

# ACTIVITY OF HAWAIIAN REEF FISHES DURING THE EVENING AND MORNING TRANSITIONS BETWEEN DAYLIGHT AND DARKNESS

EDMUND S. HOBSON<sup>1</sup>

## ABSTRACT

Activity during the morning and evening transitions between day and night was studied as part of a broad investigation of ecological relations among reef fishes in Kona, Hawaii, during 1969 and 1970.

Most of the fishes are either diurnal or nocturnal, the former being mainly inactive at night, the latter mainly inactive in daylight. During active periods their behavior is dominated by feeding, whereas inactive periods are dominated by measures to enhance security. Thus twilight behavior involves primarily a changeover from feeding to sheltering, and the reverse. Migrations of various types between shelter locations, where they rest, and feeding grounds are a major element of the transition periods.

The transition events proceed in an established, well-defined sequence. In the evening, after the diurnal fishes have descended to shelter and before the nocturnal fishes have risen into the water column, there is an interim period of about 20 min during which both diurnal and nocturnal fishes are close to the substrate; it is at this time that reef fishes are most vulnerable to predators, and the proximity of cover offers protection. Similar behavior occurs among related fishes in the Gulf of California. The interim period in Kona corresponds in time relative to sunrise and sunset to the period during which schooling fishes in the Gulf of California are under heaviest attack; however, because schooling fishes and the predators that exploit them are not major elements of the Kona fauna, overt predator-prey interactions are not prominent there. Thus the well-ordered pattern of events that characterizes twilight in Kona also occurs on other reefs widespread in tropical seas, whether or not there exists in each of these areas today a severe threat from large piscivorous predators. The twilight pattern of actions is the result of a long evolution that in any one area transcends the existing situation and species. Because predator-prey interactions among fishes have been influenced throughout time by certain basic and unchanging phenomena, the similarity of twilight activity patterns among fishes on widely separated reefs today reflects the impact of a historic threat from predators.

Most fishes on tropical reefs are active either by day or by night, with the diurnal species mostly inactive in darkness and the nocturnal species mostly inactive in daylight (Hobson, 1965, 1968; Starck and Davis, 1966). The changeover from one situation to the other is a complex process, with events following a well-defined sequence. This report describes the significant events during the evening and morning

transition periods in Kona, Hawaii, between June 1969 and August 1970. It is a segment of a broad study of ecological relations among Hawaiian reef fishes. The present report, which deals with the twilight situation, will be followed by a second report covering the situations throughout day and night, respectively, and including a detailed analysis of food habits (Hobson, in preparation). Some highlights of this program were outlined earlier (Hobson, 1970).

<sup>1</sup> National Marine Fisheries Service, Tiburon Fisheries Laboratory, Tiburon, Calif., and Scripps Institution of Oceanography, University of California, San Diego, La Jolla, Calif. Mailing address: Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92037.

## METHODS

This study is based on observations that spanned evening twilight on 20 occasions and

morning twilight on 18 occasions. Generally over 2 hr were spent on station during each observation period, although the transition events detailed in this report were concentrated into a span of about 1 hr, as discussed below. Before the data presented in this report were collected, general observations in the study area at these times of day had provided a broad understanding of the twilight transition. Also contributing significantly to this understanding were extensive observations made during twilight in other seas, especially in the Gulf of California (Hobson, 1965, 1968), where related fishes have similar behavior. With this background and using scuba, I was able to recognize and record what I knew to be significant events and to note the time and other associated characteristics. Additionally, some data from observations made at various times of day and night during other segments of the program in Kona are pertinent to the present report and thus used here. Furthermore, interpretation of the twilight activities benefited significantly from these other phases of the overall Kona program.

Throughout all twilight observation periods, Lloyd D. Richards, stationed on the sea floor nearby, recorded incident light in foot-candles each minute with a photometer facing the water's surface. In this report, all records of light levels during specific events refer to these readings. To minimize instrument error, two photometers of the same model (Weston Ranger 9, universal exposure meter, Model 348)<sup>3</sup> were alternated. The accuracy of the absolute values obtained with these inexpensive instruments is not considered critical; rather, the primary concern is that the relative values are consistent, thus permitting comparisons of behavior relative to time and light between one observation period and another.

The time of specific events are presented relative to time of sunrise or sunset, as calculated for the longitude and latitude of the study area using the *Nautical Almanac, U.S. Naval Observatory*. An event occurring at about the

same time each day relative to sunrise or sunset, will, in time of day, vary by as much as several hours over the course of the year. This fact reduced any bias that might have resulted from subconsciously looking for an event at a specific time. Although I was alert for certain events in sequence, based on familiarity with the general situation, I consciously avoided thinking in terms of time relative to sunrise or sunset during the observations. This was not difficult to do. I did not calculate time of sunrise or sunset until after a period of observation, and neither could have been directly observed, even had I not been underwater at the time; in the study area a large volcano blocks much of the eastern sky, and the western sky generally is obscured by clouds at the end of the day. Furthermore, usually a week or more elapsed between observations of morning or evening twilight, so that the time of sunrise and sunset changed substantially from one set of observations to the next. Finally, I did not translate the data from time of day to time relative to sunrise or sunset until the program in Hawaii was completed.

Obviously all events judged significant were not witnessed during each observation period. Many were evident only in certain locations, and several occurred at about the same time. Consequently, the number of times that data were recorded for each event varies widely.

Names used for the fishes generally follow those given by Gosline and Brock (1960); exceptions occur where more recent taxonomic studies have indicated changes. Most of the fishes are referred to some broad feeding category, such as being a herbivore, a plankton feeder, etc. These general designations are based on detailed study of food habits to be reported elsewhere (Hobson, in preparation).

In parentheses following the first mention of each fish species are given a mean and range of standard lengths, for example (235: 173-284 mm). These figures represent the sizes of specimens of that species that were collected for the food habit analysis (Hobson, in preparation). In collecting these specimens an attempt was made to sample individuals of sizes that showed behavior of adults. Hence these figures provide a good measure of the relative sizes of

<sup>3</sup> Reference to trade names does not imply endorsement by the National Marine Fisheries Service.

the different species, as relating to the activity described in the present report. This information is important because the size of a given fish is reflected in its behavior during twilight, as discussed below.

A number of species prominent on Hawaiian reefs are not mentioned in this report. My coverage is confined to species in which I recognized behavior relating specifically to the twilight transition period on the three reefs where twilight behavior was studied. Some other species not prominent on these reefs are abundant elsewhere and were studied during other phases of the overall project. These other segments of the work in Kona yielded no data inconsistent with what is reported or discussed below.

### STUDY LOCATIONS

The reef habitat on the Kona coast is restricted to a narrow shelf close to shore. From the base of a rough, basalt shore cliff, the sea floor in most locations slopes gently downward for distances of between 50 and 600 m from shore. At this point, where the water is generally about 20 to 25 m deep, the bottom drops abruptly to great depths.

Most of the data for this report were collected from three inshore locations, all at depths between 5 and 10 m. Each location has a distinctly different substrate. Station 1 is in Kealakekua Bay among massive heads of the coral *Porites pukoensis* rising 2 to 3 m above the sea floor. Station 2 is in Honaunau Bay among an extensive field of the coral *Porites compressus* growing in fingerlike branches 10 to 15 mm wide. Station 3 is also in Honaunau Bay, but among massive basalt boulders 2 to 3 m across that are largely overgrown with encrusting algae and corals. These boulders are variably interspersed with the forms of both *P. pukoensis* and *P. compressus* described above.

The remarkably constant weather and water conditions that characterize the Kona coast held true throughout the 15 months of observations. Consequently, variables inherent in changing environmental conditions were minimized, making it easier to recognize activity patterns associated with the twilight transition periods.

### TRANSITION FROM DAY TO NIGHT

It is difficult to determine exactly when the daytime situation begins to move toward that prevailing after dark. In large part, this difficulty reflects variations in activity of many diurnal fishes because of differing water transparencies, and even more when variable cloud cover causes light levels to fluctuate. These variations are difficult to distinguish from those associated with the lesser light levels of the advancing afternoon. Additionally, as the day progresses, activity of diurnal fishes changes subtly in many other ways that may or may not relate to a transition to the nocturnal mode. The situation prevailing throughout the day (Figure 1), including variations with changing light levels and other factors, is described elsewhere (Hobson, in preparation). This report is concerned with the more striking transformations that occur during the transition between daylight and darkness, beginning about 15 min before sunset and lasting until about 45 min after sunset—a span of about 1 hr. Three major periods are readily recognized: 1) the cover-seeking of the diurnal fishes; 2) an interim period; and 3) the mass emergence of nocturnal species.

### COVER-SEEKING OF THE DIURNAL FISHES

#### Initial Overt Phase of the Transition

An early cue to the developing transition lies with the plankton-feeding fishes that swim during the day in stationary aggregations up in the water column. Prominent among these are the damselfishes *Abudefduf abdominalis* (142: 105-162 mm), *Chromis leucurus* (57: 37-70 mm), *C. ovalis* (124: 121-138 mm), *C. vanderbilti* (38: 17-46 mm), and *Dascyllus albisella* (79: 42-95 mm). The distance of each fish from the substrate is related to its size, because the larger individuals swim at higher levels in the water column. These fishes descend progressively closer to the sea floor as light diminishes. Members of the smallest species, *Chromis vanderbilti*, are the first to take cover; they seldom move more than a meter above the reef on even the

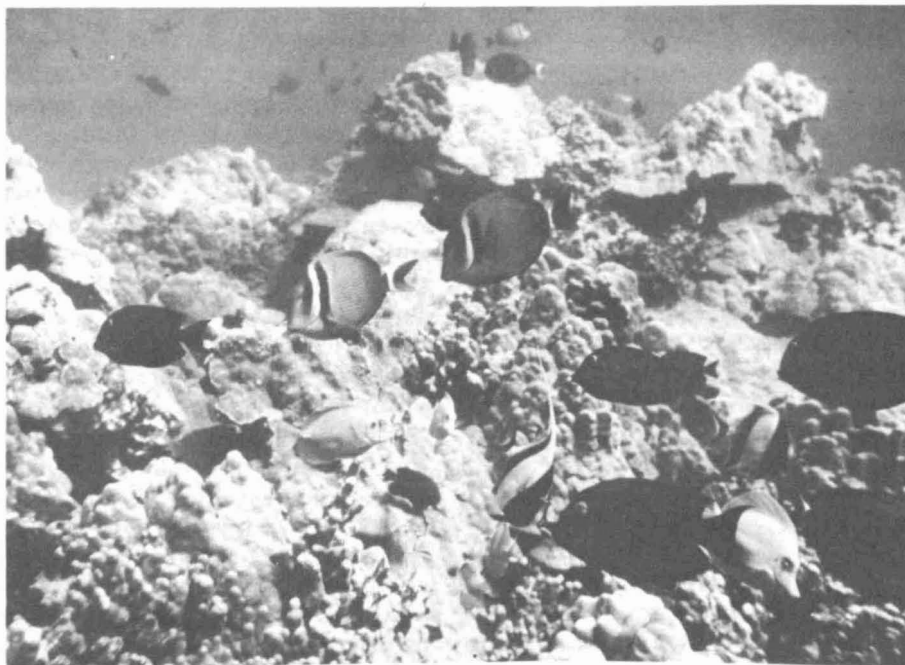


FIGURE 1.—Daytime on a coral reef in Kona, Hawaii. Most of the fishes are acanthurids, including *Ctenochaetus strigosus*, *Acanthurus leucopareius*, and *Zebrasoma flavescens*. Other fishes include *Centropyge potteri* and *Zanclus canescens*.

brightest days, and by 15 min before sunset all of them have dispersed among holes in the reef. The progressive descent of the other plankton-feeding damselfishes is treated below.

