Diurnal–Nocturnal Activity of Some Inshore Fishes in the Gulf of California

EDMUND S. HOBSON

Diurnal and nocturnal habits of some inshore fishes were observed in the southern Gulf of California. Certain patterns of behavior within and between species were consistently observed, and permit a number of tentative generalizations regarding feeding habits, schooling, and other activity in relation to time of day. Species with predominently diurnal foraging habits include: *Mycteroperca rosacea* (Streets), *Epinephelus labriformis* (Jenyns), *Chromis atrilobata* (Gill), *Eupomacentrus rectifraenum* (Gill), *Abudefduf troschelii* (Gill), *Bodianus diplotaenia* (Gill), *Thalassoma lucasanum* (Gill), *Scarus californiensis* (Pellegrin), *Heniochus nigrirostris* (Gill), *Prionurus punctatus* Gill, *Runula azalea* Jordan and Bollman, *Balistes verres* Gilbert and Starks, and *Balistes polylepis* Steindachner. Species obtaining most of their food at night include: *Holocentrus suborbitalis* (Gill), *Myripristis occidentalis* Gill, *Rypticus bicolor* (Valenciennes), *Lutjanus argentiventris* (Peters), *Apogon retrosella* (Gill), *Microlepidotus inornatus* Gill, *Anisotremus interruptus* Gill, *Haemulon sexfasciatum* Gill, *Selar crumenophthalmus* (Bloch), and *Pareques viola* (Gilbert). A number of other species are introduced as their activity relates to the discussion. The nocturnal species are predators, while the herbivorous and omnivorous fishes show predominantly diurnal feeding habits. Those species schooling in dense, relatively inactive schools inshore during the day are nocturnal feeders and the school functions in defense against diurnal predators. Members of these schools disperse to feed at night, often after moving a considerable distance offshore.

INTRODUCTION

OUR knowledge of the habits of creatures in the sea lags far behind what we know of terrestrial animals. The major barrier to obtaining this knowledge has been the aquatic environment itself. Recent technological advances, notably the development of diving equipment, have increasingly provided us with the means of overcoming this barrier. Although our knowledge has been rapidly expanding since the introduction of these tools, the effort has been confined largely to that period of the day between dawn and dusk.

The literature on nocturnal habits in fishes is sparse. Longley and Hildebrand (1941) described the nocturnal habits of some fishes at Tortugas, Florida, and information is scattered among a number of other reports (Randall 1961, 1963, and others). Most of the available information has been obtained from aquarium observations (e.g., Breder 1948, Winn 1955), while others have drawn conclusions on day–night activity largely from examination of stomach contents (Hiatt and Strasburg 1960, Randall and Brock 1960). Robert Schroeder and Walter Stark II are currently engaged in a field study of nocturnal activity in marine organisms in the Florida Keys. Some of this material has been published (Schroeder 1964).

The present report is based on observations made in the Gulf of California, off southern Baja California, Mexico. The material was gathered during 3 periods: July to December 1962, July to August 1963, and April to July 1964. Over 1,000 hr of underwater observations were made during all hours of day and night with SCUBA and by "snorkeling." Although information obtained on the differences in day and night activity of the shore fishes of this region is still fragmentary, certain patterns of behavior within and between species were consistently observed and permit tentative generalizations.

The observations were made in Bahia de Palmas, a wide (20 miles) bay almost completely bordered by a sand beach. The bottom over most of the bay is sandy from the beach out to deep water, but there are many isolated areas of rocks extending from just below low tide line to varying distances offshore. While many of these rocky areas are

quite limited in size, others extend along the water's edge for a mile or more, and out from shore for about 200 yards, where water depth is 15–40 ft. From the outer edge of the rocks, a sandy bottom slopes off gradually for perhaps a half mile before dropping abruptly to greater depths.

The activity described was centered about these rocky areas. Many of the rocks are large, rising 8–10 ft from the bottom, and contain cracks, caves, and overhangs which offer cover to many organisms. There are patches of sandy bottom among the rocks, and many of the rocks are dotted with small coral heads, notably *Porites* and *Pocillopora*.

Over 100 species of fishes occur over this rocky bottom. In this report I have considered species among those most readily observed by a diver. The fishes are designated as diurnal or nocturnal according to the periods during which most feeding takes place despite the fact that such a classification presents an oversimplified picture of day versus night activity. However, the effects of such important variables as the presence or absence of moonlight are discussed for the species treated in this report.

The diving was done from shore as well as from a 16-ft boat. Night work was integrated into the program only after several hundred hours of daylight observations had provided a thorough familiarity with the topography and fauna of the area. By that time, it was possible to operate in shallow water on clear nights of full moon with relatively little use of the 5-cell flashlight which was carried during all night dives. While greater use of the light was necessary in deeper water, or on darker nights, an effort was made to minimize the effect of the light on the fishes by alternating periods of its use with periods during which I rested quietly in the dark. The light was seldom used for periods exceeding 3–10 sec except when entering or leaving the water or when taking photographs.

The response of fishes to the diving light proved to be an important consideration in evaluating their nocturnal behavior. Some fishes, both diurnal and nocturnal, were immobilized when held in the flashlight's beam at night. At such times they could be approached and occasionally gently handled without them showing alarm. Others, however, including many diurnal fishes which had been resting on the bottom, darted away when struck by the light. Many species showed both responses under varying conditions. The response to the light was unpredictable. One night while working in 30 ft of water, the beam of light illuminated a large (40–50 lb) jack (*Caranx* sp.) approximately 40 ft away. The jack abruptly turned up the beam of light and came racing toward me. The big fish raced to within a foot of the flashlight before veering away sharply and disappearing immediately into the darkness.

A neoprene rubber jacket was worn at night. This was not so much for warmth (water temperatures ranged from 72–86 F over the months during which the observations were made) as it was to minimize the area of body surface exposed to irritating or stinging organisms. For example, isopods, many of which are ectoparasitic on fishes, were a constant source of vexation at night as they sought a point of attachment on exposed areas of my body. Minute midwater organisms, most of them crustaceans, were particularly abundant on dark nights when it was also necessary to make extensive use of the light. At those times, considerable discomfort resulted from vast numbers of those tiny organisms which swarmed about the light.

