscular. Of six individuals (138-227 mm SL, $\bar{x} = 189.5$) collected

during the hour before dawn, all contained relatively large crustaceans, including the shrimps *Lysmata californica* (12-70 mm), *Alpheus belimianus* (60 mm), and *Spirontocaris* sp. (25 mm). Greatly reduced feeding during the day was evidenced by 22 individuals (122-330 mm SL, $\bar{x} = 276.1$) collected during the afternoon from among rocks; of these, the guts of 13 (59%) were empty, and the other 9 contained material that was for the most part extensively digested—seven had each taken a single *Chromis punctipinnis* (68-135 mm SL), while other prey were the crab *Paraxanthias taylori* (16-38 mm wide), and the carideans *Lysmata californica* (38-45 mm) and *Herbstia parvifrons* (10 mm). Most of these prey had been in the guts for some time: only the two crabs appeared recently ingested. We suspect that all but the two crabs were captured during the previous night or morning twilight. We would expect the crustaceans to have been more accessible after dark, when we have seen the species in exposed locations. Further, the major prey in these collections, *C. punctipinnis*, generally swims high in the water column during the day, and would seem ill-suited then as prey of this bottom-dwelling rockfish. *Chromis punctipinnis* would be more vulnerable at night, when it settles to shelter on the seafloor (see account of *C. punctipinnis* above). However, the absence of *C. punctipinnis* in the guts of *Sebastes serriceps* taken before dawn indicates that the prey in these samples may have been captured during morning twilight, perhaps as they left cover for their ascent into the midwaters.

Haemulidae: *Xenistius californiensis*

The salema assembles in relatively inactive schools during the day, then disperses at nightfall and forages in the water column at night (Hobson and Chess 1976). This diel activity pattern is widespread among the many species of haemulids in tropical waters (Starck and Davis 1966, in the tropical Atlantic, and Hobson 1968a, in the Gulf of California). Frequently *X. californiensis* schools in the upper levels of the water column within the kelp forests, and during twilight, moves considerable distances to nocturnal feeding grounds. One location at Santa Catalina Island, known to be a nocturnal feeding ground for this species, was >400 m from the nearest point where the species had been seen during the day (Hobson and Chess 1976). On four evenings we noted when the first salema arrived on this feeding ground, and this

proved to be between 34 and 40, $\bar{x} = 37.3$, min after sunset. Once there, its behavior was much like that described above for nocturnally feeding olive rockfish. Its diet, too, proved similar to that of the rockfish. All 13 individuals (163-170 mm SL, $\bar{x} = 173.7$) collected more than 3 h after sunset were full of food, much of it fresh. Prey were organisms that are in the nearshore water column only at night, with major forms being the gammarids *Batea transversa* (2-4 mm) and *Ampelisca cristata* (3-8 mm), the caprellid *Caprella pilidigita* (6-12 mm), the cumacean *Cyclaspis nubila* (2-4 mm), the mysid *Siriella pacifica* (4-10 mm), and epitokous nereid polychaetes (15 mm).

Sciaenidae: *Seriphus politus*

The queenfish schools in relatively inactive assemblages near shore during the day and disperses to feed in the water column at night after moving away from its daytime schooling sites (Hobson and Chess 1976). Thus, its diel activity pattern is similar to that of subadult *Sebastes seranoides* and *X. californiensis*, described above. The first *Seriphus politus* appeared at a nocturnal feeding site on four occasions at 38-60, $\bar{x} = 44$, min after sunset. Food and feeding behavior of *S. politus* also are similar to the other two species. All 31 individuals (114-193 mm SL, $\bar{x} = 151$) sampled later than 3 h after sunset contained prey, much of it fresh. All were larger zooplankton that are in the water column only at night, with major forms being mysids (*Siriella pacifica*, 3-11 mm, and *Acanthomysis sculpta*, 6-11 mm), a gammarid (*Batea transversa*, 2-4 mm), and an isopod (*Paracercies* sp., 2-7 mm).

Sciaenidae: *Umbrina roncadore*

The yellowfin croaker schools close to sandy beaches during the day, and at nightfall disperses here and also to the regions immediately offshore. It feeds on organisms in the sediment, often probing with its snout to make the capture. Most of its foraging seems to occur at night. Of 20 individuals (191-255 mm SL, $\bar{x} = 210.8$) collected more than 3 h after sunset, all but 1 contained prey, much of it fresh. Major items were sand-dwelling polychaetes, many of them tubicolous, with *Onuphis* sp. (15-40 mm) and *Nothria stigmaeus* (10-20 mm) predominating; other important prey were sand-dwelling gammarids, especially *Ampelisca cristata* (2-12 mm), *Acuminodeutopus*

heteruopus (2-3 mm), and *Paraphoxus heterocrepidatus* (2-3 mm). Only limited feeding occurs by day, as attested by eight individuals (210-239 mm SL, $\bar{x} = 222.5$) collected during the afternoon. Of these, only two contained fresh material (sand-dwelling amphipods, most of them *Ampelisca cristata*). These same two, and two others, also contained extensively digested polychaetes that obviously had been in the guts for some time; the other four (50% of the sample) were empty.

Embiotocidae: *Hyperprosopon argenteum*

The walleye surfperch is the only predominantly nocturnal species among the five embiotocids considered in this paper. It schools inactively by day, often close to shore, then disperses at nightfall and moves to feeding grounds some distance away (Hobson and Chess 1976; Ebeling and Bray 1976). It forages in the water column, where it takes the larger zooplankton that are numerous there only after dark. Thus, *H. argenteum* has habits similar to those of the other nocturnal planktivores described above. Although it usually forages lower in the water column than these others, its diet and feeding behavior also are similar: of 29 individuals (100-157 mm SL, $\bar{x} = 126$) collected over nocturnal feeding grounds at night, or from recently formed schools before sunrise, 28 (97%) contained food, much of it fresh. Major prey items were the gammarids *Batea transversa* (2-4 mm), *Ampelisca cristata* (3-4 mm), and *Ampithoe* sp. (4-6 mm); the cumacean *Cyclaspis nubila* (2-4 mm); the isopod *Paracercies* sp. (2-5 mm); and the caprellid *Caprella pilidigita* (4-10 mm).