As individuals of *C. vanderbilti* are taking shelter, the transition to the nocturnal situation is clearly underway. The numbers of smaller wrasses active on the reef have been noticeably declining since at least 30 min before sunset, though many still remain in view. More obvious, an increased tendency to aggregate is exhibited by some of the smaller herbivorous fishes, including the surgeonfishes *Acanthurus nigrofuscus* (120: 100-140 mm) and *Ctenochaetus strigosus* (125: 110-145 mm) and also the parrotfish *Scarus taeniurus* (210: 180-243 mm). These aggregations continue to develop through sunset and into early twilight.

By about 5 min after sunset the last individuals of many diurnal species have taken cover, including the last of the smaller wrasses. No data are available on precisely when the larger

wrasses seek cover (those exceeding a length of about 350 mm are uncommon in the study areas). Nevertheless, my observations agree with those of Gosline and Brock (1960), who stated that all Hawaiian labrids are inactive at night.

Two species of smaller labrids are representative: *Thalassoma duperrey* (125: 103-146 mm) and *Labroides phthiropagus* (63: 33-91 mm). (I did not collect specimens of the latter species—size data are from Youngbluth, 1968.) *T. duperrey* probably is the most numerous of the readily observed species of fish overall in the various Hawaiian reef habitats and thus serves well as an indicator species. *L. phthiropagus* is not abundant, but as a cleaner fish that centers its activity around well-defined stations (Randall, 1958; Youngbluth, 1968), individuals can be readily recognized from one evening to another.

*Observations on Thalassoma duperrey.*—On five occasions I was confident that I observed

the last individual of *T. duperrey* active in my immediate area take shelter (Figure 2). Each of these individuals swam in and out of coral crevices several times before finally slipping into a hole where it remained. On subsequent close inspection I found each one lying on its side in the hole, and intermittent checks over the next hour disclosed each still in the same position. Following one such observation, a pre-dawn inspection the next morning found the fish in the same spot.

There is evidence that, on a given evening, an individual is intent on resting in a particular spot. Two incidental observations give credence to this view. One evening I lay prone and immobile across a large coral head (*Porites*), watching the many *T. duperrey* around me, and waiting to note the last one that took cover. The behavior of one individual was unusual: it circled close by regarding me more intensely than seemed normal, then swam away. Several times this same fish reappeared, repeated this behavior, then swam away again. Curious, I abandoned my position and followed when the fish reappeared. After being led in a circle, I found myself back at the original location, where the fish slipped into a coral crevice in the spot where I had been lying. Only then did it occur to me that this fish had behaved abnormally probably because I had been blocking entry to its nocturnal resting spot. Other individuals of *T. duperrey* were still active in the area when this incident occurred, making it uncertain whether the fish actually had been delayed in attaining cover. A similar incident later was more conclusive. Again, I rested motionless, watching the many individuals of this labrid during the evening transition period, this time leaning against a vertical wall of coral (*Porites*). One individual swam close by, then moved to a low ledge about 2 m away, where it then swam back and forth, watching me continuously. Several times it momentarily left the ledge, approached me, and then darted back to the ledge. Recalling the earlier incident, I did not move from my station until long after all other fish of this species had gone under cover. Finally, 12 min after sunset (light 0.8 ft-c), with the behavior of the labrid under observation still unchanged, I

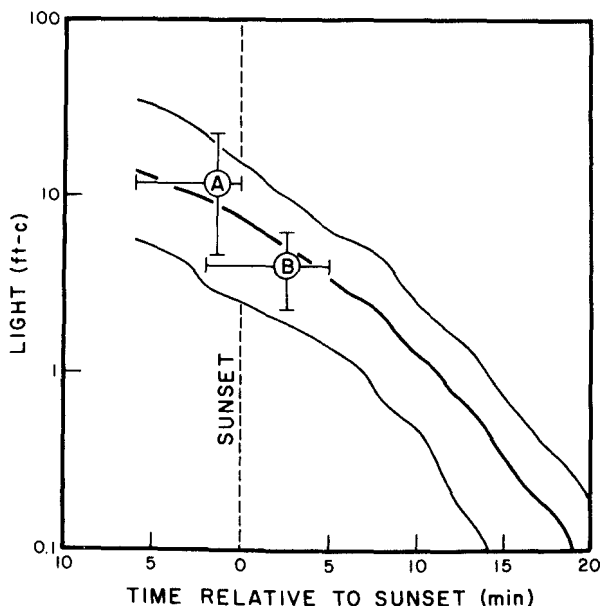


FIGURE 2.—Some characteristics of certain labrids during evening twilight. Each lettered symbol represents a species: A. *Thalassoma duperrey*—when the last individual took cover on five evenings. B. *Labroides phthirophagus*—when one individual took cover on five evenings. The circle represents mean values of both time and incident light when the event occurred; the vertical line, the range of incident light values; and the horizontal line, the range in time relative to sunset. The three diagonal lines represent: the maximum light values for each minute relative to sunset during all evening twilight observation periods (top line), the minimum values for each minute (bottom line), and the mean values (heavy median line).

moved away. Immediately, it swam to my former location and slipped into a crevice. Later, using a light, I could see this wrasse lying on its side, wedged back in the crevice. (These two incidents are not included among the data represented in Figure 2, which includes only situations judged normal.)

These observations indicate that a fish can have a strong affinity for a specific resting spot. However, I have no evidence that this is more than a short-term phenomenon. Many nocturnal resting spots of *T. duperrey*, and other fishes, were discovered incidentally during other phases of the work in Kona when I closely inspected crevices in the coral during the night. When circumstances permitted, followup observations

were made at various times during subsequent nights. Although a given resting spot was frequently occupied over several nights by what seemed to be the same fish, this did not hold true for longer than a week or so. I doubt that my repeated intrusions disturbed these fishes sufficiently to influence a change of location. Usually a spot occupied by a resting fish on one evening was vacant when next observed on a subsequent night.

*Observations on Labroides phthiophagus.*—Individuals of this species, like other labrids, seek cover for the evening during the period from immediately before to just after sunset. *L. phthiophagus*, like *T. duperrey*, finds nocturnal shelter in crevices of rock or coral. But with this species, unlike the others, individuals can readily be recognized from one day to the next, owing to their close association with well-defined cleaning stations. Thus, whereas observations of *T. duperrey* each evening involved only the last active member of the species, the cover-seeking of one particular individual *L. phthiophagus* was timed over five different evenings (Figure 2). The one instance when this fish took shelter 5 min after sunset was the latest that any of the smaller labrids were seen active.

*L. phthiophagus* cleans other fishes at its station until it takes shelter. Frequently other species still hover at the station in soliciting fashion (see Losey, 1971) after the resident cleaner has retired for the night.

### Twilight Upsurge in Activity

Visible activity among many diurnal fishes rises sharply at about the time of sunset. However, feeding generally is not involved; rather, the upsurge stems mostly from the many species on the reef that migrate from one location to another at this time, and also to increased interspecific and intraspecific aggression, at least much of which is related to territoriality. In addition, some species show at this time an increased tendency to aggregate and to swim in more visible locations.

Above, I note that prior to sunset some of the

smaller herbivores increasingly aggregate a meter or so above the reef. Beginning with this event, the phenomenon gains momentum, encompassing more and larger fishes, especially among the surgeonfishes and parrotfishes. By 5 min after sunset this activity has reached its maximum level, even though most of the smaller species among which it first appeared by then have discontinued the activity and have settled under cover.

There seem to be two major types of aggregations: Assemblages of one type, often of mixed species, mill about 1 or 2 m above certain parts of the reef; and assemblages of the other type, mostly of a single species, move with seeming purpose from one location on the reef to another. Each of these types of assemblages is treated separately below.

*The milling assemblages.*—During about a 10-min period, 5 to 15 min after sunset, the scene on many parts of the reef is dominated by large, essentially stationary, mixed-species aggregations that mill about in certain locations 1 or 2 m above the substrate. Various surgeonfishes predominate, especially *Zebrasoma flavescens* (163: 130-195 mm), *Acanthurus achilles* (182: 165-200 mm), *A. nigroris* (165: 130-180 mm), *A. leucopareius* (190: 185-210 mm), and *Naso lituratus* (180: 156-220 mm). Also prominent are the parrotfish *Scarus sordidus* (230: 205-260 mm), the triggerfishes *Melichthys niger* (165: 122-195 mm), and the filefish *Cantherines dumerili* (200: 171-240 mm).

*The twilight migrations.*—Some members of many species migrate at this time from one location on the reef to another. Although the patterns remain obscure, this activity involves movements that occur consistently in certain locations. Evening after evening specific routes are followed, in which certain species stream continuously past a given point in long drawn-out processions over a period of several minutes.

Prominent participants include members of certain species, including the surgeonfish *Naso hexacanthus* (261: 202-392 mm) and the damselfish *Chromis verater* (120: 100-141 mm), that feed on plankton during the day high in the

water column at the outer edge of the reef. Many of these fishes show a migratory pattern up into the shallower parts of the reef at nightfall, but the pattern is obscured by the circumstance that other individuals of these same species do not move inshore, but instead remain throughout the night at the outer edge of the reef, nestled among the coral on the sea floor below their midwater feeding areas.

Many of the smaller herbivores, including the surgeonfishes *Zebbrasoma flavescens* and *Ctenochaetus strigosus*, as well as the parrotfish *Scarus sordidus*, exhibit similar movements. These patterns are obscured because on any given night relatively few individuals of these species join such migrations; many others of the same species do not, including some that are prominent in the milling assemblages noted above. It remains unknown just what sort of redistribution pattern is achieved by these movements.

#### Descent of the Plankton-Feeding Damsel Fishes

Individuals of the smallest plankton-feeding damselfish *Chromis vanderbilti* have scattered among the rocks by about 15 min before sunset, as noted above. During the few minutes immediately following sunset, members of the next smallest species, *C. leucurus*, settle individually in coral crevices. On three evenings the time and light levels were recorded as the last individual of *C. leucurus* in my surroundings took shelter (Figure 3).

The larger species, including *Abudefduf abdominalis*, *Chromis ovalis*, *C. verater*, and *Dascyllus albisella*, continue to drop lower in the water column throughout this period. Precise times for the different stages of the descent are not available, but all drop at a similar rate, a fact probably related to their similar sizes. The descent begins well before sunset, when individuals in 8 m of-water, for example, are about 5 m over the sea floor. At 8 to 10 min after sunset they are about 1 to 2 m over the coral, and here contribute to the general activity, where the milling aggregations and migrating schools, described above, dominate the scene.

#### Vacating the Water Column

Throughout the time that the milling aggregations and migrating schools swim over the reef, individuals from these assemblages are descending to cover below. Nevertheless, a substantial number still swim in the water above the reef, along with the small groups of larger plankton-feeding damselfishes, at about 10 to 15 min after sunset. Then, abruptly, the vast majority of these fishes suddenly drop to the reef below, leaving the water column essentially deserted. This is a well-defined phenomenon, and on 12 evenings the time and light were recorded when it occurred (Figure 3).

#### Cover-Seeking of Other Diurnal Fishes

Also going under cover at about the time that the water column is vacated are the larger parrotfishes *Scarus rubroviolaceus* (366: 267-475 mm) and *S. perspicillatus* (348: 269-463 mm).

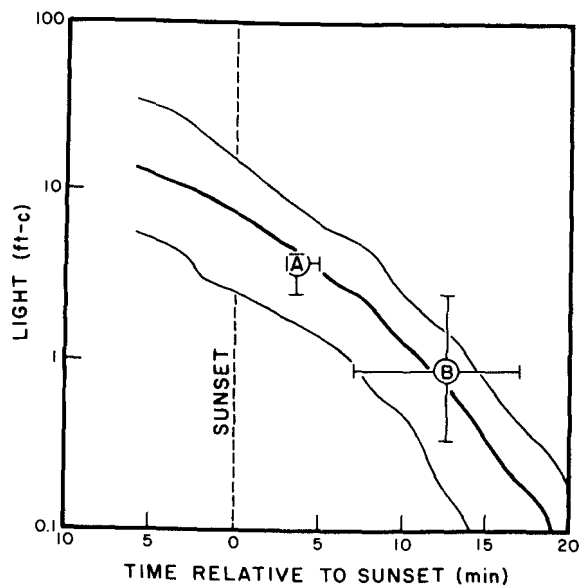


FIGURE 3.—Some characteristics of certain diurnal fishes during evening twilight. A. *Chromis leucurus*: when the last individual took cover on three evenings. B. When the water column was abruptly vacated by diurnal fishes on 12 evenings. For explanation of symbols, see legend for Figure 2.