During daylight, approximately 90% of the observations were made while snorkeling, as compared to 10% using SCUBA. At night, however, the ratio was reversed, with approximately 90% of the work being done with SCUBA as opposed to 10% with snorkel. When using SCUBA, the response of many of the fishes to the resulting bubbles often seemed more pronounced at night than during the day. Possible differences in day versus night behavior due to such a differential response have not yet been determined.

All specific references to the food habits were confirmed by stomach analysis of specimens taken with spear or slurp gun. A total of 361 specimens was taken for this purpose. The measurements presented for the specimens are all standard length.

I would like to express my appreciation to Admiral Antonio Vazquez del Mercado, Director General of Mexican Fisheries, through whom permission was obtained to carry out this study in Mexican waters. I wish to acknowledge the able assistance of Mr. Robert Kiwala of the Tiburon Marine Laboratory, U. S. Fish and Wildlife Service, and

Mr. James Freeman of Oakland, California, who accompanied me on various night dives. Mr. Gil Powell, of Rancho del Leonero, Baja California, was a capable diving partner on many daylight dives. Col. Eugene Walters graciously made available his facilities at Rancho Buena Vista. The early phase of this study was aided by a Sigma Xi-RESA Grant-in-Aid of Research award. Finally, I would like to acknowledge the many suggestions offered by Dr. Boyd W. Walker of the University of California, Los Angeles, during the preparation of the manuscript.

Diurnal Species

Serranidae

Mycteroperca rosacea (Streets). During midday, these groupers form large, inactive aggregations on or close to the bottom at the offshore edge of the rocks. Larger individuals often hover below schools of pomadasyids. At such times, these larger groupers occasionally shoot up among the pomadasyids with single, explosive feeding rushes. However, most of the feeding in this species occurs during the periods immediately before sunrise and after sunset. This is particularly evident when schools of herring, *Harengula thrissina* (Jordan and Gilbert), are located over rocks along the water's edge during the day. These herring move offshore shortly after sunset and return the following morning just before sunrise. Late in the afternoon, leopard groupers move in under the herring schools and begin feeding. As the sun falls low in the sky, less light penetrates the depths and, from above, the groupers are difficult to distinguish as they rest motionless on the darkening bottom. However, from this position on the bottom the herring in the waters above are sharply defined against the relatively bright surface. As nightfall approaches, feeding in the groupers increases in intensity, reaching a peak at the time of the herring's move offshore. The groupers follow the herring to the offshore edge of the rocks, where the herring continue out over the sand to feed while the groupers settle on the bottom among the rocks until morning. On bright moonlit nights some of these groupers are active, although I did not observe them feeding at this time. The groupers make contact with the herring again just before sunrise at the offshore edge of the rocks and follow them inshore. Feeding is intense until shortly after sunrise when most of the groupers begin moving offshore and once again form their relatively inactive midday aggregations. Ninety-two specimens (122–788 mm) were collected with spear for study of food habits. While the larger groupers are entirely piscivorous, the smaller individuals feed to a large extent on benthic crustaceans.

Epinephelus labriformis (Jenyns). This species is herein somewhat arbitrarily classified as diurnal. It rests motionless on the bottom, usually under partial cover, at all hours of day and night. While individual fish were seen making short dashes from their resting spots during the day to capture prey, feeding at night was not observed. The diet of 23 specimens (85–350 mm) collected with spear was composed of benthic crustaceans and some small fishes.

Randall and Brock (1960) remarked that while the groupers in Tahitian waters are primarily diurnal, they may feed nocturnally, especially on bright moonlight nights. Longley and Hildebrand (1941) reported that stomach analysis indicated *Epinephelus morio* (Valenciennes) at Tortugas fed indifferently by day or night, and Schroeder (1964) referred to groupers in general as nocturnal. Several serranids in the Gulf of California were largely nocturnal and will be mentioned later.

Pomacentridae

Chromis atrilobata (Gill). During the day, aggregations of these damselfish hover in "clouds" over many of the larger rocks offshore where they are particulate feeders on midwater organisms. At night, solitary individuals go under cover beneath the rocks where they remain quiet, but alert, until morning. Ten specimens (45–70 mm) collected with spear and slurp gun had fed largely on small crustaceans.

C. atrilobata also actively feeds on planktonic fish eggs, such as those of the labrid *Thalassoma lucasanum* (Gill). When spawning, *T. lucasanum* aggregates for several hours during the day over many of the rocks throughout the area. Periodically, approximately 5 to 15 individuals within these aggregations draw themselves very close together and swim rapidly upward toward the surface. After rising a distance of 3–5 ft, these small groups, which include both males and females, abruptly reverse direction and return to the aggregation below. At the apex

of the upward dash, the gonadal products of both sexes are released into the water. Similar spawning behavior in labrids of the Atlantic was described by Randall and Randall (1963). On several occasions, clouds of *C. atrilobata* hovered near spawning *T. lucasanum*, and immediately converged on each ascending group to feed on the eggs which were released. The damselfish recognized the significance of the wrasse's behavior, for they began converging on a point above the wrasse as soon as a small group of wrasse within the aggregation had drawn themselves together in preparation for the upward dash. However, the attack had to be well timed so as not to be premature. For if the damselfish arrived above the wrasse while the latter were still swimming upward, the wrasse would abort their activity and return to the aggregation below without releasing their gonadal products.

Eupomacentrus rectifraenum (Gill). The irridescent blue juveniles are abundant among the rocks during the day. Although the comparatively drab–brown adults are not as numerous, they occur over the same area. Eight specimens (78–96 mm) speared for stomach content analysis contained only benthic algae. On the approach of darkness, these fish settle out of sight among the rocks where they remain quiet, but alert, throughout the night. The closely related *E. flavilatus* (Gill) is active at the same times over essentially the same area.