Fishes That Feed Day and Night

Only two of the species studied resist classification as being either primarily diurnal or primarily nocturnal in their feeding activities. Both seem equipped to exploit circumstances that permit effective feeding during all hours of day and night. They are listed in Table 3, along with certain of their visual characteristics. The following accounts of their diel foraging activities puts their diurnal and nocturnal habits in perspective.

Cottidae: *Leiocottus birundo*

The lavender sculpin rests immobile in exposed locations on sandy substrata, usually near rocks and algae, at all hours of day and night. On the

TABLE 3.—Some southern Californian fishes that feed day and night, with the spectral absorbance maximum (λ_{\max}) of pigments extracted from their retinæ.

Family and species	$\lambda_{\max} \pm 95\% \text{ C.I.}$	N	Other pigments ¹
Cottidae:			
<i>Leiocottus hirundo</i>	500.0	2	0
Pleuronectidae:			
<i>Pleuronichthys coenosus</i>	500.9 \pm 0.5	3	T
Mean	500.5		

¹See Table 1, footnote 1.

rare occasions that feeding was observed, this fish moved only a few centimeters to snatch an object in the sand. Eight specimens (130-196 mm SL, \bar{x} = 177) were collected from a variety of habitats during the afternoon. Six (75%) contained food in their stomachs, with the predominant prey being the polychaetes *Glycera capitata* (30-85 mm), *Lumberineris* sp. (20-90 mm), and terrebellid tentacles. One had taken the gammarid *Ampelisca cristata* (12 mm), and one a holothurian (17 mm). Comparable data on nocturnal feeding was obtained from eight specimens (66-194 mm SL, \bar{x} = 136) collected during the hour before dawn. Again, six (75%) contained food in their stomachs, with polychaetes—*Glycera* sp. (35 mm), *Nothria stigmatis* (8 mm), and a terrebellid (30 mm)—the major prey, though less so than during the day. Gammarids, especially *Ampelisca cristata* (2-6 mm) were important to these nocturnal individuals, as was the clam *Solemya valvus* (8-10 mm). But these differences in prey selection between day and night may relate to fish size rather than to time of feeding: two *Leiocottus hirundo* collected during the night were smaller (66 and 84 mm) than any taken by day, and it was these that had preyed mostly on gammarids. Aside from these minor differences in food composition, feeding habits appear similar day and night: stomachs of the day feeders averaged 75% full, and contained \bar{x} = 4.2 items, compared with an average of 69% full and \bar{x} = 4.8 items for the night feeders.

Pleuronectidae: *Pleuronichthys coenosus*

The C-O turbot rests immobile on sandy substrata at all hours of day and night—usually exposed but sometimes under a thin layer of sediment. Often it occurs in the same habitat as *L. hirundo*, but more so than the cottid it ranges into regions of open sand, where its highly variable coloration often matches the surroundings. We have observed feeding only in daylight, when typically this species rests motionless, with body

somewhat elevated on dorsal and anal fins and head poised above the substratum (Figure 12). Its mobile, closely set eyes are oriented vertically on a bony ridge, and function almost as if set in a turret. This arrangement permits the fish to scan the seafloor close at hand, probably for moving sediments or other signs of prey that are just below the surface. Occasionally we have seen individuals that had been immobile in one spot for some time move a meter or so across the seafloor, pause for a moment, and then drive their heads into the sediment. Usually we were unable to see what they had taken, but daytime quarry were identified in the 11 specimens that contained food out of 14 (161-212 mm SL, \bar{x} = 186) collected from sandy substrata during the afternoon (stomachs averaged 47% full). The major prey were polychaetes, especially terrebellid tentacles. Although we did not observe feeding at night, prey were identified in all 11 specimens (159-220 mm SL, \bar{x} = 183.5) collected during the hour before dawn (stomachs averaged 72% full). Again, polychaetes, especially terrebellid tentacles, predominated. Clearly its trophic relationships are similar to those of *L. hirundo*, except that it may be more able to feed at night.

DISCUSSION

Events during twilight and at night in Californian marine habitats can be compared with equivalents on tropical reefs. Tropical activity patterns have been described (Hobson 1965, 1968a, 1972, 1974; Starck and Davis 1966; Collette and Talbot 1972; Smith and Tyler 1972; Vivien 1973), as has scotopic vision in tropical fishes (Munz and McFarland 1973). Below we relate our findings with Californian coastal fishes to these and other studies made elsewhere. First we consider crepuscular and nocturnal activity patterns and then scotopic spectral sensitivity, first in relation to ambient light, and then to bioluminescence.

Activity Patterns

In relating diel activity patterns of fishes in Californian waters near Santa Barbara to fishes on tropical reefs, Ebeling and Bray (1976) referred to the Californian species as "kelp-bed" fishes. We assume they implied a broad concept of this term that includes fishes sometimes in kelp forests, but more characteristic of other habitats. This is because the tropical side of their comparison (which



FIGURE 12.—*Pleuronichthys coenosus*, which feeds day and night, largely on sand-dwelling polychaetes, has eyes on either side of a bony ridge set almost as if in a turret. This arrangement increases its ability to scan the surrounding seafloor for prey and threatening predators.

is based on observations by Hobson 1965, 1968a, 1974; Starck and Davis 1966; and others) involves species (often referred to as coral-reef fishes) from a variety of contiguous habitats. A comparison of diurnal and nocturnal behavior requires a multi-habitat view because so many fishes move from one habitat to another between day and night.