The smaller parrotfishes had sought shelter earlier. Gone now too are the triggerfishes *Sufflamen bursa* (140: 109-164 mm) and *Rhinecanthus rectangulus* (142: 114-170 mm), as well as the filefishes *Pervagor spilosoma* (85: 64-120 mm) and *Cantherines sandwichiensis* (116: 84-132 mm), all of which had remained close to the substrate throughout their active periods during daylight and early twilight. Because most of these and many other diurnal species are not especially numerous on all of the study areas, often none are in view for long periods even during those times of day when they are most active; therefore, it would not have been meaningful to record the last individual of each species that was seen to take cover, as was done with the ubiquitous *Thalassoma duperrey* and a few other species treated in this report. This procedure is meaningful only with species whose members are so numerous and widespread that in all study areas some of them are always in view during their active periods. Nevertheless, these species, as described above, are only rarely seen in exposed positions after the water column has been vacated.

Many sedentary diurnal fishes find shelter during this period too. One suddenly realizes that such species as the hawkfishes *Paracirrhites forsteri* (139: 93-181 mm), *P. arcatus* (82: 49-101 mm), and *Cirrhitops fasciatus* (76: 39-91 mm) are only occasionally visible in locations where they are numerous during daylight. The same is true of the blennies *Exallias brevis* (94: 70-106 mm) and *Cirripectus variolosus* (73: 66-80 mm). Relative activity in species that are at least overtly inactive is difficult to quantify. Nevertheless, after the nocturnal situation prevails, about 30 min after the free-swimming fishes vacate the water column, these sedentary diurnal fishes rarely occur in exposed positions.

#### THE EVENING INTERIM PERIOD

When the last of those diurnal fishes swimming above the coral abruptly descend to the ocean floor, about 10 to 15 min after sunset, the evening interim period begins. At the outset, many diurnal fishes still mill about in pockets among the coral, close to the substrate. Promi-

nent among these are the medium-sized surgeonfishes, such as *Acanthurus achilles*, that were prominent in the milling aggregations earlier. In addition, a few of the larger surgeonfishes, like *A. dussumieri* (340: 302-390 mm), still swim slowly over the coral in small scattered schools, but these do not diminish the prevailing quiescence. The closely related moorish idol, *Zanclus canescens* (108: 74-137 mm), still swims in groups of three or four, but close to the substrate. The butterflyfishes, family Chaetodontidae, often remain paired, as during midday, but some already show colorations that are different from those seen in daylight; these include *Chaetodon auriga* (151: 132-160 mm), *C. ornatissimus* (119: 95-140 mm), *C. multicinctus* (84: 78-94 mm), and *C. unimaculatus* (85: 66-102 mm), which become progressively less active and stay close to the coral. Damselfishes too, including *Pomacentrus jenkinsi* (89: 80-100 mm), and *Plectroglyphidodon johnstonianus* (60: 39-70 mm), though generally solitary, remain active close to coral and rock shelter at this time. The chaetodontid *Centropyge potteri* (80: 69-86 mm) behaves much like these damselfishes.

Into this situation of rapidly diminishing activity among diurnal species, the nocturnal species begin to emerge from the caves and crevices of the reef, in which they have passed the daytime. The first to appear is the cardinalfish *Apogon snyderi* (96: 82-130 mm), which remains close to the substrate, frequently mixing with the diurnal species that are settling there. A second cardinalfish, *A. menesemus* (114: 90-134 mm), soon follows its congener into the open. The initial sightings of *A. snyderi* and *A. menesemus* moving away from shelter were recorded on four and five evenings, respectively (Figure 4).

Several minutes later, when the diurnal species still in view are becoming more and more quiescent, the first of the squirrelfishes, the relatively large *Holocentrus sammara* (162: 128-202 mm), appears. This event was recorded on four evenings (Figure 5). Throughout the day, some individuals of both *A. snyderi* and *H. sammara* hover in view at the entrances to their diurnal retreats; consequently, one must be thoroughly familiar with these fishes to recognize



the subtle behavioral distinctions that characterize their initial moves away from shelter in the evening.

The interim is aptly termed the "quiet period," because so little activity is visible to an observer. The small fishes, both diurnal and nocturnal, are close to the sheltering substrate at this time. The term "quiet," as used here, refers to an absence of observable activity, not to an absence of sound. In fact, vocalizing of many animals increases throughout the transition period (see, for example, Cummings, Brahy, and Herrnkind, 1964).

During the latter part of the interim, or quiet period, a few individuals of *Myripristis* spp. move out of their caves but stay close to the substrate. When the members of these species sud-

denly boil out of their caves 30 to 35 min after sunset, this striking event marks an abrupt end to the evening interim period.

## THE MASS EMERGENCE OF NOCTURNAL FISHES

### Reoccupation of the Water Column

The darkening water column suddenly becomes reoccupied by a horde of fishes when squirrelfishes of the genus *Myripristis* come streaming out of their diurnal retreats. The timing of this spectacular event was recorded on eight different evenings (Figure 5). Three species prominent on the study reefs, *Myripristis argyromus* (176: 116-210 mm), *M. multiradiatus*

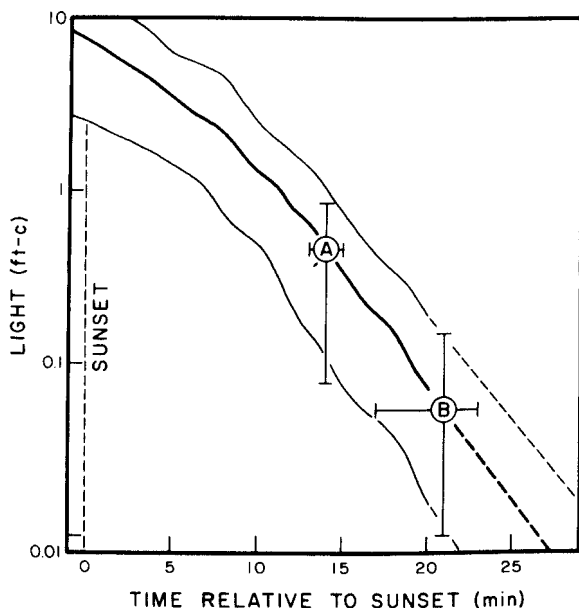


FIGURE 4.—Some characteristics of certain apogonids during evening twilight. A. *Apogon snyderi*: when the first individual left cover on four evenings. B. *Apogon menesemus*: when the first individual left cover on five evenings. For explanation of symbols, see legend for Figure 2. In addition, the broken diagonal lines represent estimated light values. Because of instrument limitations, light readings later than about 20 min after sunset were often unreliable, and therefore values beyond this point were estimated by projecting the established lines.

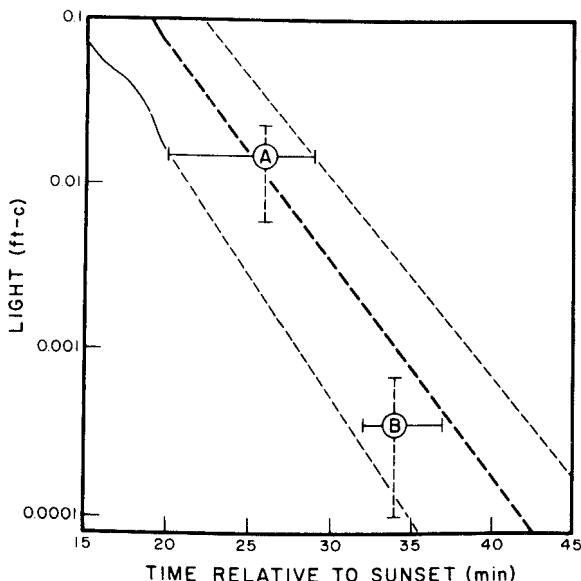


FIGURE 5.—Some characteristics of certain holocentrids during evening twilight. A. *Holocentrus sammara*: when the first individual left cover on four evenings. B. *Myripristis* spp: when large numbers of these fishes abruptly appeared in the water column on eight evenings. For explanation of symbols, see legends for Figures 2 and 4. In addition, broken lines representing range of light values in species symbols indicate that these were estimated for each observation by projecting the established line beyond 20 min after sunset.

(120: 74-145 mm), and *M. berndti* (169: 136-270 mm), all emerge at the same time. All move right up into the water column, although *M. multiradiatus*, the smallest of the three, stays closer to the reef than the other two. Almost immediately, many individuals of *M. argyromus* and *M. berndti* move offshore in mass. That fishes of this genus migrate offshore at night was noted by Gosline (1965), and their nocturnal plankton-feeding habits have been established (Hobson, in preparation).

At about the same time, bigeyes, *Priacanthus cruentatus* (173: 115-255 mm), rise from the rock and coral crevices that had sheltered them in daylight and, forming schools high above the reef, most of them swim offshore. The offshore migration at night by *P. cruentatus* was noted by Gosline (1965), and the feeding habits of this fish were studied (Hobson, in preparation).

At about the same time that fishes are reoccupying the water column, many other nocturnal

fishes that are active only close to the substrate begin to be seen for the first time. These are mostly small species under about 200 mm long, and all are predators. Included are a number of squirrelfishes of the genus *Holocentrus*, including *H. xantherythrus* (106: 88-123 mm), *H. diadema* (109: 85-127 mm), *H. lacteoguttatus* (88: 52-104 mm), *H. tiere* (141: 67-235 mm), and *Holotrachys lima* (91: 70-113 mm); also the scorpionfishes *Dendrochirus brachypterus* (99: 80-118 mm), *Pterois sphex* (83: 58-121 mm), and *Scorpaena conioarta* (46: 26-67 mm), and the brotulid *Brotula multibarbata* (169: 73-250 mm). The nocturnal feeding habits of these fishes were studied (Hobson, in preparation).

To the human eye, it is nighttime on the reef at about 50 min after sunset, although the last vestige of daylight is still visible on the water's surface overhead. By this time the nocturnal situation prevails and will continue to do so until morning (Figure 6).



FIGURE 6.—Nighttime on a coral reef in Kona, Hawaii. The fishes swimming above the reef are squirrelfish, *Myripristis* spp. At lower right center a single surgeonfish, *Zebra-soma flavescens*, is nestled among the coral; the horizontal white bar on its side is, in adults, a feature of its nocturnal coloration.

## TRANSITION FROM NIGHT TO DAY

As is true of the transition from day to night, it is difficult to determine exactly when the nighttime situation begins to give away to that prevailing during daylight. In large part, this difficulty reflects the great variation in activity among fishes at night relative to the amount of moonlight. The situation throughout the night, including variations under different levels of moonlight, is described elsewhere (Hobson, in preparation). This report is concerned with the more striking transformations that occur during the transition from darkness to daylight, beginning about 45 min before sunrise and lasting until about 15 min after sunrise—a total of about 1 hr. As is true of the evening transition, described above, three major periods are readily recognized: 1) the cover-seeking of the nocturnal fishes; 2) the morning interim period; and 3) the mass emergence of diurnal species.

### COVER-SEEKING OF THE NOCTURNAL FISHES

#### Return of the Offshore Feeders

When there is no moonlight, an underwater observer notices the first trace of sunlight on the waters surface overhead about 1 hr before sunrise. Nevertheless, not for another 10 to 15 min do the fishes display overt signs that the transition to their daytime behavior is underway. Then, about 40 to 50 min before sunrise, the numbers of *Myripristis* spp. and *Priacanthus cruentatus* increase sharply near the caves where they pass the daylight hours. To some extent this is the assembling here of those individuals that had remained on the reef during the night, but mostly this marks the return to the reef of individuals that had migrated elsewhere.