Abudefduf troschelii (Gill). During the day aggregations of 10 to 30 of these omnivores swim in midwater, or just under the surface, where they feed on minute organisms. They occur over rocky bottom, and much of their food consists of material taken from the rock surfaces. The diet of 15 specimens (98–141 mm) collected with spear was composed of algae and small crustaceans. While solitary individuals remain quiet but alert among the rocks on dark nights, they are active close to the bottom when there is a bright moon. However, lack of food in the digestive tracts of 5 active individuals speared under bright moonlight between midnight and first light in the morning indicated that little, if any, feeding had occurred during this period.

Diurnal habits seem to be characteristic of the pomacentrids. Breder (1948) found that *Abudefduf saxatilis* (Linn.) in aquaria rested quietly on the bottom at night in the proximity of shells, but did not take shelter. He also noted that *Eupomacentrus leucostictus* (Müller and Troschel) disappeared into empty shells after dark. Hiatt and Strasburg (1960) reported that *Chromis atripectoralis* Welander and Schultz formed "clouds" over coral heads in the Marshall Islands during the day.

Labridae

Bodianus diplotaenia (Gill). Juvenile hogfish are prominent cleaners (i.e., removers of ectoparasites from other fishes), and are active close to the surfaces of many of the larger rocks offshore during the day. Here, these little fish "service" other species, such as pomadasyids and adults of their own species, which station themselves motionless close to the surfaces of these rocks. Randall (1958, 1962) reported cleaning by juvenile *Bodianus* in the Society Islands and in the Caribbean Sea. At night, juvenile *B. diplotaenia* are quiescent in crevices among the rocks, often encased in well-developed mucous envelopes. While the adults also lie quietly in crevices at night they do not form envelopes, nor are they cleaners. During the day, the larger hogfish swim alone or in groups of 2 or 3 over rocky bottom where they feed. Two specimens (250 and 400 mm) were speared. The digestive tracts of both contained a wide variety of benthic organisms including algae, crustaceans, and mollusks. The larger individual also contained a small fish. Hogfish often closely follow the large parrotfish, *Scarops perrico* (Jordan and Gilbert), and feed on scraps torn loose from the bottom by the powerful jaws of the larger fish.

Thalassoma lucasanum (Gill). During the day, this wrasse swims in small aggregations of 2 to 20 individuals close to the surface of rocks. Most feeding consists of "picking" small benthic organisms from these rocks. The diet of 6 specimens (60–72 mm) collected with spear and slurp gun included crustaceans, algae, and soft coral. Like many small fishes which feed on minute organisms from rock surfaces, this labrid, the juvenile in particular, engages in some cleaning of other species incidental to its regular feeding activity. As with most wrasses, they are among the first fishes retiring to shelter for the night, and among the last to appear in the morning. During the night, they lie quietly on their sides in crevices among the

rocks, usually at least partially covered with sand. Other labrids active at essentially the same time and over the same area include *Halichoeres dispilus* (Günther) and *H. nicholsi* (Jordan and Gilbert).

Labrids are widely reported to go undercover at night, a characteristic apparently shared by all members of the family. For example, Breder (1948) reported that *Halichoeres bivittatus* (Bloch) in aquaria at Bimini disappeared into shells or buried themselves in sand at night. Similarly, the California wrasse *Oxyjulis californica* (Günther) buries itself in sand at night (Herald 1961). The mucous envelopes surrounding juvenile *B. diplotaenia* were similar to those described in some scarids by Winn (1955), and in the small labrid *Labroides pthirophagus* Randall by Gosline and Brock (1960). Charles Turner and Earl Ebert of the California Department of Fish and Game (pers. comm.) have seen similar mucous envelopes about juveniles of the large eastern Pacific labrid *Pimelometopon pulchrum* (Ayres), typically among branches of gorgonians. Adult *P. pulchrum* lie in crevices and holes at night, as do adult *B. diplotaenia*. The presence of mucous envelopes in *Labroides* and in juvenile *Bodianus* and *Pimelometopon* may reflect an increased need for protection in the smaller individuals. Winn and Bardach (1959), working at Bermuda, presented evidence suggesting that the mucous envelope of the parrotfish *Scarus croicensis* Bloch provided defense against predation by the moray eel *Gymnothorax moringa* (Cuvier) at night. The widespread habit of burying themselves in sand, or taking shelter in empty mollusk shells, may be the solution of most other small labrids to the predation problem.

Scaridae

Scarus californiensis (Pellegrin). During daylight, parrotfish, solitary or in groups of 2 or 3, swim over rocky bottom where they scrape benthic organisms from the surfaces of rocks. Although no stomachs were examined, it appeared that algae composed at least the bulk of the material ingested. At dusk, males often chase one another among the rocks. This may be a display of territoriality, perhaps in defense of resting spots. For with darkness, the parrotfish settle on the bottom, usually under at least partial cover, where they remain quiet throughout the night. Although there was often a variable amount of mucous covering on these parrotfish at night, the only individual observed having actually formed an envelope was a female of approximately 350 mm which had suffered a large wound on its side. This suggests that at least the adults of this species form envelopes only when injured, or perhaps under stress. Juvenile parrotfish were not observed at night, so it is possible that mucous envelopes are regularly formed by the smaller individuals, as was the case with the labrids noted above. When one considers the relatively small size of most nocturnal predators in this area (see section on nocturnal species below) it becomes apparent that while the juveniles and smaller species are undoubtedly potential prey, necessitating special protective measures, large, healthy adults may be relatively safe. Winn and Bardach (1959, 1960) noted that the occurrence of envelopes was variable between, as well as within, species at Bermuda and Bimini.

Other scarids consistently observed in the area, including *Scarops perrico* and *Scarops jordani* (Jenkins) showed similar behavior.