The general scene in Californian nearshore habitats differs dramatically between day and night. A major aspect of this difference is the sharp drop in observed activity among fishes on reefs after dark. Describing an "aura of desolation..." in the "notably lackluster night life..." Ebeling and Bray (1976) considered this feature of kelp forests to be in contrast to tropical reefs. But on tropical reefs, too, one notes less activity at night than during the day (e.g., Starck and Schroeder 1965). Nevertheless, there may be an especially pronounced difference where Ebeling and Bray studied, because the relative dearth of nocturnal activities there led them to conclude: "...in kelp beds there is no broad replacement for the 'day

shift' of fishes at night." In particular, they reported an absence of fishes that move from daytime assemblages on reefs to nocturnal feeding grounds on adjacent sand, and also to there being relatively few nocturnal planktivores. But the situation they described is unlike that which prevails in the more southerly waters around Santa Catalina, where many species are most active at night. Following a pattern widespread in the tropics, for example, *Xenistius californiensis*, *Umbrina roncadore*, *Seriphus politus*, and *Hyperprosopon argenteum* (to mention species considered in this report) are relatively inactive in schools near shore, reefs, or kelp forests by day, and disperse over feeding grounds elsewhere at night. It may be significant, however, that with the exception of *H. argenteum*, these are species with close tropical affinities (Table 4). In contrasting the relative absence of nocturnal planktivores at their Santa Barbara study site, with the many such forms at Santa Catalina (as reported by Hobson and Chess 1976), Ebeling and Bray suggested

TABLE 4.—Geographic affinities¹ of the fishes studied.

I.	Warm-temperate representatives of basically tropical families or genera; species that do not range into the colder waters northward from central California. Twelve species:	
	<i>Scorpaena guttata</i>	<i>Girella nigricans</i>
	<i>Paralabrax clathratus</i>	<i>Chromis punctipinnis</i>
	<i>Xenistius californiensis</i>	<i>Hypsypops rubicunda</i>
	<i>Seriphus politus</i>	<i>Halichoeres semicinctus</i>
	<i>Umbrina roncador</i>	<i>Oxyjulis californica</i>
	<i>Medialuna californiensis</i>	<i>Semicossyphus pulcher</i>
II.	Temperate representatives of basically tropical families; species that range widely into the colder waters northward from central California. Two species:	
	<i>Atherinops affinis</i>	<i>Coryphopterus nicholsi</i>
III.	Warm-temperate representatives of temperate families or genera; species that do not range northward from central California. Five species:	
	<i>Sebastes atrovirens</i>	<i>Alloclinus holderi</i>
	<i>S. serripiceps</i>	<i>Gibbonsia elegans</i>
	<i>Leiocottus hirundo</i>	
IV.	Representatives of temperate families or genera; species that range widely northward from central California. Eight species:	
	<i>Sebastes serranoides</i>	<i>Embiotoca jacksoni</i>
	<i>Brachyistius frenatus</i>	<i>Hyperprosopon argenteum</i>
	<i>Cymatogaster aggregata</i>	<i>Heterostichus rostratus</i>
	<i>Damalichthys vacca</i>	<i>Pleuronichthys coenosus</i>

¹Based on ranges given in Miller and Lea (1972).

that the difference may reflect the proximity of Santa Barbara to Point Conception, the northern boundary of the warm-temperate zoogeographic region (Hubbs 1960; Quast 1968; Briggs 1974).

Certainly there is a strong tropical influence in many of the more clearly defined crepuscular and nocturnal activity patterns among southern Californian fishes. Species with the most distinctive patterns tend to be warm-temperate representatives of what basically are tropical families. The three Californian labrids, for example, seek and leave nocturnal shelter at precise times relative to sunset and sunrise, just as their tropical relatives do. And the two Californian pomacentrids shelter under reef cover at night in the same manner as tropical pomacentrids. Similarly, of the species listed above that school inactively by day and disperse to feed at night, most represent the predominantly tropical families Haemulidae and Sciaenidae. Clearly these behavior patterns are rooted deeply in their tropical ancestry, and are as characteristic of their kind as the more generally recognized morphological features that define their families. Ebeling and Bray recognized the strong influence that ancestral relationships exert on activity patterns, and distinguished "temperate derivatives" from "tropical derivatives." (Unaccountably, however, they considered *Paralabrax clathratus* and *Coryphopterus nicholsi* to be of temperate stock, even though the affinities of both are predominantly tropical.) These relationships,

then, are insightful in understanding how activity patterns are integrated in southern Californian nearshore fish communities. The geographical affinities of the various species (Table 4) are helpful in gaining an overview of these relationships.

Because nearshore communities in warm-temperate southern California mix fishes of temperate and tropical affinities, it is tempting to interpret behaviors in terms of interactions between these two lineages. Such comparisons are risky. For example, Ebeling and Bray (1976) stated: "It is paradoxical that the 'tropical derivatives'... persist in their complex... shelter-seeking while many primarily temperate fishes remain exposed." We see no paradox here. On tropical reefs, too, many diurnal fishes remain exposed at night, while others seek cover. Size often influences which strategy is used. For example, while smaller acanthurids (surgeonfishes) and chaetodontids (butterflyfishes) generally are sheltered, larger members of their families often rest exposed (Hobson 1972, 1974). Ebeling and Bray went on to suggest: "... the 'tropical derivatives' may... compete more successfully against primarily temperate species such as surfperches for shelter on the reef." This speculation, too, is unsupported by our observations. Most of the temperate species involved here are widespread northward (see Table 4, Group IV), well beyond the ranges of the tropical derivatives, and there too they are exposed at night (E. S. Hobson pers. obs.).

We doubt that nocturnal shelter sites are in short supply on California reefs except under exceptional circumstances. The places we identified as resting sites of *Semicossyphus pulcher* were just sporadically occupied, which seems an unlikely circumstance if there is strong competition for these sites. But clearly there is a shortage of shelter sites where the diurnal planktivore *Chromis punctipinnis* is so numerous that at night resting individuals overflow from the rocks and actually pile up on the adjacent sand. Apparently this exceptional situation exists where the zooplankters on which this fish feeds are abundant by day, but appropriate nocturnal shelter is limited. Significantly, however, the competition for this shelter appears to be intraspecific.