The species of *Myripristis* become simultaneously so abundant everywhere that it is uncertain to what extent they have arrived together in schools or have converged simultaneously as solitary individuals onto the reef. The behavior of *P. cruentatus* is clearer. Being far less abundant than *Myripristis*, individuals of *P. cruentatus* are seen arriving in discrete schools, swimming high above the reef. These schools

were especially apparent when an arrival point for the species was discovered at Honaunau, at a location near a coral cave midway down a steep slope. The crest of the slope is in water 12 m deep, the base is about 35 m deep, and the cave is at a depth of about 20 m. On six mornings, I witnessed the arrival here of a large school of *P. cruentatus* (Figure 7). Although a few early arrivals had already been in the area for as long as 10 min, the sudden appearance of the school, containing 30 to 50 fish, was a readily recognized event. After arriving together, many of these fish remained as a unit, milling close to the substrate just outside the entrance to the cave; however, many others of the group dispersed along the face of the slope, where much cover is available under overhanging coral growths. After about 10 min, during which these fish hovered close to the coral, all gradually took shelter: the majority entered the cave, whereas others, either as individuals or groups of a few fish, found cover in the varied crevices and smaller caves along the face of the slope. On the two occasions when the time was noted, the last of these fish were seen entering shelter at 29 and 32 min before sunrise, respectively.

After the initial upsurge in their numbers on the reef, some *Myripristis* go under cover right away, but most continue to swim above the coral for 10 min or so. On eight mornings I noted when the last of these had entered their caves (Figure 7).

#### Cover-Seeking of Other Nocturnal Fishes

About the time that *Priacanthus cruentatus* and *Myripristis* spp. are reappearing on the reef in large numbers, members of at least most of the other, less conspicuous nocturnal species are still active close to the substrate. It remains uncertain just when, in response to the approaching dawn, many nocturnal fishes cease to range into exposed positions. *Holotrachys lima*, *Dendrochirus brachypterus*, *Pterois sphex*, *Scorpaena conioarta*, *Brotula multibarbata*, and others are among the species that are seen only irregularly during the night, partly because they are not especially numerous. The behavior of the more numerous squirrelfishes of the genus *Holocentrus* is less obscure. Individuals of any one

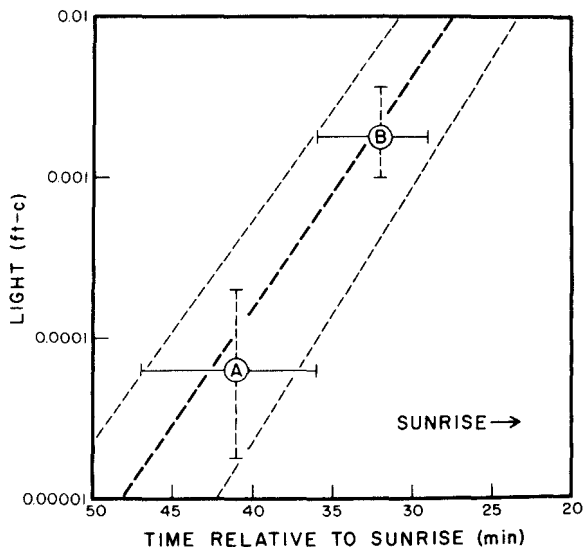


FIGURE 7.—Some characteristics of certain nocturnal fishes during morning twilight. A. *Priacanthus cruentatus*: when a certain school returned to the reef on six mornings. B. *Myripristis* spp. when the last individual descended to the reef on eight mornings. For explanation of symbols, see legends for Figures 2, 4, and 5, except that this figure represents morning events.

species of *Holocentrus* do not go under cover at about the same time, as is true for *Myripristis* spp. Instead, their numbers gradually diminish over a period of about 20 min during early twilight, approximately 50 to 30 min before sunrise. By the time holocentrids of the genus *Myripristis* have gone under cover, about 30 min before sunrise, the only nocturnal fishes consistently in view are scattered individuals of *Holocentrus sammara*, *Apogon menesemus*, and *A. snyderi*. At this point the morning interim period has begun.

#### THE MORNING INTERIM PERIOD

As the midwaters are being vacated by the species of *Myripristis*, it is getting light enough for the human observer to visually distinguish details of the reef around him. It is about 30 min before sunrise, and relatively few fishes are seen. Scattered individuals of several nocturnal species, especially *Holocentrus sammara*, *Apogon menesemus*, and *A. snyderi*, still hover in

view close among the coral but are not active. Among diurnal fishes, a number of chaetodontids, many paired, move about close among the coral; the nocturnal colorations of many are just now giving way to their diurnal hues. Despite these active fishes, the overall aspect on the reef is quiet. Thus, the morning interim, like the evening interim, is termed the "quiet period."

About 5 min into the interim, or quiet, period, when sunrise is still about 25 min away, and when the last *Holocentrus sammara* is now under shelter, the first strong indications of increasing activity in diurnal fishes is seen. At this time the large and medium-sized surgeonfishes begin to assemble in depressions between the towering heads of the coral *Porites*. The timing of this event was recorded on six different mornings (Figure 8). These assemblages, which include

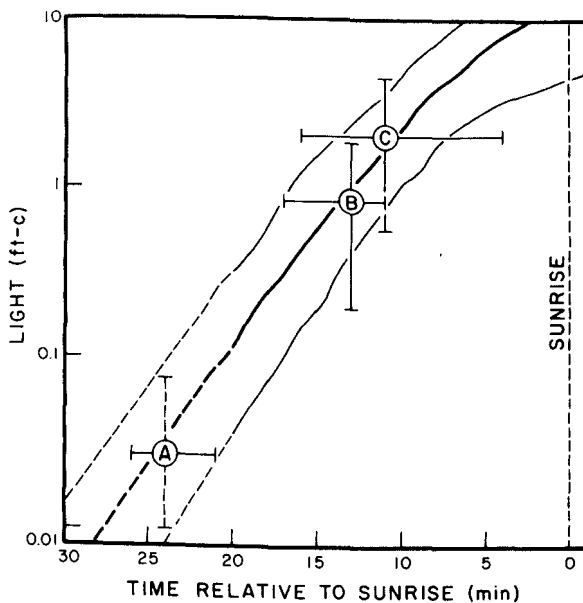


FIGURE 8.—Some characteristics of certain diurnal fishes during morning twilight. A. When species of acanthurids began to assemble in reef depressions on six mornings. B. When diurnal fishes first surged into the water column on nine mornings. C. When the first scarid appeared away from cover on nine mornings. For explanation of symbols, see legends for Figures 2, 4, and 5, except that this figure represents morning events.

*Acanthurus achilles* and *A. leucopareius*, continue to develop for about 5 min. *Zanclus canescens* soon joins in, swimming in groups of four to six, as do various chaetodontids, most notably the many species of *Chaetodon*. These become increasingly active, while at the same time staying close to the substrate. Pomacentrids, including *Pomacentrus jenkinsi* and *Plectroglyphidodon johnstonianus*, have become noticeably active close to the coral and rocks. The chaetodontid *Centropyge potteri* becomes active in the same area, and joins the pomacentrids in feeding on benthic organisms at this time. In this benthic activity, these fishes swim among the stragglers of *Apogon snyderi* and *A. menesemus*, which are now gradually going under cover.

At about 20 min before sunrise the assemblages that have been developing in depressions among the towering corals begin to rise out of the depressions and range over the reef. At first they stay close to the substrate, but then, in an action comparable in abruptness to their vacating the water column in the evening, these diurnal fishes rise 1 to 2 m above the reef. This event marks the end of the morning interim period.

### THE MASS EMERGENCE OF DIURNAL FISHES

#### Twilight Upsurge in Activity and Reoccupation of the Water Column

The sudden surge of diurnal fishes into the water column was noted on nine mornings (Figure 8). Surgeonfishes, and to a lesser extent parrotfishes, are the predominant forms here, just as they are during the increased activity during evening twilight. As in the evening, they swim in aggregations that move back and forth 1 to 3 m over the reef, or in schools that move with seeming purpose from one location on the reef to another.

*The milling assemblages.*—The assemblages that develop above the reef in the morning are more segregated by species than are those that occur in these same locations during the evening. The initial surge of activity into the water col-

umn 10 to 15 min before sunrise involves mostly medium to larger herbivorous species, including surgeonfishes *Acanthurus achilles*, *A. leucopareius*, and *Naso lituratus*. These do not show any purposeful direction; rather, they mill about over a defined part of the reef. Also swimming in and around these assemblages are a number of larger diurnal fishes that occur as individuals, or groups of two or three fish: these include the filefish *Cantherines dumerili*, the triggerfishes *Sufflamen bursa* and *Melichthys niger*, and the parrotfishes *Scarus perspicillatus* and *S. rubroviolaceus*.

The time that the first parrotfish was seen was noted on nine different mornings (Figure 8). This observation included all species, yet *S. perspicillatus* or *S. rubroviolaceus*, the two largest species, were seen first in five of the nine instances, despite their being by far the least numerous species of the genus *Scarus*. The smaller, but much more numerous *Scarus* species, *S. sordidus*, *S. dubius*, and *S. taeniurus*, generally appeared later. During the time that the smaller parrotfishes are appearing, the remnants of numerous mucous envelopes, in which many of them had spent the night (see, for example, Winn, 1955; Casimir, 1971), drift about close to the substrate.

*The twilight migrations.*—Just as they do during evening twilight, many species migrate from one location on the reef to another at this time. As in the evening, they travel in schools that frequently are drawn out as long processions. Again, specific routes are followed morning after morning, indicating that well-defined patterns exist. Although these patterns remain obscure for most participants, some individuals clearly reverse their evening direction. Thus, having spent the night sheltered on the shallower parts of the reef, many individuals of the plankton-feeding surgeonfish *Naso hexacanthus*, along with many of the damselfish *Chromis verater*, return to their deeper water feeding grounds high above the offshore edge of the reef. As mentioned above, this pattern is obscured by the many other individuals of these species that do not migrate inshore at nightfall, but instead spend the night sheltered on the deeper parts of

the reef, directly below their midwater feeding grounds.

Just as they do in the evening, many smaller herbivores, including the surgeonfishes *Zebra-soma flavescens* and *Ctenochaetus strigosus*, as well as the parrotfish *Scarus sordidus*, migrate from one area to another, but the patterns are not yet defined. Again, the picture is obscured by the many other individuals of these same species throughout the study areas that do not join these migrations. Thus, as in the evening, it remains unknown just what sort of redistribution most of these fishes achieve. Nevertheless, the patterns seem to relate to the transition toward the diurnal situation.

#### Ascent of the Plankton-Feeding Damsel-fishes

Adults of the larger plankton-feeding damselfishes, *Abudefduf abdominalis*, *Chromis ovalis*, *C. verater*, and *Dascyllus albisella*, join the surge of diurnal fishes that rise into the water column 10 to 15 min before sunrise. Because they all ascend above the reef at about the same rate, the most readily observed, *D. albisella*, is representative. On five mornings, stationed in one location where the water was 8 m deep, I noted when a particular aggregation of *D. albisella* was clear of cover, and then as it gradually ascended into the water column, I estimated when it had attained levels of 3 m, and (on three mornings) 5 m above the reef (Figure 9).

The smaller plankton-feeding damselfishes *Chromis leucurus* and *C. vanderbilti* rise above the reef later than do these larger species. On nine mornings, at a variety of locations, I noted when the first individual of *C. leucurus* moved out away from shelter (Figure 10). These fish remained in about this position, solitary and with shelter close at hand, for some time; at 15 min after sunrise they had moved a little farther from shelter, but otherwise their position was unchanged. *C. vanderbilti* follows an even later schedule. On the one occasion that it was recorded, solitary individuals first appeared close to shelter at 1 min after sunrise, and 11 min later had just begun to aggregate in pockets among the rocks.