Many authors (e.g., Winn 1955; Winn and Bardach 1959, 1960; Schroeder 1964; and others) have reported the quiescence of parrotfishes at night. This habit seems to be a characteristic shared by all scarids.

Chaetodontidae

Heniochus nigrirostris (Gill). Large aggregations of these active cleaners maintain "stations" at specific locations among the rocks during the day. These stations are visited by a wide variety of other species, including pomadasyids, lutjanids, serranids, mullids, and many others. In addition to cleaning, *H. nigrirostris* also feeds on organisms taken from surfaces of rocks. Items found in the digestive tracts of 13 specimens (95–165 mm) taken with spear included crustaceans, minute gastropods, algae, and fish scales, the latter often with attached bits of flesh. On dark nights, solitary butterflyfish rest quietly, but remain alert, among the rocks. However, on bright moonlit nights they are active close to the bottom, often in groups of 2 or 3. Nevertheless, the digestive tracts of 4 active individuals speared between midnight and 1:00 AM when there was a bright moon contained only well-digested food in the posterior part of their intestines.

Thus, it appeared that little, if any, feeding had occurred during that period.

Another chaetodont often observed in this area, *Holacanthus passer* Valenciennes, feeds diurnally on midwater as well as benthic organisms. At night, solitary individuals are alert as they rest quietly on the bottom, usually under cover. Unlike *H. nigrirostris*, they are not active on nights of bright moonlight.

Acanthuridae

Prionurus punctatus Gill. During the day, these surgeonfish are active in aggregations over rocks in specific areas offshore where they graze on benthic algae. Fifteen specimens (115–420 mm) were speared. Although a few minute crustaceans and gastropods were found in the digestive tracts of these specimens, these were probably taken incidentally with the algae. On dark nights, solitary *P. punctatus* settle on the bottom, usually under at least partial cover. However, when there is a bright moon many are active in aggregations similar to those formed during daylight. It appears that at least some nocturnal feeding occurs at this time. Two solitary specimens were speared shortly before first light in the morning as they rested quietly on the bottom following a night during which there had been no moon. Neither had any food in its digestive tract. A third specimen was speared the same morning, approximately 30 min after the aggregation had formed at first light, but still 30 min or so before sunrise. While this fish also had an empty intestine, its stomach was full of algae. Five specimens were speared after 11:00 PM during nights of bright moonlight. All were taken from the aggregations that form with moonlight, including 2 that were speared just before first light in the morning. While none of these specimens had food in their stomachs, all had intestines full, or nearly full, of algae. Six specimens taken from aggregations during the day all had full stomachs and intestines. While the data here are limited, they indicate that at least some nocturnal feeding occurs when the aggregations form with moonlight.

Randall (1961) reported that the Hawaiian surgeonfish *Acanthurus triostegus sandvicensis* Streets rests on the bottom at night in sheltered, although not confining locations. Breder (1948) noted similar activity in *Acanthurus chirurgus* (Bloch) in aquaria at Bimini.

Blenniidae

Runula azalea Jordan and Bollman. Although some of these blennies periodically occupy mollusk or worm tubes on the rocks during the day, where they are highly territorial, most swim in small aggregations of 2 to 6 individuals above these rocks. Often, they swim with the labrid *T. lucasanum*, which they superficially resemble. From their position over the rocks, they attack the posterior surfaces of many larger fishes which pass nearby, invariably causing the larger fish to start and swim rapidly away. They attack only from behind, and will abort their attack if the intended victim turns toward them. At nightfall, these blennies take shelter, usually entering tubes on the rocks, where they remain until morning.

Wickler (1961) described the predatory habits of *Runula* on larger fishes in aquaria.

Balistidae

Balistes verres Gilbert and Starks. During the day, these solitary triggerfish are active about rocks where they feed on benthic organisms taken from the rock surfaces. Often, when one of these triggerfish has worked over that part of a particular rock which is exposed above the sand, it will then lie on its side and, with a rapid undulation of dorsal and anal fins, produce water currents which carry away the sand next to the rock, thus exposing additional surface to feeding. In this manner, these rocks may be exposed to depths of over a foot below the original sandline. Six of these triggerfish (230–255 mm) were speared. A wide variety of benthic organisms are present in their diet, including crustaceans, mollusks, soft corals, annelids, sea urchins, and algae. While feeding, the triggerfish is often followed by small labrids, notably *T. lucasanum*. The labrids not only feed vigorously on scraps torn loose from the substrate by the triggerfish, but also converge to pick through clouds of debris which the triggerfish periodically vents from its gill slits when feeding. At night, these triggerfish lie quietly on their sides in holes usually small enough so that they cannot be forcibly extracted when their triggers (modified dorsal fin spines) have locked the long first spine in an erect position.

Balistes polylepis Steindachner. This triggerfish is active individually, as well as in aggregations, feeding over sandy bottom adjacent to rocky areas. It, and to a lesser de-

gree *B. verres*, feeds on sand-burrowing invertebrates after exposing them with a jet of water from the mouth. During this operation the triggerfish hovers vertically in the water, its head down, 2 to 3 inches from the bottom. Seven specimens (223–305 mm) were speared. Digestive tract contents included crustaceans, mollusks, and the remains of some fishes. Unlike *B. verres*, many of these triggerfish remain active during nights when there is a bright moon. On dark nights, however, they lie on their sides under rocks, as does *B. verres*. The nocturnal activity of many *B. polylepis* during nights of bright moonlight may be related to the relatively high level of illumination over the white sand bottom where it feeds. That *B. verres* is not active at this time may, in turn, reflect the relatively low level of illumination among the dark rocks where it feeds. Clark (1950) and others have reported triggerfish resting on the bottom at night.

Nocturnal species

Holocentridae

Holocentrus suborbitalis (Gill). Only an occasional glimpse is had of squirrelfish during the day when they momentarily appear at openings of dark recesses beneath rocks near shore. However, when the last daylight fades underwater, they emerge from shelters and solitary individuals forage close to the rocky bottom throughout the night. Five individuals (88–110 mm) taken with spear had fed upon crustaceans. With the first trace of morning light underwater, the squirrelfish return to shelter. Although the data are limited, there was no indication that these squirrelfish feed while under cover during the day.