A casual appraisal of southern Californian fishes agrees with Ebeling and Bray (1976) that activities among fishes of the kelp-bed community are "... more loosely 'programmed'" than among fishes in tropical reef communities. A similar condition has been described for temperate lake fishes

(Helfman 1979). This position is strengthened by the more clearly defined behavior in the Californian representatives of tropical families. But at least two considerations complicate this comparison. First, activity patterns, no matter how highly structured, will be less evident in temperate fish communities because a greater proportion of the species there are sedentary. As stated for tropical fishes (Hobson 1972), relative activity in sedentary species is difficult to quantify. Second, and perhaps more important, because there are far fewer species in the temperate habitats, community activity patterns will be less distinct if only because they are defined by fewer forms. It need not follow that activities of each species are less structured. Despite these cautions, however, it is generally accepted that organisms tend to have less specialized habits where species are fewer, and this circumstance should produce more loosely structured activities.

Whether or not activities of individual species are less structured in California than in the tropics, certainly the overall community patterns in California are less clearly defined. In examining the changeovers between diurnal and nocturnal

modes, for example, we found little evidence of the detailed community transition-patterns that typically characterize these phenomena on tropical reefs (Hobson 1972; Collette and Talbot 1972; Domm and Domm 1973; McFarland et al. 1979). In particular, we were unable to clearly define a "quiet period," that 15-20 min segment of twilight on many tropical reefs when smaller fishes—both diurnal and nocturnal—have vacated the water column. Based on studies in the tropics (Hobson 1968a, 1972; Munz and McFarland 1973), the quiet periods are considered times of increased danger from predators when smaller fishes find it adaptive to avoid exposed positions. So if the quiet periods are less evident in California, it could indicate reduced crepuscular predation there.

When the sequence of twilight events identified at Santa Catalina Island is related to the timing of the quiet period at Kona, Hawaii (Figure 13), there might appear to be more overlap between the diurnal and nocturnal modes in California. For instance, as the nocturnal juveniles of *Sebastes serranoides* move into exposed locations (Figure 13, event 5), they sometimes pass above active labrids (Figure 13, events 2, 3, and 4) and close to the

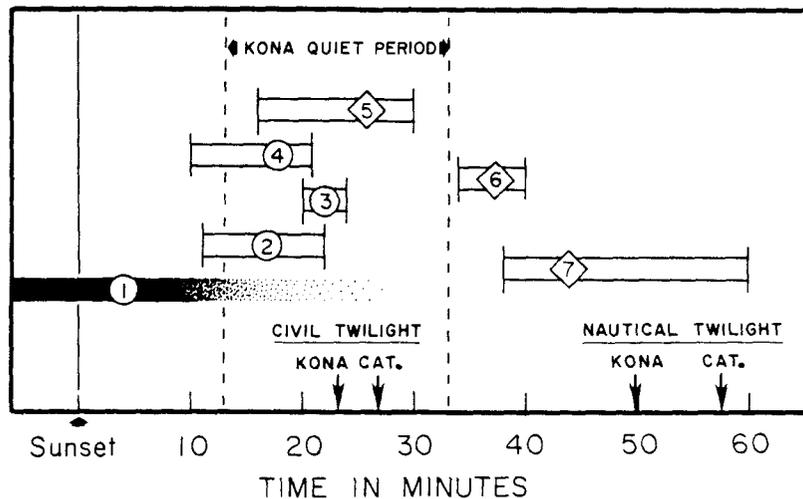


FIGURE 13.— Events during the evening changeover between day and night at one southern Californian site from August to November 1973, relative to timing of the quiet period at Kona, Hawaii (Hobson 1972). (The Californian site is illustrated in Hobson and Chess 1976: fig. 2, 3.) Circles represent diurnal species, diamonds represent nocturnal species. Event 1 is based on estimates, events 2-7 on counts, with bars encompassing range, and numbers located at mean. 1. Migration of *Chromis punctipinnis* to nocturnal resting area: progressive disintegration of bar represents decreasing numbers of individuals in migrating groups ($n = 6$). 2. Time last *Oxyjulis californica* was seen active ($n = 4$). 3. Time last *Halichoeres semicinctus* was seen active ($n = 6$). 4. Time last *Semicossyphus pulcher* departed observation site for nocturnal resting places elsewhere ($n = 4$). 5. Time first *Sebastes serranoides* appeared at open water feeding ground ($n = 5$). 6. Time first *Xenistius californiensis* arrived on feeding ground ($n = 4$). 7. Time first *Seriphus politus* arrived on feeding ground ($n = 4$). Times of civil and nautical twilight are from Nautical Almanac (U.S. Naval Observatory, Washington, D.C.) and are means of times on dates observations were made.

last migrating *Chromis punctipinnis* (Figure 13, event 1). But this apparent overlap can be explained without evoking a more relaxed regime. Although the three species of Californian labrids retire relatively late (even considering the longer twilight at temperate latitudes), they grow larger than most of their tropical relatives, and it is generally true that among diurnal fishes larger individuals retire later (Hobson 1972). Similarly, there are tropical equivalents to the relatively early shift made by juvenile *S. serranoides* to its nocturnal mode. In the western tropical Pacific Ocean, for example, the largely transparent nocturnal juveniles of some apogonids move away from shelter long before their larger adults. Some of them—many < 30 mm long—move out as early as 10 min after sunset (E. S. Hobson unpubl. obs.). This entry into exposed locations at a time when many piscivorous predators hunt most effectively might seem in conflict with the quiet-period concept. But in the dim twilight we are not surprised that these inconspicuous little fishes seem to go unseen by the visual hunters that so seriously threaten the more visible adults. Certainly these juveniles go unseen by human eyes at this time, except upon close inspection with a diving light, and so fail to detract from the aura of inactivity that characterizes the quiet period.

So what might appear to be a more loosely structured sequence of events during twilight in California may instead reflect the lesser number of species that define the transition pattern there. At least some semblance of a quiet period is evident. On the occasions depicted in Figure 13, the numbers of migrating *C. punctipinnis* declined sharply about 10 min before the juvenile *S. serranoides* first appeared, and after that only scattered small groups passed that way. Considering the tremendous numbers of *C. punctipinnis* in that area (we have never seen a single species so dominant on coral reefs), numerous exceptions from the norm should be expected. Furthermore, major species that occupy the water column at night—*Xenistius californiensis* and *Seriphus politus*—did not arrive until about 20 min after the vast majority of *C. punctipinnis* had passed through. So although crisp definition is lacking, there is evidence of a quiet period in Californian waters from about 15 to 35 min after sunset.