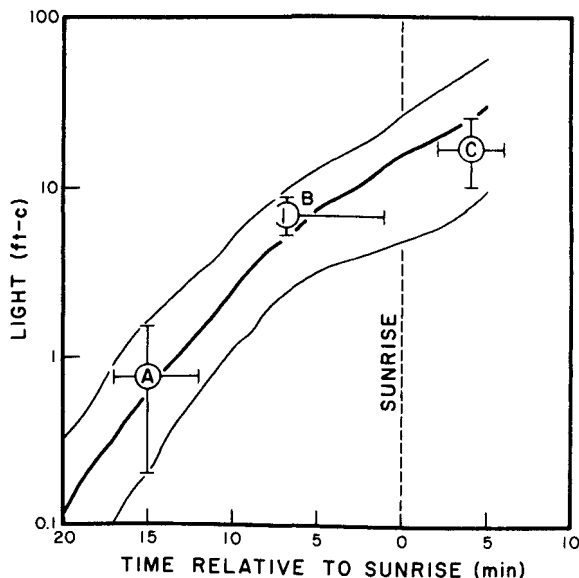


FIGURE 9.—Ascent of an aggregation of *Dascyllus albisella* into the water column during morning twilight. A. When the aggregation was first clear of cover above the reef on five mornings. B. When the aggregation had risen to 3 m above the reef on five mornings. C. When the aggregation had risen to 5 m above the reef on three mornings. For explanation of symbols, see legends for Figures 2 and 4, except that this figure represents morning events.

#### Emergence of Other Diurnal Fishes

Throughout the time that the diurnal fishes noted above are resuming activity on the reef, the many sedentary diurnal fishes become increasingly evident, including the hawkfishes *Paracirrhites forsteri*, *P. arcatus*, and *Cirrhitops fasciatus* and also the blennies *Exallias brevis* and *Cirripectus variolosus*. These begin moving out from shelter during the interim period, but so unobtrusively that their initial appearance usually goes unnoticed.

When the milling assemblages and migrating schools dominate the scene, additional fishes become active close among the rocks and corals, including the triggerfishes *Sufflamen bursa* and *Rhinecanthus rectangulus*, as well as the filefishes *Cantherines sandwichiensis* and *Pervagor spilosoma*. These too, being scattered and relatively inconspicuous, often go unnoticed at first appearance.

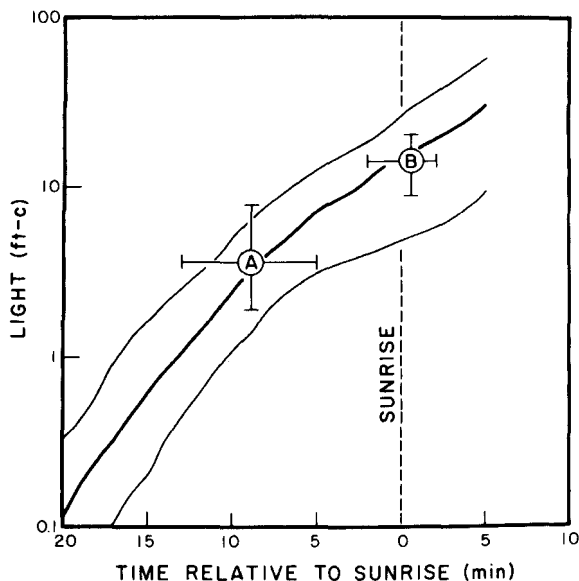


FIGURE 10.—Some characteristics of certain diurnal fishes during morning twilight. A. *Chromis leucurus*: when the first individual left cover on nine mornings. B. *Acanthurus nigrofuscus*: when individuals first appeared in school above the reef on three mornings. For explanation of symbols, see legend for Figure 2, except that this figure represents morning events.

#### Late Risers

*Observations on Acanthurus nigrofuscus.*—The assemblages of larger and medium-sized surgeonfishes that have been swimming above the reef since the initial upsurge in activity, begin to break up about the time of sunrise. Initially these aggregations become less active, then dissolve into smaller, discrete groups, now closer to the sea floor, that increasingly range out over the reef. Soon they assume activity typical of daylight. At about the time that these aggregations are breaking up, the small surgeonfish *Acanthurus nigrofuscus* makes its first appearance. Soon after, individuals of this species assemble in large schools over the reef and proceed to follow a course of action much like that taken earlier by their larger relatives. The initial appearance of *A. nigrofuscus* in a school above the reef was noted on three occasions (Figure 10). They maintain these large, active schools, as did the large species, for about 20 min, when

finally these schools too dissolve into smaller discrete groups that range out over the reef.

*Observations on Thalassoma duperrey.*—As is true in the Gulf of California (Hobson, 1965, 1968), the smaller labrids are among the last diurnal fishes to become active in the morning. The initial appearance of the ubiquitous *Thalassoma duperrey* in the morning is representative of this group, just as is its cover-seeking in the evening. It is much easier to recognize the first individual to appear in the morning than the last individual to take cover in the evening, and on 16 mornings I noted the first *T. duperrey* to become active in my immediate surroundings (Figure 11). These fish are often unmistakable when they are just resuming activity; for several seconds after emerging from their resting places many “yawn,” opening the mouth wide, and “stretch,” drawing their body into various contortions.

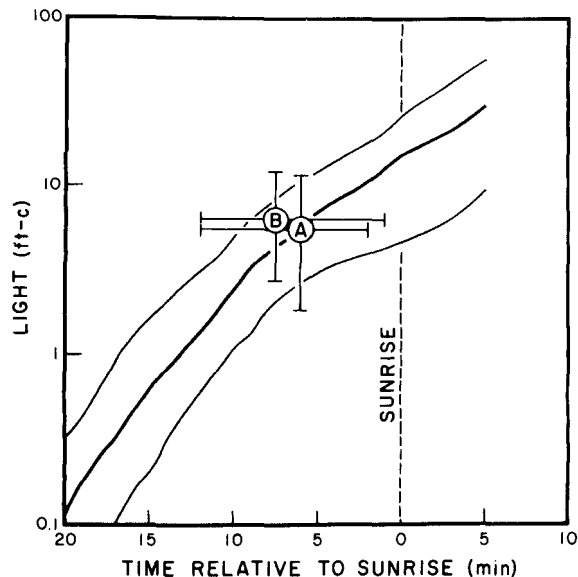


FIGURE 11.—Some characteristics of certain labrids during morning twilight. A. *Thalassoma duperrey*: when the first individual left cover on 16 mornings. B. *Labroides phthirophagus*: when the first individual left cover on nine mornings. For explanation of symbols, see legend for Figure 2, except that this figure represents morning events.

*Observations on Labroides phthiophagus.*—In describing evening cover-seeking by *Labroides phthiophagus* above, data are presented on just one individual. At least five individuals of this species are involved in the nine observations of the initial morning appearance (Figure 11).

Other fishes seeking cleaning from this species often hover in typical soliciting fashion at the cleaning stations (see Losey, 1971) for some time before the cleaners have made their initial morning appearance.

### SUMMARY

The data presented above are summarized in Figures 12 and 13.

### DISCUSSION

Most fishes on the reefs at Kona behave differently in daylight than they do at night, and during twilight their actions express a transition between these two modes of behavior. In essence, we are concerned with predominantly diurnal or nocturnal fishes changing from active to relatively inactive states, or the reverse, and the influence that certain characteristics of twilight itself have on these actions. These considerations underlie the following discussion.

#### FEEDING LOCATIONS VERSUS SHELTER LOCATIONS

The daily activities of tropical reef fishes show the overriding influence of two primary concerns: to eat and to avoid being eaten. Reef fishes must contend with predators at all times, but during those periods of day when they are active their actions seem dominated by their own feeding. On the other hand, during those periods of the day when they are relatively inactive, resting, their major consideration seems to be security. Thus, for example, the small parrotfish *Scarus taeniurus* grazes in exposed positions during daylight, but rests in coral crevices at night, often encased in a mucous envelope. Winn and Bardach (1959) discussed the function of the mucous envelope as a defense against nocturnal predators.

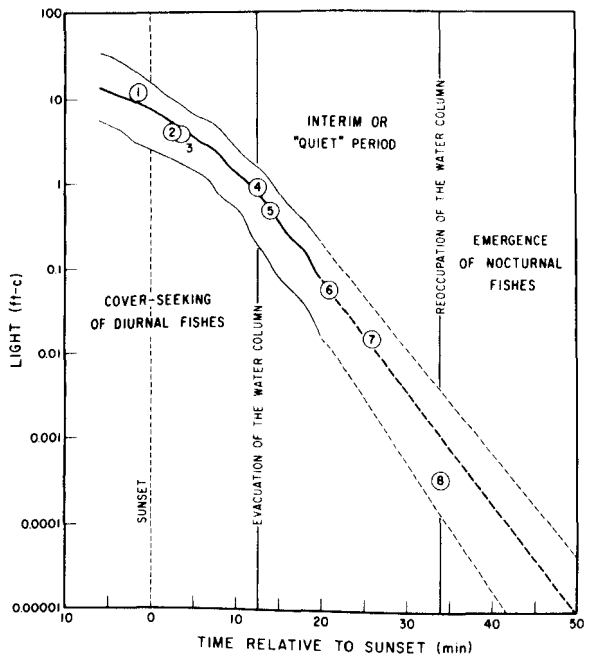


FIGURE 12.—Summary of events during the evening transition period. For explanation of symbols, see legends for Figures 2, 4, and 5. In addition, numbered points represent mean values for events. 1) When the last *Thalassoma duperrey* took cover on five evenings. 2) When a certain *Labroides phthiophagus* took cover on five evenings. 3) When the last *Chromis leucurus* took cover on three evenings. 4) Abrupt vacating of water column by diurnal fishes; the beginning of the interim, or "quiet," period: 12 evenings. 5) When *Apogon snyderi* first left cover on four evenings. 6) When *Apogon menesemus* first left cover on five evenings. 7) When *Holocentrus sammara* first left cover on four evenings. 8) When *Myripristis* spp. abruptly appeared in large numbers above the reef; the end of the interim, or "quiet," period: eight evenings.