Myripristis occidentalis Gill. During the day, these holocentrids remain deep in the shadows of overhanging rocks, or just inside the entrances to small caves. Upon being threatened, they dart rapidly back and forth from one end of their confines to the other. With darkness, they emerge from cover and are active throughout the night when they feed over the rocks, or in small aggregations near the surface. Food items in the stomachs of 27 specimens (72–102 mm) collected with spear and slurp gun were largely small crustaceans. I found no evidence indicating that this species takes food during the day.

Nocturnal habits in members of this family are widely recognized. Longley and Hildebrand (1941) described behavior in *Holocentrus ascensionis* (Osbeck) at Tortugas, Florida, which is similar to that of *H. suborbitalis*. Hiatt and Strasburg (1960) also reported nocturnal feeding habits in *Myripristis* and *Holocentrus* in the Marshall Islands. Schroeder (1964) cited nocturnal habits of squirrelfishes in the Florida Keys.

Serranidae

Rypticus bicolor (Valenciennes). During the day, soapfish remain under cover among the rocks where they are difficult to distinguish due to their characteristic habit of remaining motionless, flush against the sheltered faces of rocks. At night, solitary individuals swim in the open, usually close to rocky bottom, but occasionally in midwater. Thirteen individuals (78–248 mm) were speared at various times of both day and night. While benthic crustaceans made up the bulk of their diet, one had ingested a small fish. Although most feeding occurs at night, some food is taken while the soapfish is under cover during the day.

At least 1, and perhaps 2, other small serranids in this area appear to have nocturnal habits. *Alphestes multiguttatus* (Günther) hides amongst algae in shallow water during the day but is active in the open at night. *Petrometopon panamensis* (Steindachner) has secretive habits among the rocks during the day and, although it has not been observed at night, does venture a short distance from cover at dusk when *Alphestes* and *Rypticus* also first appear in the open.

Lutjanidae

Lutjanus argentiventris (Peters). During the day, many of these snappers swim in large aggregations close to the rocky bottom offshore. Some of the larger individuals tend toward solitary habits, often retiring to caves among the rocks during the day. At dusk, the aggregations disperse among the rocks where the snappers forage on crustaceans and, to a lesser degree, fishes throughout the night. Thirteen individuals (179–446 mm) were speared for food habit study. Although most feeding occurs with dusk or darkness, 2 individuals collected during midafternoon were full of recently ingested herring.

Longley and Hildebrand (1941) reported nocturnal feeding habits in the snappers at Tortugas. Similarly, Randall and Brock (1960) concluded from stomach analyses that

Lutjanus vaigiensis (Quoy and Gaimard) in Tahiti was primarily a nocturnal feeder. However, they found fresh food in the stomachs of *L. vaigiensis* during the day, indicating that at least some diurnal feeding occurred.

Apogonidae

Apogon retrosella (Gill). During the day, this cardinal fish schools beneath rocks or in the shadow of overhanging ledges. At night, they emerge and form "clouds" over many of the same rocks, and in the same manner as does the pomacentrid *Chromis atrilobata* during the day. *A. retrosella* feeds on midwater organisms at night much as *C. atrilobata* does during the day. At dawn and dusk, these species school together about the bases of the rocks, as one species is emerging and the other is going under cover. The stomachs of 18 individuals (57–90 mm) taken with spear and slurp gun showed their diet to be composed largely of crustaceans. Although some food is ingested during the day while this fish is undercover, most is captured at night when the cardinal fish is in the open.

Longley and Hildebrand (1941) noted the secretiveness of *Apogon maculatus* (Poey) at Tortugas during the day, but expressed uncertainty of its habits at night. Hiatt and Strasburg (1960) suspected nocturnal habits in a Marshall Islands cardinal fish *Gymnapogon philippinus* (Herre) due to its secretive habits during the day. However, they reported that most of the apogonids in that area forage diurnally. Randall (1963) in the Virgin Islands, and Schroeder (1964) in the Florida Keys, both observed nocturnal habits in cardinal fishes.

Hiatt and Strasburg (1960) noted that females of the Marshall Island apogonids cease to take food when their ovaries are well developed. A similar situation occurs in *A. retrosella* of the Gulf of California, except that in this species it is the male which ceases to feed. The only male taken during this period which contained material in its digestive tract had its stomach filled with eggs. These may have been eggs which the fish had held in its mouth and swallowed when speared. It is well known that many members of this family are mouth breeders (Herald 1961 and others). The cessation of feeding by the males and the male taken with eggs in its stomach suggest that in *A. retrosella* it is only the males which orally incubate the eggs.

Pomadasyidae

Microlepidotus inornatus Gill. This species illustrates one of the more striking aspects of the contrast in the underwater scene between daylight and darkness. During the day, the sandy expanses offshore are relatively devoid of larger fishes. However, after dark this area supports a vast number of foraging fishes. *M. inornatus*, which feeds on sand-dwelling invertebrates, is one of the more numerous species over the sand at night. These grunts pass the daylight hours in dense, relatively inactive schools over rocks and sandy bottom inshore. As evening approaches, they become increasingly active and finally move offshore where they disperse over the sand after dark. Twenty-three individuals (204–310 mm) were speared. Their diet consisted of small crustaceans, both midwater and benthic, along with small bivalve mollusks. When there is a bright moon, many *M. inornatus* are active throughout the night in small schools over the sand, close to and sometimes over, the outer edge of the rocks. On darker nights, however, relatively few of these pomadasyids are seen in this area, and those present tend toward solitary habits. However, even on the darkest nights some remain together in groups of 2 or 3. On these dark nights, the numbers of *M. inornatus* begin to increase at the outer edge of the rocks about the time of first light in the morning, about an hour before sunrise. Although no light is evident to a human being on the bottom at this time, the surface above is showing the first trace of morning light. As light increases, the numbers of these pomadasyids increases, as well as the density of the school. Then, about 30–40 min before sunrise, the school, having reached daytime proportions, streams in over the rocks to return to its daytime location near the beach.