It remains uncertain whether the dangers smaller fishes face during twilight in southern Californian coastal waters are as intense as those faced on tropical reefs. Limited data from gut contents

indicate that such major predators as *Paralabrax clathratus* and *Sebastes serriceps* are primarily crepuscular when capturing smaller fishes. Unfortunately, we can no longer directly observe much of the predation that has influenced the evolution of coastal fishes in southern California. This is because during recent decades populations of the larger predators involved—including the giant seabass, *Stereolepis gigas*, and the white seabass, *Cynoscion nobilis*—have been decimated by fishermen. Nevertheless, as we discuss next, the possibility that Californian fishes have faced intensified selection pressures during twilight is also indicated by the nature of their scotopic visual pigments. Significantly, despite the varied forms and habits of these fishes, the maximum absorptions (λ_{\max}) of their scotopic pigments cluster about 500 nm, which indicates strong selection for enhanced photosensitivity over this segment of the spectrum.

Scotopic Spectral Sensitivity and Ambient Light

Tropical reef fishes have scotopic pigments that cluster about wavelengths that spectrally match twilight, which underwater is bluer than the light of day or night (Munz and McFarland 1973). In developing their Twilight Hypothesis, Munz and McFarland pointed out that because dawn and dusk are the most dangerous times for fishes on tropical reefs (Hobson 1972), even slightly increased photosensitivity during twilight may be crucial.

The Twilight Hypothesis is a variation of the Sensitivity Hypothesis (Lythgoe 1966), which declares that visual sensitivity is improved when absorption of photo pigments matches ambient light. The scotopic pigments of both aquatic and terrestrial vertebrates are known to cluster about narrow wave bands, but at different regions of the spectrum (for review, see McFarland and Munz 1975b). Among fishes, the scotopic pigments broadly match the spectral transmission of the water in which the fishes live (Lythgoe 1972). Deep sea fishes, for example, have scotopic pigments that tend to be even more blue sensitive (λ_{\max} from 478 to 490 nm: Denton and Warren 1956; Munz 1957), than tropical marine fishes (λ_{\max} from 489 to 500 nm: Munz and McFarland 1973), and the pigments of freshwater fishes are green sensitive (λ_{\max} from 503 to 540 nm: McFarland and Munz

1975b). The present study shows that fishes associated with Californian kelp forests have pigments that are most sensitive to blue-green light (λ_{\max} from 496 to 506 nm).

If the adaptive advantage of matching ambient light lies in heightened photosensitivity, then the match should be to light that prevails when selection for improved vision is most intense. We are not surprised, therefore, that the λ_{\max} values for fishes in a given habitat match not the light of day or night, but rather the bluer twilight, and thus the fishes are equipped to meet an intensified threat from crepuscular predators. In clear tropical waters, for example, the λ_{\max} values of the scotopic pigments in reef fishes cluster about 492 nm, which in that habitat matches twilight, rather than the greener light of day or night (Munz and McFarland 1977). Of course, the spectral position of this match is influenced by the light transmission characteristics of water in that particular habitat. For example, in most fresh waters the match is made above 520 nm, but this position nevertheless approximates the λP_{50} of twilight in these very green waters and is in fact toward the blue from light that prevails there during day and night (McFarland and Munz 1975c).

As could have been predicted from the Sensitivity Hypothesis, the scotopic pigments of fishes in the blue-green coastal water of California cluster at wavelengths intermediate between those of fishes on coral reefs and those of fishes in freshwater, at about 500 nm (Tables 1-3). The match with twilight, however, is less clear in Californian waters than in the other two environments because, we believe, photic conditions in Californian waters are more variable. Nevertheless, the tight clustering of scotopic pigments around 500 nm in the Californian fishes better matches ambient light during twilight than at night. Both moonlight and starlight are richer in red light than daylight or twilight (Munz and McFarland 1977), and for all water conditions we encountered at Santa Catalina Island downwelling light at night would have λP_{50} values well above 520 nm (Figure 5). Only during twilight does ambient light underwater shift far enough toward the blue-green region of the spectrum (Figures 3, 4) to produce a close match with the visual pigment λ_{\max} .

In evaluating the impact of crepuscular predators on the spectral position of scotopic pigments, however, we must not forget that other selection pressures are operating. We would expect scotopic pigments in fishes to be particularly responsive to

such alternate pressures at night, which is especially "short of light" (Dartnell 1975). Certainly fishes must be sensitive to the emissions of bioluminescent organisms, because few visual cues could be more apparent than a flash of light in the dark.

Scotopic Spectral Sensitivity and Bioluminescence

Bioluminescence often signifies underwater movement. According to Hobson (1966), "In many areas of the sea at night, a moving object is readily observed due to the luminescence of many minute planktonic organisms, mostly protozoans, which light up when disturbed. These organisms are often so numerous that while making observations underwater I have been able to identify, to species, fishes that swam actively among them. This was not because the fish itself was illuminated, but rather because there were so many minute luminescent organisms about the fish that its form was essentially traced out in tiny flecks of light." If such cues are evident to human eyes, adapted to a diurnal, terrestrial existence, the capacity to sense and to orient by them must be highly refined in animals like fishes that have evolved in this environment.