Tropical reef fishes exhibit either one of two general means of reducing predation during their inactive periods: they school or they seek cover (Hobson, 1968). Thus, many fishes that forage at night, including various clupeids, pomadasyds, mullids, lutjanids, and carangids, characteristically spend the day in large inactive schools that hover in exposed positions on or near the reef. The advantage of such schools in reducing predation was discussed earlier (Hobson, 1968). Significantly, no diurnal fish is known



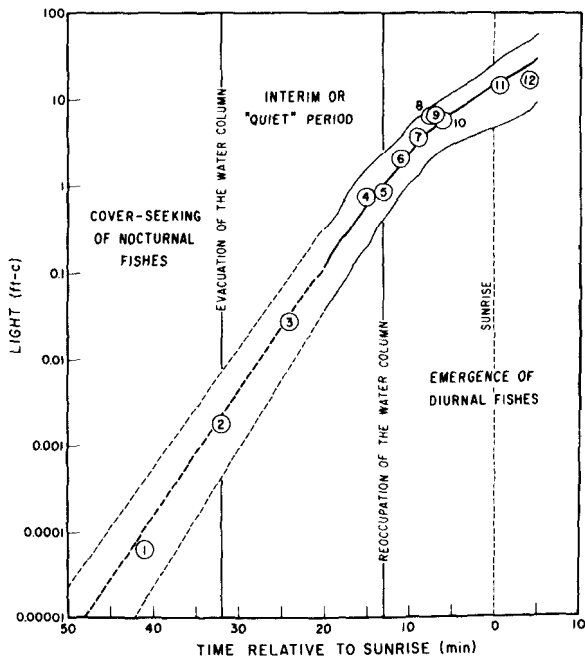


FIGURE 13.—Summary of events during the morning transition period. For explanation of symbols, see legends for Figures 2, 4, and 5, except that this figure represents morning events; in addition numbered points represent mean values for events. 1) When a particular school of *Priacanthus cruentatus* returned to the reef on six mornings. 2) When last *Myripristis* spp. took cover on reef; the beginning of the interim, or "quiet," period: eight mornings. 3) When acanthurids began assembling in depressions in the reef on six mornings. 4) When an aggregation of *Dascyllus albisella* in a particular location had moved away from cover, above the reef, on five mornings. 5) When diurnal fishes first surged 1 to 2 m into the water column; end of the interim, or "quiet," period: nine mornings. 6) When the first scarid appeared away from cover on nine mornings. 7) When the aggregation of *Dascyllus albisella* (see #4), had risen 3 m above the reef on five mornings. 8) When *Chromis leucurus* first left cover on nine mornings. 9) When *Labroides phthirophagus* first left cover on nine mornings. 10) When *Thalassoma duperrey* first left cover on 16 mornings. 11) When *Acanthurus nigrofuscus* first appeared in school above the reef on three mornings. 12) When the aggregation of *Dascyllus albisella* (see #4 and #7) was 5 m above the reef on three mornings.

to similarly school during its nocturnal inactive period. Fishes that form large schools in exposed locations when inactive are not well rep-

resented on Kona reefs; possible reasons are given below. The other means of attaining security while inactive—seeking shelter under rocks or coral—is characteristic of many diurnal as well as nocturnal fishes, including labrids, scarids, balistids, holocentrids, and apogonids. This second tactic is employed by most reef fishes in Kona. The advantage of cover in reducing predation is obvious. Some of the nocturnal fishes, for example, species of *Myripristis* and *Holocentrus*, as well as *Priacanthus cruentatus*, characteristically aggregate under cover on the reef in daylight; in contrast, none of the diurnal species were noted to aggregate when sheltered in their nocturnal resting spots.

Each of the wide variety of fishes on the Kona reef has its own specific feeding habits (Hobson, in preparation), and these relate in large part to where each is active. A suitable feeding location for any given species may or may not be near areas that offer it suitable security during its inactive period. Consequently, the major actions of these fishes characteristic of twilight relate to moving between feeding locations and shelter locations.

## TWILIGHT REDISTRIBUTION

Most of the readily observed movements of Kona reef fishes during twilight fit within a framework of three broad, overlapping categories: 1) individuals of some species migrate extensively between offshore feeding grounds and shelter locations on the reef; 2) other species migrate from one part of the reef to another; and 3) still others make short but well-defined vertical migrations between plankton-feeding locations in the water column and shelter locations on the reef below. These movements are all performed by fishes swimming in groups. The movements of most reef fishes, which remain poorly known, do not seem referable to any of these categories; nevertheless, limited evidence indicates that at least many of them follow well-defined patterns of some sort. There is much overlap between the different categories and the activity of many species comprise elements of more than one type. It is for convenience in

presentation that each category is discussed separately below.

### Offshore Migrations

*Nocturnal fishes.*—In many seas, certain reef fishes are known to make extensive feeding migrations away from the reef at nightfall; outstanding examples include certain clupeids, pomadasysids, carangids, and other schooling fishes in the Gulf of California (Hobson, 1965, 1968) and tropical Atlantic (Starck and Davis, 1966). These migrations are best known among those nocturnal predators that school on or near the reef during their inactive periods. Although such schooling fishes and their offshore migrations during twilight are a major characteristic of some areas, they are not prominent on Kona reefs. This is understandable. The reefs where these schooling fishes and their offshore migrations are so pronounced in the Gulf of California and in the tropical Atlantic are surrounded by extensive open sand flats or grass beds. These vast stretches are nocturnal feeding grounds of the fishes that migrate away from the reefs. The importance of proximate feeding grounds of this sort to such fishes is well known (Longley and Hildebrand, 1941; Randall, 1963; Hobson, 1968). Similar feeding grounds do not surround Kona reefs, which are instead bordered by a precipitous drop into deep water. Not surprisingly, the relatively few species that migrate offshore at nightfall from Kona reefs, including *Priacanthus cruentatus* and *Myripristis* spp., seek open-water prey. Furthermore, whereas fishes migrating over the extensive sand flats and grass beds adjacent to reefs elsewhere often travel considerable distances (Starck and Davis, 1966; Hobson, 1968), comparable data are not available for *Priacanthus* and *Myripristis*. It is possible that these fishes do not go much beyond the outer edge of the reef, an area known to be a rich feeding ground for diurnal plankton-feeding fishes (see below).

*Diurnal fishes.*—Offshore feeding migrations comparable to those made by nocturnal fishes have not been reported for diurnal fishes. In the Gulf of California, the exodus of fishes away

from the reef during twilight, transforming the stretches of open sand offshore into centers of activity, is strictly a nocturnal phenomenon; there is no diurnal equivalent, as these open expanses are comparatively without active fishes in daylight (Hobson, 1968).

In Kona, several diurnal fishes, including some individuals of the surgeonfish *Naso hexacanthus* and the damselfish *Chromis verater*, migrate to the offshore edge of the reef during morning twilight. They swim to where the seaward reef-face drops abruptly to great depths and here become part of a large assemblage of plankton-feeding fishes. Apparently plankton is exceptionally rich in this area. The migrations seem to terminate here, but the larger *Naso hexacanthus*, and perhaps other species, periodically range farther offshore during the day. During evening twilight many individuals of these species return inshore to the shallower parts of the reef, a pattern obscured by the many other individuals of these species that shelter themselves on the offshore parts of the reef, below their mid-water feeding grounds. It may be that there is not enough suitable cover here to accommodate all of the many fishes that concentrate to feed in this location. This would account for the fact that while some shelter themselves here, others migrate from other areas.

### Intrareef Migrations

Conspicuous elements of the transition period are the long drawn-out processions that migrate from one point on the reef to another, following the same routes day after day. Although the redistribution pattern achieved by these movements remains undefined, the phenomenon seems limited to herbivorous fishes, especially the small to medium-sized acanthurids and scarids, and to some plankton feeders. Herbivorous reef fishes are widely reported to be strictly diurnal (Hobson, 1965, 1968; Starck and Davis, 1966). The migratory patterns shown by these fishes are obscured by the many other individuals of the migrating species that do not join these movements.

Some herbivorous species, for example certain parrotfishes (see Bardach, 1958), range far

across the reef in schools while grazing on benthic algae during the day. The intrareef migrations during evening twilight of such fishes may be a return from such excursions to established resting areas at day's end.

### Vertical Migrations

The movements discussed so far involve fishes that traverse considerable distances. Many other fishes, some diurnal, others nocturnal, move between feeding grounds and shelter locations in a well-defined pattern that covers no more than a few meters. These are the many plankton feeders that forage in the water column, and find shelter on the reef directly below. Some species, like the diurnal *Naso hexacanthus* and the nocturnal *Myripristis argyromus*, both discussed above, undertake such vertical movements but also make extensive lateral excursions across the reef and beyond. Nevertheless, many plankton feeders, especially smaller species like *Dascyllus albisella*, restrict their activity to a limited area on the reef. Restricted though these movements may be, they follow patterns as well defined as any of those discussed above.

These plankton feeders are either diurnal or nocturnal. Without overlap, those feeding in daylight are inactive after dark, and those feeding at night are inactive in daylight. The respective feeding periods of the two groups are separated by the 15 to 20 min interim, or quiet, period. I noted a similar absence of overlap between diurnal and nocturnal plankton feeders in the Gulf of California (Hobson, 1968), as did Starck and Davis (1966) in the tropical Atlantic. Obviously conditions of plankton feeding differ between day and night. Emery (1968) reported that the composition of plankton over Florida reefs differs between day and night, and I found the same true in Kona (Hobson, in preparation).

### Twilight Movements of Other Reef Fishes

The patterns of movement described above are readily recognized because each involves many individual fish moving together. Most reef fishes do not operate in large assemblages but instead are active solitarily or in small groups.

Unifying patterns in such species are difficult to recognize, because many discrete units are simultaneously behaving independently at different points on the reef. Nevertheless, limited data show that patterns do exist. Probably the movements of some fall into the broad categories outlined above, but the actions of others, once recognized, probably would represent additional categories. Chaetodontids, labrids, pomacentrids, scarids, balistids, and other diurnal species, as well as many holocentrids, apogonids, scorpaenids, and other nocturnal fishes, all display distinctive nocturnal and diurnal habits. The twilight activities of most of these fishes do not include extensive movements; most change from an active to a relatively inactive state, or the reverse, within a limited area on the reef. Data presented in this report show well-defined temporal patterns in their seeking and everging from cover. Limited additional data indicate that in at least many of these fishes the patterns also have a strong spatial element: consider, for example, the circumstance that at least some individuals of *Thalassoma duperrey* and other species occupy specific resting spots at nightfall.

### PATTERNS OF TWILIGHT ACTIVITY

I have developed the thesis that activity of most Kona reef fishes during twilight relates to a transition between diurnal and nocturnal modes of behavior. If these fishes were concerned only with shifting from one mode of behavior to another, the timing of the various transition events could well as not be random. In fact, however, the transition events proceed in an established, well-defined sequence, with characteristics indicating that some force exerts a strong controlling influence. The general pattern has been outlined above (Figures 12 and 13). Some additional characteristics of the transition events warrant discussion.

#### Fish Size as Expressed in Transition Activity

The time during the transition at which a given fish joins certain of the activities is related to that fish's size. During evening twilight

some of the transition activities are performed by the smaller fishes first. Thus, for example, the increased tendency of many fishes to aggregate, as seen especially in acanthurids and scarids, occurs first in the smallest species of the respective groups: *Acanthurus nigrofuscus* among the acanthurids, and *Scarus taeniurus* among the scarids. Consider too the plankton-feeding damselfishes, which during the transition period progressively descend closer to the sea floor and finally take cover on the reef. The smallest species, *Chromis vanderbilti*, is first to seek cover, and the next smallest, *C. leucurus*, is second. The other, larger damselfish species follow later. Similarly, the smallest of the surgeonfishes, *Acanthurus nigrofuscus*, is the first of that family to go under cover, and the others follow in order roughly corresponding to increasing size. Most acanthurids on the reef are of about the same size and therefore show similar timing in seeking cover; nevertheless, the larger species, like *A. dussumieri*, are the last to settle down. The same pattern occurs among the filefishes, where the smaller *Cantherines sandwichiensis* takes cover long before the larger *C. dumerili*; and among the parrotfishes, where the smallest, *Scarus taeniurus*, is no longer seen when such larger relatives as *S. rubroviolaceus* and *S. perspicillatus* are still active. The effect operates within species, just as it does between species; thus, for example, large adults of *Scarus rubroviolaceus* are still active long after all the small juveniles of this species have gone under cover.

In the morning the situation in these same species is reversed. The larger individuals are the first of the diurnal fishes to emerge from cover, and the others appear in order roughly according to decreasing size to perform their characteristic transition activity.

It remains uncertain to what extent fish size relates to the transition activity of nocturnal fishes. *Holocentrus sammara*, *Apogon menesemus*, and *A. snyderi*, which are consistently the first nocturnal species to leave shelter in the evening and the last to seek shelter in the morning, are the largest of their respective groups common in Kona; however, additional data are lacking.

### Increased Activity During Twilight

One senses a marked increase in activity among fishes at two times during the twilight periods: in the evening, from just before sunset to about the time that the diurnal fishes abandon the water column, and in the morning, from the time the diurnal fishes reoccupy the water column to just after sunrise. This impression of heightened activity derives mostly from a combination of the following: 1) fishes migrating from one location to another; 2) increased territorial aggression (evening only); and 3) an increased tendency to aggregate in locations more visible to the observer.

*Migrations.*—The migrations are discussed above. Their contribution to a general impression of increased activity is obvious.