Two other pomadasyids, *Lythrulon flaviguttatum* (Gill) and *Orthostoechus maculicauda* Gill show similar behavior.

Anisotremus interruptus (Gill). After passing the daylight hours in relatively inactive schools close to rocky bottom offshore, these grunts disperse with darkness. Many individuals move into shallow water where they forage on a wide variety of benthic organisms. Study of the stomach contents of 20 specimens (240–410 mm) taken with spear showed a diet that included crustaceans, soft coral, annelids, sea anemones, holothurians,

chitons, gastropods, pelecypods, sea urchins, small fishes, algae, sand, and debris. Some feeding occurs in this species during the day as individuals, or groups of 2 or 3, move about among the rocks.

Haemulon sexfasciatum Gill. During the day, most of these grunts hover in large, relatively inactive schools over sand adjacent to rocky bottom. Although a few individuals periodically nose into the sand at this time, presumably for food, most members of the school show no sign of feeding. However, a few solitary individuals swim close to the bottom inshore at all hours of the day where they feed on organisms in the sand among the rocks. The large schools disperse at night and their members spread out among the rocks where they forage on organisms in the sand. Twenty-three individuals (245–355 mm) were speared. Their diet consisted of crustaceans, mollusks, annelids, and, in the case of one individual, ophichthyid eels.

While operating a small 2-man submarine over sandy bottom in the vicinity of a large, inactive school of *H. sexfasciatum* during the day, we found that when turbulence created by the propeller action stirred up sand in our wake, many of the pomadasyids from the school followed and actively fed on organisms which had been uncovered.

Pomadasyids have been consistently described as nocturnal feeders. Longley and Hildebrand (1941), noting the relative freshness of food taken from pomadasyids at Tortugas in the morning, concluded that grunts were nocturnal feeders. They also reported that schools of *Haemulon sciurus* (Shaw) broke up at nightfall and individuals scattered over the reef to feed. Schroeder (1964) also noted the dispersal of pomadasyid schools after dark.

All of the pomadasyids observed during this study were preyed upon during the day by a number of large predators, including *Mycteroperca rosacea* and the carangids *Nematistius pectoralis* Gill, *Caranx hippos caninus* Günther, and *Seriola colburni* Evermann and Clark.

The formation of schools by the pomadasyids during the day appears to function in lowering the incidence of predation. The pomadasyids, *H. sexfasciatum* in particular, often tightened up their school when a predator threatened. This is illustrated by the following account.

A large school of *H. sexfasciatum* appeared at a cleaning station maintained by butterflyfish (*Heniochus nigrirostris*). At this particular station the cleaners were active at several different points within a defined area. The grunt school broke up into segments of 20–30 fish each, with each segment visiting a different group of cleaners. Suddenly, the grunts abruptly terminated the cleaning activity and rapidly regrouped into a single, large, very tight school. This behavior puzzled me until I realized that a large (60–70 lb) carangid, *Nematistius pectoralis*, had entered the area. The big fish passed close to the school, made a wide turn, and then disappeared in the direction from which it had come. Shortly after the large predator disappeared, the school of grunts moved out of sight. Ten minutes later, however, the grunts returned and the school broke up into segments about the cleaning station as before.

It might seem that a predator would find fishes in a tightly packed school more readily obtainable as prey than those in a more loosely packed school. This is probably not the case with the predators and prey involved here. As Manteifel and Radakov (1961) pointed out, many predators must direct their attack at a single individual in order to achieve any degree of success in capturing a meal. It becomes increasingly difficult to single out an individual as the schools close up, particularly when the schooling fishes then increase their swimming speed and often begin weaving in and out among one another. When a predator makes a feeding rush into this tightly packed aggregation, the school parts before the attacker. The visual effect produced as the schooling fishes radiate out in all directions probably functions in further confusing the predator.

Carangidae

Selar crumenophthalmus (Bloch). These small carangids swim in dense schools close to shore during the day. These schools, which often form a mill, are under periodic attack by the same diurnal predators noted above feeding on pomadasyids. The scad become increasingly active as dusk approaches. Then, with darkness, they spread out over the sand where they feed on both benthic and midwater organisms. Items found in the stomachs of 10 specimens (185–209 mm) taken with spear included crustaceans, small fishes, pebbles, sand, and algae.