Bioluminescence offers an especially effective way to detect predators or prey because predator-prey interactions generally involve movement, and luminescence by plankton is greatly increased in the turbulent water around moving objects. We believe, as did Burkenroad (1943), that this fact has had enormous impact on the nocturnal tactics of both predators and prey. The motionless attitude that characterizes nocturnal planktivorous fishes when they hunt probably is enforced by the need to minimize turbulence in the water about them. By minimizing turbulence they minimize the firing of luminescent organisms that would betray their presence, and so hover unseen in the dark, ready to strike when nearby prey advertise their positions by disturbing the plankton. This tactic is in essence an ambush and probably is effective only at short range. Reasons for this limitation are two. First, an attack, once launched, is immediately identified by flashing plankton, thus giving prey more than a short distance away time for evasive maneuvers. Second, a long-range attack directed at plankton luminescing around a particular prey may be led to the prey's wake, because the targets that elicited the attack are left behind when the prey darts away. Probably pred-

ators can be led by luminescent plankton to prey over some distance (Nichol 1962), but we suggest the approach must be made with great stealth to avoid turbulence and resulting luminescence. Surely such limitations preclude many kinds of predatory activities after dark, especially when the prey are as agile as most small fishes. In fact, the diminished threat from predators that smaller reef fishes enjoy at night (Hobson 1973, 1975, 1979) may stem largely from the difficulties predators have at this time moving undetected to within striking range.

If fishes use luminescent plankton to detect predators and prey, undoubtedly they have experienced strong selection pressures to enhance this detection. An obvious adaptive response to such pressures would be a match of the scotopic visual pigments to the emission spectra of the luminescent plankton. Certain vertebrates living at great depths, or in the open ocean, reportedly have scotopic pigments that match the luminescent emissions of organisms with which they interact, socially or as predator or prey (Clarke 1936; Munz 1958a; Lythgoe and Dartnall 1970; McFarland 1971; Lockett 1977). These animals, however, interact directly with the luminescent organisms, whereas we stress indirect interactions. Of course, the principle is the same either way—detection is enhanced by matching visual pigment absorption to a luminescent emission.

The emission spectra of most luminescent plankton, as exemplified by *Noctiluca miliaris* and *Gonyaulax polyedra* (Figure 5), indicate that fishes would sense the emitted photons best with blue-sensitive visual pigments that have λ_{\max} values near 490 nm. But this holds only before the light has passed through water. As noted above, the spectrum of light changes as it travels through water, with the degree of change sharply affected by the water's clarity. Clearly any such change will favor a different λ_{\max} value in visual pigments.

The relative effectiveness of visual pigments with differing λ_{\max} values in waters of differing clarities can be estimated with some simple calculations. Given the relative attenuation of light at each wavelength, which is a function of water type, we can compare the relative photoabsorption of different visual pigments at increasing distances from the luminescent source. Let us consider, for example, how a series of pigments with λ_{\max} values at 10 nm intervals between 450 and 550 nm, each at 0.4 absorbance units, would ab-

sorb the light emitted by *Noctiluca* as this light passes through differing clarities of seawater, as defined by Jerlov (1968). The relative photoabsorption of each pigment at a given distance from the source can be estimated by multiplying that pigment's percentage absorption at each wavelength by the relative amount of light available at that wavelength and then integrating the products over all wavelengths (Figure 14). Thus, to see

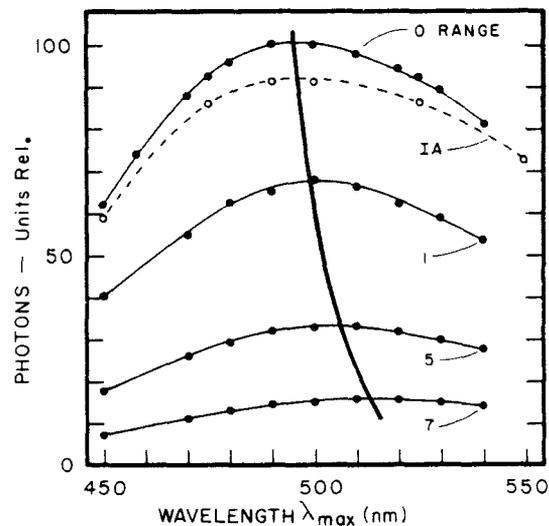


FIGURE 14.—Expected relative effectiveness of visual pigments with differing λ_{\max} values (positioned at wavelengths indicated by circles) in sensing luminescent emissions of *Noctiluca miliaris* under varying circumstances. Top curve, for reference, represents effectiveness at zero range (no alteration of emission spectrum by intervening water); dashed curve (with open circles), for comparison, represents effectiveness at distance of 3 m in clear tropical water (water type 1A of Jerlov 1968); three lower curves represent relative effectiveness in waters of decreasing clarity (water types 1, 5, and 7 of Jerlov 1968). Vertical line crosses each curve at the optimal λ_{\max} position. Method of calculation in text.

luminations from an organism like *N. miliaris* at a distance of 3 m in coastal waters (as at Santa Catalina), fishes would best have visual pigments with λ_{\max} values between 500 and 510 nm. And as range increases, and water clarity decreases, photodetection of this luminant source would be improved by shifting the λ_{\max} position slightly, but continuously, toward the greener wavelengths (Figure 15).

In reality, of course, the reduced visibility in turbid water sharply limits the practical extent of such a shift. During heavy phytoplankton blooms, for example, even large objects in full daylight are

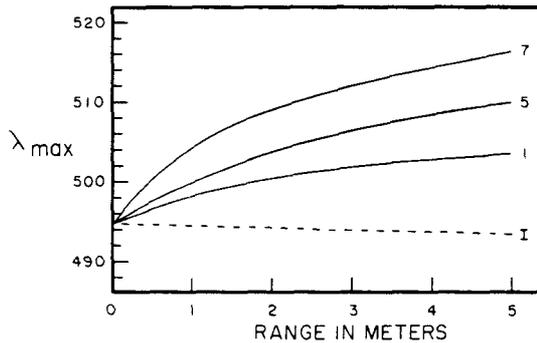


FIGURE 15.—Calculated optimum λ_{\max} position for absorption of luminescent emissions of *Noctiluca miliaris* at increasing range in waters of differing clarity. Water types I, 1, 5, and 7 of Jerlov (1968). Solid lines = coastal waters of increasing turbidity; dashed line = clear tropical water.

invisible beyond 2-3 m. Obviously under such conditions bioluminescence, too, would be invisible at these distances. Probably most meaningful interactions involving fishes and the bioluminescent emissions of plankton occur over distances of just a few meters or less, and to see bioluminescence at these ranges in the waters of varying visibility that surround Santa Catalina fishes probably would best have visual pigments with λ_{\max} values at a little above 500 nm (Figure 15).