*Territorial aggression.*—A minor element of the increased activity during evening twilight is increased territorial aggression. During the day there are frequent territorial disputes among many of these fishes, often, if not generally, relating to feeding areas; this is a frequent source of conflict among the acanthurids (see, for example, Jones, 1968). Aggression during evening twilight, which was noted only in diurnal fishes, seems unrelated to feeding; rather, it may express conflict over resting spots. It is significant not so much that such aggression occurs, but that there is so little of it. With such a vast number of fishes settling into resting positions on the reef at nightfall, one might expect individuals with similar requirements to compete strongly for optimum spots. That relatively little aggression of this sort occurs suggests that some mechanism establishes spatial distribution without overt conflict. One possibility is that each individual has a well-established resting spot; this is suggested by the two individual *Thalassoma duperrey* that were observed to be strongly attached to particular locations. However, this hypothesis is not widely supported. Overall, I recognized only a relatively few cases where what seemed to be the same individual returned to a particular spot on

a number of different nights, and even these did not seem to have a long-standing attachment to such locations. More important, I was unable to recognize attachments to particular locations in most of the diurnal species that occupy resting spots when inactive. There are scattered reports of reef fishes returning to established resting spots: Winn and Bardach (1960), for example, noted that a certain species of parrotfish in Bermuda has "home caves," and Starck and Davis (1966) suspected the same to be true of two parrotfish species in Florida. Nevertheless, pending accumulation of additional data from a variety of fish groups the question on a broad scale remains unresolved.

Nocturnal fishes seeking cover in the morning were not seen in conflict over resting spots. A major general behavioral difference between diurnal and nocturnal fishes may account for this. Unlike diurnal fishes, which generally are solitary in their resting places, many nocturnal species, including *Myripristis* spp., *Holocentrus* spp., and *Priacanthus cruentatus*, aggregate in their daytime shelters.

*Increased tendency to aggregate in locations more visible to the observer.*—The general impression of increased activity during the periods of twilight defined above stems mainly from the many diurnal fishes that congregate one to several meters above certain parts of the reef at these times. These fishes, which concentrate over areas where at least most of them seek shelter, mill about actively, but without recognized direction. Although surgeonfishes predominate in these aggregations, species from many families of diurnal fishes are represented. However, it can be questioned whether or not this phenomenon does in fact involve increased activity. At least to some extent the fishes only appear to be more active. At this time, compared to other times of day, they are more concentrated and swim in locations that are more visible to the observer. Mostly these are gregarious species, but the groups in which they swim during midday are less visible than the twilight assemblages, being smaller, more loosely organized, and occurring closer to the substrate at many different places on the reef.

## THE INFLUENCE OF PREDATORS ON TWILIGHT ACTIVITY

I have emphasized that the twilight activity in reef fishes proceeds in an established, well-defined sequence. Now I suggest that this well-ordered series of events is shaped by the threat of crepuscular predators.

In the Gulf of California (Hobson, 1965, 1968) and certain parts of the tropical Atlantic (Starck and Davis, 1966), large piscivorous fishes are primarily crepuscular. The increased vulnerability of smaller free-swimming fishes during twilight, especially those in schools, has been discussed (Hobson, 1968). Mechanisms that reduce the threat from predators during daylight and darkness apparently are less effective during the transition between these two major segments of the diel cycle. Thus attacks by large piscivores on schooling clupeids, pomadasyids, and small carangids in the Gulf of California become increasingly frequent at about the time of sunset, and peak about 20 min later. After peaking, the predation ceases, and the piscivores withdraw. Most of the schooling prey, which are nocturnal predators, then migrate to their offshore feeding grounds (Hobson, 1968). Because this activity is a dominant feature of the reef situation in the Gulf of California, one can relate it to the concurrent actions there of such smaller nonschooling fishes as labrids, pomacentrids, chaetodontids, acanthurids, and balistids. The pattern of cover-seeking in these fishes, and the subsequent emergence of such nocturnal forms as holocentrids and apogonids, follows much the same pattern in the Gulf as that of their close relatives in Kona, described in this report. Observations on the transition events in the Gulf of California were not detailed to the extent of those in Kona; nevertheless, many of the same phenomena were reported from the Gulf. For example, referring to evening observations I pointed out that labrids are among the first of the diurnal fishes there to seek cover and that the emerging *Apogon* mix with some of the diurnal fishes close among the rocks as the latter are taking cover (Hobson, 1965, 1968). I am confident that the techniques used in Kona, if

repeated in the Gulf of California, would generate data much like those presented in this report. Although the faunas of the two areas have only a few species in common, there are many generic parallels. Genera common to both areas include: *Bodianus*, *Thalassoma*, *Halichoeres*, and *Hemipteronotus* (labrids); *Abudefduf*, *Chromis*, and *Pomacentrus* (pomacentrids); *Chaetodon* and *Holacanthus* (chaetodontids); *Acanthurus* (acanthurids); *Balistes* and *Sufflamen* (balistids); *Holocentrus* and *Myripristis* (holocentrids); *Apogon* (apogonids); and many others. Congeners from these two widely separated areas behave similarly.

In the Gulf, one can readily relate the distances small fishes are from shelter at different times during the transition period with the concurrent attacks by large piscivores on the schooling fishes; when this piscivorous activity peaks, most of the small nonschooling fishes are under cover. As I pointed out (Hobson, 1968, p. 84), "... during those periods of morning and evening twilight, when schooling fishes are most heavily exploited, neither diurnal nor nocturnal plankton feeders (mostly *Chromis*, *Abudefduf*, *Myripristis* and *Apogon*) are in midwater."

Significantly, the reef fishes in Kona all are close to shelter at the time, relative to sunrise or sunset, that schooling fishes in the Gulf of California are under heaviest attack (Figures 14 and 15). At the same time that predation upsurges in the Gulf, the water column is vacated in Kona, both by nocturnal fishes during early morning twilight and by diurnal fishes during early evening twilight. Furthermore, the water column is not then reoccupied in Kona, either

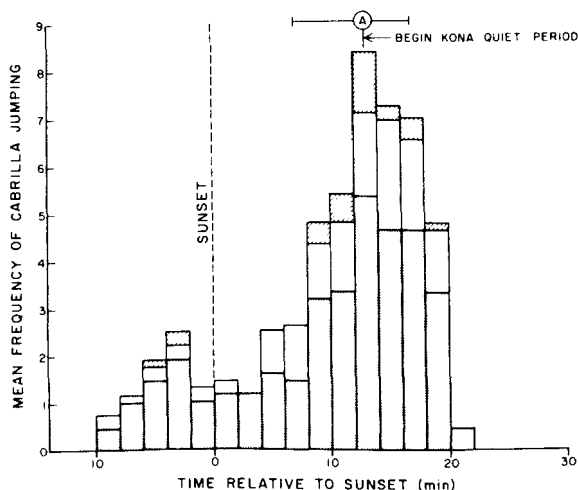


FIGURE 14.—Time of peak predation (*Mycteroperca rosacea*) when preying on schooling *Harengula thrissina* in the Gulf of California relative to the evening interim, or "quiet," period in Kona. Duration of twilight is similar in the two areas as the difference in latitude is only about 4°. Stippled area of the bars represents the frequency of attacks involving one *M. rosacea*; white area of bars, the frequency of attacks involving two to seven *M. rosacea*; hatched areas of bars, the frequency of attacks involving eight or more *M. rosacea* charging simultaneously. Also plotted is the mean (A) and the range of times, relative to sunset, that diurnal fishes vacated the water column in Kona. (For further information regarding this figure, see text footnote 3.)

\* When preying on schooling flatiron herring, *Harengula thrissina*, in shallow water in the Gulf of California, the cabrilla, *Mycteroperca rosacea* attacks from below. Its charge carries the cabrilla up through the herring school and momentarily out of the water (see Hobson, 1968). Because the herring schools are close to the beach throughout the day and into twilight, an observer on the beach can obtain an index of predatory activity by noting the incidence of attacks—seen as cabrilla jumping out of the water amid the herring. These data were collected on seven consecutive evenings and were presented earlier (Hobson, 1968, Figure 18).

In Figure 14, I have pooled these data, and present the mean values in time relative to sunset (when presented in Hobson (1968) these data were broken down by days, and shown against time of day). The graph also reflects the fact that discrete attacks involve vary-

ing numbers of cabrilla charging simultaneously. Unfortunately, the attacks by cabrilla on herring do not provide an index of predation beyond about 20 min after sunset; at this time, with the cabrilla and other predators still highly active, the herring migrated offshore. Thus the sudden drop in attacks shown in the figure reflects the herring's departure, not a decline in predation. The predators continued to attack other schooling fishes in the area, mostly pomadasysids, for a short while longer, and these prey schools did not leave the inshore waters until the predators had withdrawn (Hobson, 1968). In any event, because the attacks by cabrilla on herring provided an index only for the initial upsurge in predatory activity, it is meaningless to relate these data to the latter stages of the Kona quiet period.

\* Data on predation by cabrilla on flatiron herring were collected on three consecutive mornings (see Hobson, 1968). Unlike the evening situation in the Gulf of California, where the herring leave the inshore waters while the cabrilla and other predators are still highly active, in the morning the herring arrive inshore before the predators have begun feeding. Therefore, the attacks by cabrilla on flatiron herring in the morning provide an index of predatory activity spanning all of the twilight period, and thus can be related to the entire interim, or "quiet," period in Kona.

by diurnal fishes during morning twilight, or by nocturnal fishes during evening twilight, until after the time that predation in the Gulf has subsided. Thus, the time of maximum predation in the Gulf is equivalent to what is aptly called the "quiet" period in Kona. Obviously the term "quiet" would be a misnomer if applied to this part of the transition period in certain parts of the Gulf, it being the time when the schooling fishes are under heaviest attack. These schooling species, for example the herring *Harengula*, cannot take shelter under rocks or coral on the reef, as have the other smaller fishes, and thus are exposed to predators during a time when they seem to be especially vulnerable. The disadvantage of schooling fishes at this time, as compared to other potential prey of the piscivores, was pointed out earlier (Hobson, 1968). Thus, if there is an advantage in being close to shelter when predators are most effective, the actions of Kona reef fishes during twilight are adaptive to any increased threat from predators that might exist at that time.

Other behavioral characteristics of Kona reef fishes during the day-night transition period can

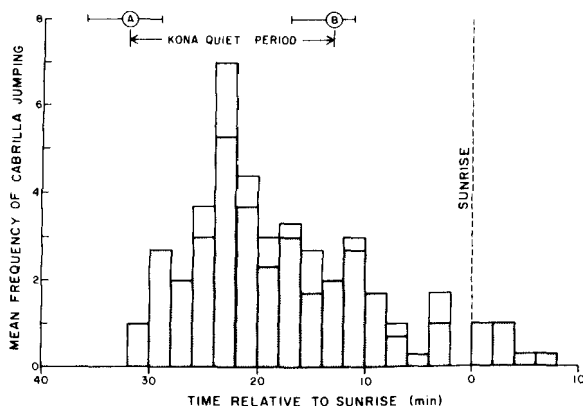


FIGURE 15.—Time of peak predation (*Mycteroperca rosacea*) when preying on schooling *Harengula thrissina* in the Gulf of California relative to the morning interim, or "quiet," period in Kona. For explanation of symbols, see legend for Figure 14. The mean and ranges of both the beginning (A) and end (B) of the Kona quiet period, defined by events described at length in this report, are plotted. (For further information regarding this figure, see text footnote 4.)

be interpreted as mechanisms to reduce predation. If one accepts the premise that smaller fishes are more vulnerable to predation than larger ones, it is significant that smaller individuals seek cover earlier in the evening, when danger from predators apparently is progressively intensifying. The same significance can be attributed to their leaving cover later in the morning when danger from predators apparently is progressively diminishing. Consider too the increased tendency to aggregate among so many fishes that just mill over a given section of the reef. Although this behavior probably has other functions as well, it may also contribute some measure of security from predators. It was pointed out earlier (Hobson, 1968) that fishes in such aggregations attain the same protection from predators as do those in schools (if one wishes to distinguish between such assemblages).