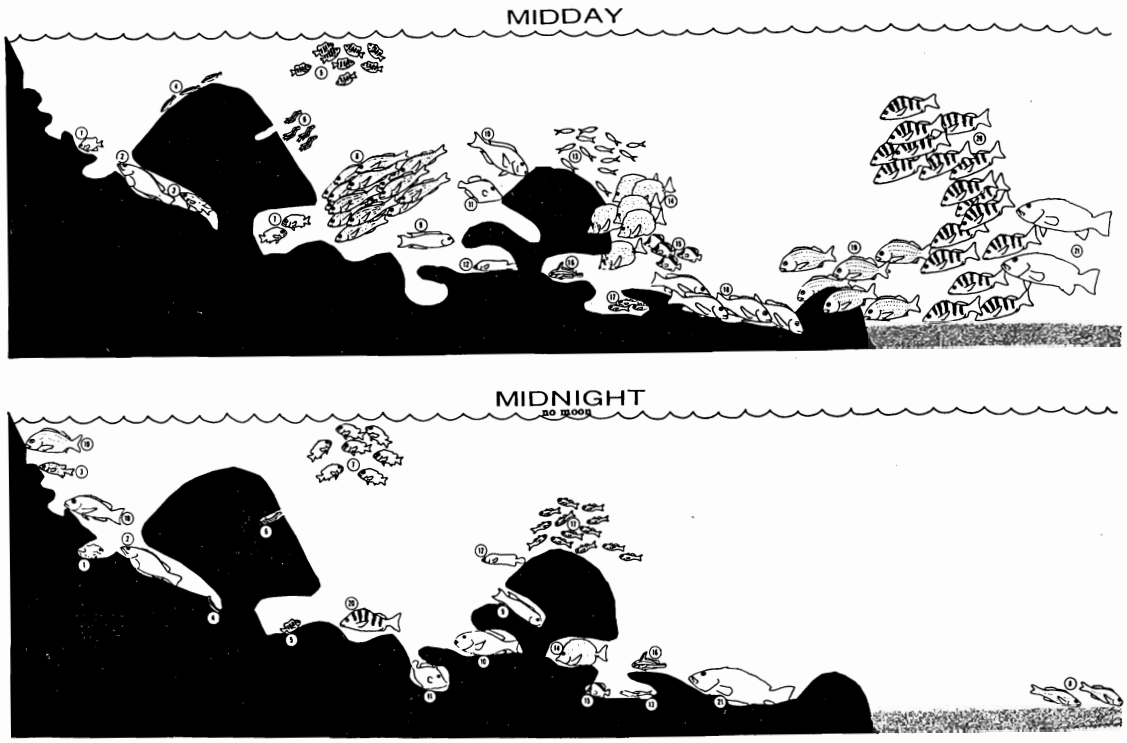

Fig. 1. Diagrammatic representation of an inshore rocky bottom in the southern Gulf of California off Baja California, Mexico. The fishes figured, all of which are treated in this report, are among those most readily observed by a diver. They are shown in positions typically occupied during midday and midnight with no moon. The species illustrated, by number, are: 1) *Eupomacentrus rectifraenum*, 2) *Epinephelus labriformis*, 3) *Holocentrus suborbitalis*, 4) *Thalassoma lucasanum*, 5) *Abudefduf troschelii*, 6) *Runula azalea*, 7) *Myripristis occidentalis*, 8) *Microlepidotus inornatus*, 9) *Bodianus diplotaenia*, 10) *Scarus californiensis*, 11) *Balistes verres*, 12) *Rypticus bicolor*, 13) *Chromis atrilobata*, 14) *Prionurus punctatus*, 15) *Heniochus nigrirostris*, 16) *Pareques viola*, 17) *Apogon retrosella*, 18) *Lutjanus argentiventris*, 19) *Anisotremus interruptus*, 20) *Haemulon sexfasciatum*, and 21) *Mycteroperca rosacea*.

Sciaenidae

Pareques viola (Gilbert). During the day, this croaker, solitary or in groups of 2 to 5, swims in the shadow of low, overhanging ledges or within small caves under the rocks. At night, they emerge into the open where solitary individuals are active close to the bottom. Twelve specimens (20–160 mm) speared or taken in slurp gun, showed a diet that was composed of small crustaceans. Although most feeding occurs at night, some food is ingested during the day when this croaker is under cover.

Longley and Hildebrand (1941) reported similar behavior in *Equetus acuminatus* (Bloch and Schneider), a closely related form in the Atlantic Ocean.

General Remarks

Most, if not all, of the fishes show a difference in their behavior between periods of light and periods of darkness (Fig. 1). Time of major activity tends to be consistent within most of the families of fishes. Thus, species of Acanthuridae, Balistidae, Chaetodontidae, Pomacentridae, Labridae, and Scaridae are most active during daylight, while species of Apogonidae, Holocentridae, Lutjanidae, and Pomadasyidae are more active at night.

Outstanding exceptions occur in many of the large predaceous groups, such as the Serranidae and Carangidae. These families, which contain species varying greatly in size as well as habits, include both nocturnal and diurnal forms.

Although it is clear that many fishes are basically either diurnal or nocturnal, this distinction is not so apparent in many predators. For example, while the serranid *Mycteroperca rosacea* has been classified as diurnal in this report, major feeding activity occurs at dawn and dusk. It is relatively inactive during midday as well as during the night. Perhaps this species, and others with

similar habits, might better be regarded as crepuscular.

The nocturnal species are predators. Most of these are relatively small fishes feeding largely on invertebrates. Included here are the Apogonidae, Holocentridae, and Pomadasyidae, as well as many species of the Carangidae, Clupeidae, Lutjanidae, Sciaenidae, and Serranidae. There is an increase in activity among many, if not most, invertebrates after dark. Many invertebrate species that are inactive under rocks or beneath the sand during the day, emerge at night to feed and, in so doing, expose themselves to predation. The exodus of many pomadasyids and other species out over the sand at night coincides with the emergence of many sand-dwelling invertebrates. On dark nights in particular, many of the minute midwater organisms, notably some of the crustaceans, are especially abundant. Some of these are readily seen due to their luminescence, a factor which may enable fishes feeding on these organisms to orient visually on their prey.

The fishes aggregating in dense, relatively inactive schools close to shore during the day are nocturnal feeders. Included here are many species of the Clupeidae, Lutjanidae, Pomadasyidae, and Carangidae. These large schools disperse at nightfall, often after moving a considerable distance offshore, and the fishes spread out to feed. At dawn they return to their relatively inactive daytime locations. Some diurnal feeding occurs in many of these fishes. In most cases, however, those feeding during the day are not members of the large schools, but rather are solitary or in small groups.

Schooling nocturnal species are a principal source of food for many diurnal piscivores, such as large carangids and serranids. Present evidence indicates that the formation of the school inshore during the day by these nocturnal species functions in defense against this predation. Although predation occurs throughout the day, it is particularly intense early in the morning and late in the evening, reaching a peak at dawn and dusk.

The herbivorous and omnivorous fishes feed during the day, as for example do members of the Acanthuridae and Scaridae which graze on benthic algae. Also included here are those relatively small-mouthed species, including many chaetodontids, pomacentrids, and labrids which feed on minute organisms taken from the surfaces of rocks and coral. Many members of these groups are also particulate feeders on plankton and, in some, the feeding habits have become specialized to varying degrees as cleaners of ectoparasites from other fishes.