One might expect diurnal fishes to be less sensitive than nocturnal or crepuscular fishes to selection pressures on scotopic pigments because they are less active under low light. But among species studied at Santa Catalina the λ_{\max} values scarcely differ between the two groups (diurnal feeders: \bar{x} = 499.1 nm; range = 496.1-505.8—Table 1; nocturnal feeders: \bar{x} = 501 nm, range = 496.1-505.1—Table 2). Perhaps there is little difference here

because many of these diurnal feeders are exposed at night and need means to detect threatening predators. In fact, if the fishes are grouped according to their relative exposure after dark, rather than by how active they are at this time, their λ_{\max} values show a clear pattern (Table 5). Those fishes that are exposed at night, compared with those that are sheltered, tend to have scotopic pigments with spectral sensitivities closer to what we consider optimum for detecting bioluminescence in Californian coastal waters. This would mean that, despite their apparent quiescence, at least many diurnal fishes remain visually alert for potential threats during the night.

So the similar λ_{\max} values in the diurnally feeding *Atherinops affinis* (505.8 nm) and the nocturnally feeding *Hyperprosopon argenteum* (505.1 nm) may answer the similar threats both face while exposed in the water column at night. We assume the increased sensitivity to bioluminescence would also benefit *H. argenteum* in feeding, but suspect this advantage would be less forceful. The need to evade predators should be sharper than the need to capture prey. Both needs are critical, but there is less tolerance for error on defense than on offense. A fish as prey is likely to be eliminated the first time it errs in responding defensively to an attack, but the same fish as an attacker may err many times without serious consequences.

Bioluminescence, triggered by movement, represents a well-defined indicator of immediate danger that can effectively focus selection pressures on a narrowly defined adaptive response. Moonlight and starlight would seem less suited for this because neither so effectively identifies specific threats and because the impact of both

TABLE 5.—Relative exposure at night, and λ_{\max} position of scotopic visual pigments in certain southern Californian marine fishes.¹

Relative exposure at night	Species	λ_{\max} mean	λ_{\max} range
I. Fully exposed in water column	<i>Atherinops affinis</i>	502.1	500.4-505.8
	<i>Brachyistius frenatus</i>		
	<i>Sebastes serranoides</i>		
	<i>Cymatogaster aggregata</i>		
	<i>Xenistius californiensis</i>		
II. Fully exposed on or near seafloor, often on open sand	<i>Seriphus politus</i>	501.1	500.0-503.1
	<i>Umbrina roncadore</i>		
	<i>Damalichthys vacca</i>		
	<i>Leiocottus hirundo</i>		
III. Partially or fully sheltered by rocks or algae	<i>Embiotoca jacksoni</i>	497.3	496.1-499.7
	<i>Scorpaena guttata</i>		
	<i>Sebastes atrovirens</i> ²		
	<i>Semicossyphus pulcher</i>		
	<i>S. serripes</i>		
	<i>Alloclinius holderi</i>		
	<i>Paralabrax clathratus</i>		
	<i>Heterostichus rostratus</i>		
<i>Girella nigricans</i>			
<i>Chromis punctipinnis</i>			
<i>Coryphopterus nicholsi</i>			

¹Of species studied, *Medialuna californiensis* is excluded because its nocturnal habits remain uncertain (see text), and *Halichoeres semicinctus* and *Oxyjulis californica* are excluded because they have a different type of visual pigment (see Table 1, footnote 3).

²Even though *S. atrovirens* feeds in the water column at night, these activities occur close to rising kelp stipes or just beneath the surface canopy.

tends to be diffused over a greater range of visual circumstances. Bioluminescence is more constant: the spectral compositions of moonlight and starlight change with water depth and atmospheric conditions, but the spectral composition of bioluminescence is independent of these variables. And, of course, there is less light from moon or stars with increased water depth, which, again, is untrue of a bioluminescent emission. So it is not surprising that the narrow range of λ_{\max} positions in visual pigments of Californian fishes more closely matches bioluminescence than it does moonlight or starlight (Figure 16).

Undoubtedly moonlight and starlight have strong influences on nocturnal relationships

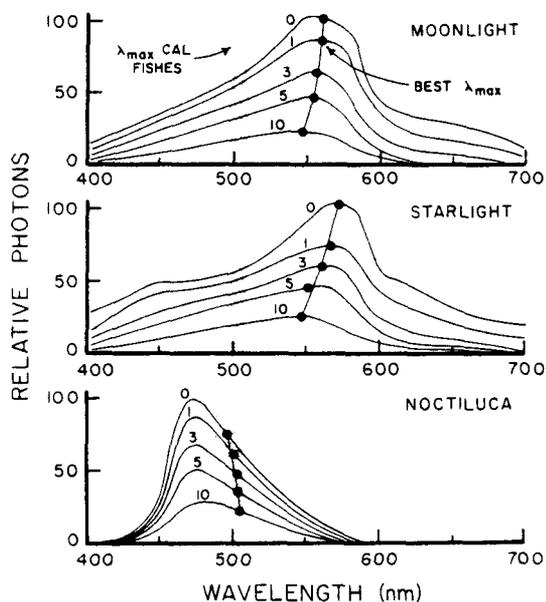


FIGURE 16.—Relationships between the spectral distributions of moonlight, starlight, and bioluminescence (as produced by *Noctiluca miliaris*) in seawater typical of southern California and the spectral sensitivities of fishes that live there. The five curves for each type of light represent the spectral distribution expected to reach a fish at the distance (in meters) indicated by the number that accompanies each curve. The curves depict moonlight and starlight off a flat reflector at a depth of 3 m (using values from Munz and McFarland 1977), and the luminescence of *N. miliaris* (using values from Nicol 1958), in water equivalent to typical conditions at Santa Catalina Island (Coastal Type 1 of Jerlov 1968). The solid circle on each spectral curve identifies the wavelength to best match with a visual pigment for maximum photosensitivity, and the stippled column represents the spectral range of maximum photosensitivity in scotopic pigments of Californian fishes (λ_{\max}). Note that these coincide only with bioluminescence.