Clearly the overall pattern of activity in Kona reef fishes during twilight can be interpreted as being strongly influenced by crepuscular predators. Yet, critics of this hypothesis can point out that an obvious piscivorous threat is absent, at least relatively so when the Kona habitats are compared to those of the Gulf of California.

Hawaiian reefs have been known to be lacking in some of the major predatory fish-groups that are common on most other tropical Pacific reefs. Most notable among these are the shallow water groupers (Serranidae) and snappers (Lutjanidae)—Gosline and Brock, 1960; Randall and Brock, 1960. There are several large carangid species in Hawaii, but the only one that is numerous in Kona, *Caranx melampygus*, is represented mostly by small individuals. Possibly heavy pressure from fishermen along Hawaiian shores keeps the numbers of large carangids at a low level. Because the major piscivorous fishes on the reef at Kona (aside from some of the moray eels, which probably do not prey significantly on free-swimming fishes) are relatively small, they do not seriously threaten the adults of the species being considered here. These include such predators as *Fistularia petimba*, *Aulostomus chinensis*, *Paracirrhites forsteri*, *Parupeneus chryserydros*, and *Bothus mancus*. The predatory activity of these and other species

is detailed elsewhere (Hobson, in preparation). The occasional occurrence during twilight of large barracuda, *Sphyraena barracuda*, and sharks, especially *Carcharhinus milberti*, would not seem to have much impact on the general behavior patterns of the reef fishes. However, any behavior that reduces vulnerability to predators certainly would enhance survival on the occasions when such predators do appear, and the effect of this circumstance may be greater than is readily apparent. Nevertheless, with neither schooling prey nor the predators that exploit them being major elements of the fauna, the vigorous interactions such fishes so prominently generate during twilight in the Gulf of California are essentially missing in Kona.

The absence of large piscivores on the Kona reef as compared, for example, with the Gulf of California, may bear on the relative scarcity in Kona of prey fishes in large schools. Reason for the relative absence of such fishes in Kona was discussed above. The many schooling prey in the Gulf of California was held to be a major factor in the occurrence there of so many large piscivores (Hobson, 1968). For whatever reason these faunal elements are missing in Kona, the question remains: if the threat from predators strongly influences the well-defined sequence in which fishes in the Gulf seek and leave cover during the day-night transition, how is it that reef fishes in Kona show essentially the same pattern when the threat of large piscivores to them is comparatively mild?

We have been focusing on the situations in Kona and the Gulf of California, when in fact it seems that related fishes on most, if not all, tropical reefs, show similar behavior during twilight. Data are lacking for most areas, so this conclusion remains tentative. Nevertheless, not only do related fishes common to Kona and the Gulf of California behave similarly, as described above, but limited data from other seas, including the tropical Atlantic (Starck and Davis, 1966) show essentially the same pattern. The similar pattern of events in these widely separated areas indicates a long evolution that in any one locality transcends the existing situation, even the existing species.

One would expect predator-prey relations among fishes to have responded similarly throughout time to certain basic, unchanging phenomena. Among others, these phenomena would have included the characteristics of light underwater and the effect of these characteristics on visually feeding predators at different times of the day, as well as the probable difficulties such predators experience in choosing a target from among the many confronting them in a fish school (Allen, 1920a, 1920b; Hobson, 1968; and others). With this common heritage, it would be surprising if behavior patterns relating to predator-prey interactions did not show today deep-rooted parallels on even widely separated reefs. I suggest, therefore, that the behavior of tropical reef fishes during twilight in all seas, including Kona, reflects the impact of a historic threat from predators.

## CONCLUSIONS

1. At least most of the reef fishes at Kona, Hawaii, behave differently in daylight than they do at night, and during twilight their actions express a transition between these two modes of behavior. Most of these fishes are either diurnal or nocturnal, with the diurnal species relatively inactive at night and the nocturnal species relatively inactive in daylight.

2. During their period of major activity, the actions of these fishes are dominated by behavior relating to their own feeding, and often this takes them to specific feeding grounds. During their inactive periods their behavior relates strongly to their own security, and usually they take shelter. Consequently, the actions of these fishes during twilight relate primarily to moving between feeding locations and shelter locations.

3. The twilight movements of many of these fishes involve well-defined migrations. A) Some members of certain nocturnal species migrate extensively between shelter locations on the reef and feeding grounds offshore; species in this category include *Myripristis* spp. and *Priacanthus cruentatus*. B) Some members of certain other species migrate between shelter locations on one part of the reef and feeding grounds on another; species in this category are mostly di-



urnal herbivores and plankton feeders, including certain acanthurids, scarids, and pomacentrids. C) Many small plankton-feeding species make short, but well-defined vertical migrations between shelter locations on the reef and feeding locations in the water column directly above; diurnal species in this category include certain pomacentrids and chaetodontids, and nocturnal species include certain apogonids and holocentrids.

4. Activity associated with the transitions from day to night, and from night to day, proceeds in an established, well-defined sequence. Both evening and morning periods of changeover comprise three distinct segments. In the evening, these are: 1) *the shelter-seeking of the diurnal fishes* (from about 30 min before sunset to about 13 min after sunset), which ends when the last group of diurnal fishes still milling above the reef, mostly acanthurids, abruptly descend to cover; 2) *the evening interim, or "quiet," period* (beginning about 13 min after sunset and ending about 20 min later), which is characterized by the water column being essentially deserted of fishes; and 3) *the emergence of the nocturnal fishes* (from about 33 to 50 min after sunset), which begins when the surge of nocturnal fishes, mostly *Myripristis* spp., rise into the water column. In the morning, the sequence is reversed, being: 1) *the shelter-seeking of the nocturnal fishes* (from about 50 to 30 min before sunrise), which ends when the last of the nocturnal fishes in the water column, usually *Myripristis* spp., have descended to cover; 2) *the morning interim, or "quiet," period* (beginning about 33 min before sunrise and ending about 20 min later), when the water column is essentially deserted; and 3) *the emergence of the diurnal fishes* (from about 13 min before sunrise to a point soon after sunrise), which begins when the surge of diurnal fishes, mostly acanthurids, rise into the water column.

5. In the evening, diurnal fishes, both within and between species, seek cover in an order that corresponds roughly to increasing size. That is, the larger fishes seek cover last. In the morning, the same fishes emerge from cover in an order that corresponds roughly to de-

creasing size. That is, the larger fishes emerge from cover first.

6. There is some territorial aggression among diurnal fishes during evening twilight that expresses conflict over resting spots. However, the aggression is minimal considering how many fishes settle into resting positions on the reef at this time. Limited evidence suggests that overt conflict is reduced because at least some individuals have established resting spots.

7. Reef fishes are most vulnerable to predators during twilight because mechanisms that reduce predation during the day and night are less effective during the transition between these two major segments of the diel cycle. The interim, or "quiet," period in Kona is the time of greatest potential danger and corresponds in time relative to sunrise and sunset to the period when schooling fishes in the Gulf of California are under heaviest attack. Similar overt predator-prey interactions are relatively infrequent at this time in Kona because the schooling prey and the predators that exploit them are not major elements of the Kona fauna.

8. The well-ordered pattern of twilight activity among Kona reef fishes, which is essentially the same among tropical reef fishes in other seas, has been shaped by a historic threat from crepuscular predators. In areas where predators are only a relatively mild threat, as in Kona, twilight activity follows the same pattern as it does in areas where predators are a severe threat, as in the Gulf of California. Because predator-prey relations among fishes have responded throughout time to certain basic, unchanging phenomena, the similarity of twilight activity patterns among fishes on widely separated reefs today is the result of a long evolution that in any one area transcends the existing situation and species.

#### ACKNOWLEDGMENTS

Lloyd D. Richards assisted in collecting the data for this study. I thank Carl L. Hubbs and Richard H. Rosenblatt, Scripps Institution of Oceanography, and John R. Hunter, National Marine Fisheries Service, for helpful comments

on a draft of the manuscript. Kenneth Raymond, National Marine Fisheries Service, drew the figures.

### LITERATURE CITED

- ALLEN, W. E.  
1920a. Behavior of loon and sardines, *Ecology* 1: 309-310.  
1920b. Behavior of feeding mackerel. *Ecology* 1: 310.
- BARDACH, J. E.  
1958. On the movements of certain Bermuda reef fishes. *Ecology* 39:139-146.
- CASIMIR, M. J.  
1971. Zur Morphologie, Histochemie, Tagesperiodik und Biologie der Operculardrüse bei Labriden und Scariden (Pisces). [English synopsis.] *Mar. Biol. (Berl.)* 8:126-146.
- CUMMINGS, W. C., B. D. BRAHY, AND W. F. HERRNKIND.  
1964. The occurrence of underwater sounds of biological origin off the west coast of Bimini, Bahamas. In W. N. Tavolga (editor), *Marine bioacoustics*, p. 27-43. Pergamon Press, N.Y.
- EMERY, A. R.  
1968. Preliminary observations on coral reef plankton. *Limnol. Oceanogr.* 13:293-303.
- GOSLINE, W. A.  
1965. Vertical zonation of inshore fishes in the upper water layers of the Hawaiian Islands. *Ecology* 46:823-831.
- GOSLINE, W. A., AND V. E. BROCK.  
1960. *Handbook of Hawaiian fishes*. Univ. Hawaii Press, Honolulu, 372 p.
- HOBSON, E. S.  
1965. Diurnal-nocturnal activity of some inshore fishes in the Gulf of California. *Copeia* 1965:291-302.  
1968. Predatory behavior of some shore fishes in the Gulf of California. U.S. Fish Wildl. Serv., Res. Rep. 73, 92 p.  
1970. Behavior and ecology of inshore fishes. In *Progress in sport fishery research 1969*, p. 204-208. U.S. Fish Wildl. Serv. Bur. Sport Fish. Wildl., Resour. Publ. 88.
- JONES, R. S.  
1968. Ecological relationships in Hawaiian and Johnston Island Acanthuridae (surgeonfishes). *Micronesica* 4:309-361.
- LONGLEY, W. H., AND S. F. HILDEBRAND.  
1941. Systematic catalogue of the fishes of Tortugas, Florida, with observations on color, habits, and local distribution. Pap. Tortugas Lab. 34, Carnegie Inst. Wash. Publ. 535, 331 p.
- LOSEY, G. S., JR.  
1971. Communication between fishes in cleaning symbiosis. In T. C. Cheng (editor), *Aspects of the biology of symbiosis*, p. 45-76. Univ. Park Press, Baltimore.
- RANDALL, J. E.  
1958. A review of the labrid fish genus *Labroides*, with descriptions of two new species and notes on ecology. *Pac. Sci.* 12:327-347.  
1963. An analysis of the fish populations of artificial and natural reefs in the Virgin Islands. *Caribb. J. Sci.* 3:31-47.
- RANDALL, J. E., 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.* 89:9-16.
- STARCK, W. A. II, AND W. P. DAVIS.  
1966. Night habits of fishes of Alligator Reef, Florida. *Ichthyol. Aquarium J.* 38:313-356.
- WINN, H. E.  
1955. Formation of a mucous envelope at night by parrot fishes. *Zoologica (N.Y.)* 40:145-148.
- WINN, H. E., AND J. E. BARDACH.  
1959. Differential food selection by morray eels and a possible role of the mucous envelope of parrot fishes in reduction of predation. *Ecology* 40: 296-298.  
1960. Some aspects of the comparative biology of parrot fishes at Bermuda. *Zoologica (N.Y.)* 45: 29-34.
- YOUNGBLUTH, M. J.  
1968. Aspects of the ecology and ethology of the cleaning fish, *Labroides phthirophagus* Randall. *Z. Tierpsychol.* 25:915-932.