On dark nights, most diurnal species are relatively inactive, with many on or close to the bottom, often under cover of some sort. While many remain alert and move about somewhat, including many chaetodontids and pomacentrids, others, for example labrids, scarids, and balistids rest quietly on the bottom, often lying on their sides in crevices, under rocks, or buried in the sand.

When sufficient light is available from the moon, many diurnal fishes are active at night. Examples include *Mycteroperca rosacea, Balistes polylepis,* and *Prionurus punctatus.* As availability of food during the day often elicits feeding in otherwise inactive nocturnal species, such as *Haemulon sexfasciatum,* feeding in some diurnal species probably occurs at night when suitable food is made available through increased illumination from moonlight.

Literature Cited

Breder, C. M., Jr. 1948. Observations on coloration in reference to behavior in tide pool and other marine shore fishes. Bull. Am. Mus. Nat. Hist. 92 (5) :285–311.

Clark, E. 1950. Notes on the behavior and morphology of some West Indian plectognath fishes. Zoologica 35 (13) :159–168.

Gosline, W. A., and V. E. Brock. 1960. A Handbook of Hawaiian Fishes. Univ. Hawaii Press, Honolulu, Hawaii.

Herald, E. 1961. Living Fishes of the World. Doubleday. New York, N. Y.

Hiatt, R. W., and D. W. Strasburg. 1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. Ecol. Monogr. 30:65–127.

Longley, W. H., and S. F. Hildebrand. 1941. Systematic catalogue of the fishes of Tortugas, Florida. Carneg. Inst. Wash. Publ. 535, 34:1–331.

Manteifel, B. P., and D. V. Radakov. 1961. The adaptive significance of schooling behavior in fishes. Rus. Rev. Biol. 50 (3) :338–345.

Randall, J. E. 1958. A review of the labrid fish genus *Labroides,* with descriptions of two new species and notes on ecology. Pac. Sci. 12 (4) :327–347.

———. 1961. A contribution to the biology of the convict surgeon fish of the Hawaiian Islands, *Acanthurus triostegus sandvicensis. Ibid.* 15 (2) :215–272.

———. 1962. Fish service stations. Sea Frontiers. 8 (1) :40–47.

———. 1963. An analysis of the fish populations of artificial and natural reefs in the Virgin Islands. Carib. J. Sci. 3 (1) :1–16.

———, AND V. E. BROCK. 1960. Observations on the ecology of epinepheline and lutjanid fishes of the Society Islands, with emphasis on food habits. Trans. Am. Fish. Soc. 89 (1) :9–16.

———, AND H. A. RANDALL. 1963. The spawning and early development of the Atlantic parrotfish *Sparisoma rubripinne*, with notes on other scarid and labrid fishes. Zoologica 48 (2) : 49–60.

SCHROEDER, R. 1964. Photographing the night creatures of Alligator Reef. Natl. Geog. 125 (1) : 128–154.

WICKLER, W. 1961. Über das Verhalten der Blenniiden *Runula* und *Aspidontus* (Pisces, Blenniidae). Z. f. Tierpsych. 18 (4) :421–440.

WINN, H. E. 1955. Formation of a mucous envelope at night by parrotfishes. Zoologica 40: 145–147.

———, AND J. E. BARDACH. 1959. Differential food selection by moray eels and a possible role of the mucous envelope of parrotfishes in reduction of predation. Ecology 40 (2) :296–298.

———, AND ———. 1960. Some aspects of the comparative biology of parrotfishes at Bermuda. Zoologica 45 (1) :29–34.

DEPARTMENT OF ZOOLOGY, UNIVERSITY OF CALIFORNIA, LOS ANGELES, AND TIBURON MARINE LABORATORY, U. S. FISH AND WILDLIFE SERVICE.

Reproduction in the Nototheniid Fish *Trematomus bernacchii* Boulenger at McMurdo Sound, Antarctica

JOHN H. DEARBORN

The reproductive cycle of the nototheniid fish *Trematomus bernacchii* was studied by observations of the gonads of 549 individuals collected near the U. S. McMurdo Station, Ross Island, Antarctica. The developmental conditions of ovaries from 286 females were divided into 5 stages, and the numbers of fish in each stage were compared by month. The data show that spawning may occur between August and January, but mostly occurs between mid-December and mid-January. Numbers of eggs representing a single spawn range from 1,154 to 3,123. At spawning, eggs are 3.7 to 3.9 mm in diameter. Other aspects of reproduction are discussed. It is suggested that the variable breeding times of Antarctic fishes are due to the specific ecological requirements of the individual species, or of populations of the same species, and are not variable in time because the environment is so stable that one period of the year is as favorable as any other.

INTRODUCTION

THE purpose of this paper is to describe the spawning period and the number and size of eggs of *Trematomus bernacchii* from McMurdo Sound, to compare these data with other accounts of reproduction in this species, and to comment briefly on reproduction in Antarctic fishes in general. Results are based upon an examination of the gonads of 549 specimens collected between 1958 and 1963.

Although *T. bernacchii* is widely distributed in high southern latitudes (Norman 1938), and is common in the shallower waters of the Ross Sea, only limited mention of its reproductive habits is made in the literature. Regarding material collected at Cape Royds, McMurdo Sound, Waite (1911:12) stated, "Specimens examined were in full ripe roe when taken on August 25, 1908; the ova are bright yellow in colour and very large, measuring 3.8 mm. in diameter." Regan (1916: 130) noted that the genital glands of *T. bernacchii* and *T. hansoni* from the "SOUTHERN CROSS" and "DISCOVERY" collections "are much larger in April than in October" and that the probable spawning time is July. Hureau (1964) described the reproductive cycle of *T. bernacchii* from an examination of specimens collected off the Adélie Coast during the Eleventh French Expedition.

Published information on the breeding habits of Antarctic fishes is mostly derived from species taken at South Georgia or various subantarctic islands rather than the continental coastal areas (Lönnberg 1905, 1906;