among predators and prey. But probably both help fishes more on offense than on defense. Predators can position themselves, and time their attacks, to play both types of light to their advantage, and to the prey's disadvantage. By charging at prey from below, for example, predators view their targets against the water's relatively light surface, while their own movements are masked by the surrounding gloom (Hobson 1966). Certainly attacks that so often spring from the shadows would greatly dilute a defensive advantage prey might gain with spectral sensitivities that match moonlight or starlight. Under these circumstances prey face a broad range of threats that calls for a more generalized response. So we can understand why many smaller reef fishes that habitually range into the water column at night stay closer to shelter under moonlight (Hobson 1968a).

Despite the offensive advantage that certain predators likely gain from moonlight (or starlight), their scotopic visual pigments tend to be better matched to bioluminescence (or twilight), probably because this answers a more pressing need on defense. So it would seem that even those species that have special tactics to use moonlight or starlight to better see their prey must compromise with visual pigments less than optimal for this task. Included are those nocturnal planktivores, like subadult *Sebastes serranoides*, that characteristically hover tail-down in the water column, where apparently prey are visible to them against moonlight or starlight from above. Included, too, are those predominantly diurnal fishes, like *Paralabrax clathratus* and *Cymatogaster aggregata*, that apparently are able to hunt at night close to sand where light levels are elevated by reflected moonlight and starlight. We suggest not that their visual pigments are unsuited to see prey by moonlight or starlight, but rather that these pigments simply could have better spectral sensitivities for this particular job (Figure 16).

These arguments, favoring bioluminescence over moonlight and starlight as a selective force in determining λ_{\max} position, would also favor bioluminescence over twilight. But there is an important difference in this last comparison. Moonlight and starlight would select for spectral positions different from that selected for by bioluminescence, and so a conflict would exist. Twilight, on the other hand, would select for essentially the same spectral position as bioluminescence, so that the two would act in concert (see below).

If scotopic visual pigments with spectral positions slightly above 500 nm are optimally located to detect bioluminescence in Californian coastal waters, one can see why such pigments occur there in fishes exposed to nocturnal predators. But questions remain concerning why fishes apparently less threatened are consistent in having scotopic pigments positioned slightly under 500 nm. Why are these pigments not loosely positioned above, as well as below, the optimum location? The answer to this question might lie in ancestral relationships. In grouping the Californian fishes according to whether their geographical affinities are tropical or temperate (Table 4), our concern was with current relationships. In fact, all these fishes belong to groups that stem from tropical origins (Berg 1940). The radiation of acanthopterygian⁵ fishes from a relatively few ancestral forms early in the Cenozoic (Patterson 1964; Romer 1966) has been related (by Hobson 1974) to the concurrent development of modern coral reef communities (Newell 1971). And we have seen that conditions under which coral reefs flourish, compared with conditions in temperate Californian waters, favor in fishes' scotopic visual pigments that are more sensitive to slightly shorter wavelengths. The mean λ_{\max} of 492 nm that Munz and McFarland (1973) found in the scotopic pigments of coral-reef fishes, compared with the values around 500 nm that characterize Californian fishes, is consistent with the fact that water around coral reefs is generally clearer and more transparent to blue light than water around Santa Catalina (Figure 2). The extent that λ_{\max} values of scotopic pigments in Californian coastal fishes have shifted toward the green from what may have been ancestral positions near 490 nm, and, especially, have become located slightly above 500 nm (the optimal position in California), may roughly measure the relative strength of nocturnal or crepuscular predation pressures on each species in these greener waters.

The argument that scotopic pigments may be positioned to detect bioluminescence can be extended to coral reef fishes. Our calculations show that visual pigments with different λ_{\max} values would trap percentages of the light from *Noctiluca miliaris* as follows: P450 nm = 62%, P475 nm =

94%, P490 nm = 100%, P500 nm = 99%, P525 nm = 93.5%, P550 nm = 79%. Although the peak is broad, the central wavelength for maximum absorption at zero range would be near 495 nm (Figure 14), which is close to the λ_{\max} of 492 nm in the scotopic pigments of coral-reef fishes. And as distance from the source increases the match becomes even better (Figure 15).

Twilight or Bioluminescence?

Whether the clustering and spectral position of visual pigments in warm-temperate and tropical reef fishes is the result of natural selection, or is simply fortuitous, is a complex question. If, as we believe, these features have been refined by intense selection pressures from predators, it remains problematical whether the advantage lies in detecting bioluminescence, or in enhancing photoabsorption during twilight—as suggested by the Twilight Hypothesis. Indeed, both may be important. The scotopic pigments have spectral positions that would be effective in both functions, and the benefits of one would complement the other. Unquestionably, there has been ample time to influence evolution. Bioluminescent plankton have existed since before the first fishes (Seliger 1975), and so has twilight's unique spectrum. Because fishes have experienced these features throughout their history, the slightest favorable adjustment could have been adaptive. Although a 5-10 nm shift in λ_{\max} position would improve photoabsorption by no more than a few percentage units, even this could have been meaningful. And if selection pressures to detect bioluminescence have, in fact, acted in concert with those to enhance crepuscular vision, which to us seems likely, then their combined impact certainly would have been a powerful evolutionary force.

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⁵All fishes considered in this paper have been included among the acanthopterygians, or spiny-finned teleosts, although one, *Athernops affinis*, would be relegated by some systematists (e.g., Greenwood et al. 1966) to another group.

(NMFS), NOAA, typed the manuscript, and Susan Smith, Southwest Fisheries Center Tiburon Laboratory, NMFS, NOAA, drew Figure 1. Portions of this study were supported by N.I.H. Research Grant EY-00323 from the National Eye Institute.

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