Pacific Science (1973), Vol. 27, No. 2, p. 128–135
Printed in Great Britain

The Sequence of Appearance at Dawn and Disappearance at Dusk of Some Coral Reef Fishes[1]

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ABSTRACT: Coral reef fishes were observed from the Hook Island Underwater Observatory and the light intensity and time at which each species appeared at dawn and disappeared at dusk were measured. For the species considered there was a definite sequence of disappearance at dusk (showing family groupings) that more or less reversed itself in the appearance at dawn. Light is probably a factor governing this behavior but whether it is light intensity, rate of change of light intensity, or a change in light quality (wavelength) is not known. It is postulated that the sequential appearance at dawn and disappearance at dusk of the fishes may have evolved to reduce confusion and hence the likelihood of predation at this time.

Collette and Talbot (in press) have obtained detailed information on the diurnal-nocturnal changeover pattern of many coral reef fishes in the Virgin Islands, but these authors did not report a sequential pattern in the diurnal-nocturnal changeover.

This study was conceived to investigate the possibility of a sequence in the disappearance of diurnal fishes at dusk and a corresponding sequence in the appearance of these fishes at dawn.

The observations were made at the Hook Island Underwater Observatory. Hook Island (lat 20°07′ S, long 148°55′ E) is considered to be a part of the Great Barrier Reef of Australia. It is 12 miles from shore and near the central Queensland town of Proserpine. Hook Island like the other islands of the Whitsunday Group is a high island, surrounded by a well-developed fringing coral reef. The reefs in this area support many species of tropical coral reef fishes.

The Hook Island Underwater Observatory consists of a large rectangular viewing chamber 4 meters wide by 6 meters long by 2½ meters high and contains 36 windows. A platform 2 meters wide surrounds the viewing chamber and supports the living corals that make up the viewing area. The depth of the platform varies from 2½ meters at low tide to 6 meters at high tide. A large number of fishes frequented the viewing area (51 species identified), and there were no enclosures to prevent their movement. Their behavior seemed undisturbed by the observers' presence. The owners of the Observatory, however, did encourage the larger carnivores by occasional feeding. From the Observatory we were able to make close-range observations on fish behavior without the disadvantages of continual diving and the disturbance caused by diver presence.

METHODS

Before observations commenced, the fishes frequenting the Observatory were identified. In fishes without distinct color patterns and in fishes that are known to change their coloration with age (e.g., some Labridae), the identifications can only be taken as tentative. Although this is a disadvantage, it should not impair the value of this study. Identifications were made visually using the following reference texts: Schultz et al. (1960 and 1966), Smith (1949), Smith and Smith (1963), Marshall (1964), Munro (1967), Gosline and Brock (1960), and Choat (1969).

From 16 August 1970 to 5 September 1970 repeated visits were made to the Observatory during the times of dusk and dawn. Observations on the presence and relative abundance of the most common species (Table 1) and the

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TABLE 1

Fishes of the Hook Island Underwater Observatory from Which Data were Obtained

CENTROPOMIDAE
Psammoperca melanopus

HOLOCENTRIDAE
Holocentrus sp.

SERRANIDAE
Plectropomus maculatus
Cephalopholis miniatus
Epinephelus fasciatus
Anyperodon leucogrammicus
Epinephelus merra
Epinephelus tauvina
Epinephelus fuscoguttatus
Epinephelus lanceolatus
Cephalopholis pachycentron
Cephalopholis cyanostigma
Diploprion bifasciatum
Cromiliptes altivelis

APOGONIDAE
No species differentiated

LUTJANIDAE
Caesio chrysozonus

CHAETODONTIDAE
Chaetodon aureofasciatus
Chaetodon rainfordi
Chelmon rostratus
Chaetodontiplus personifer

POMACENTRIDAE
Abudefduf palmeri
Abudefduf melas
Abudefduf bankieri
Pomacentrus sufflavus
Chromis dimidiatus

LABRIDAE
Lienardella fasciatus
Hemigymnus melapterus
Labroides dimidiatus
Thalassoma lunare
Epibulus insidiator
Choerodon albigena
Choerodon venustus

SCARIDAE
Scarus fasciatus
Scarus ghobban
Scarus venosus
Scarus flavipectoralis
Scarus microrhinos
Scarus spp.

ACANTHURIDAE
Acanthurus xanthopterus

SIGANIDAE
Siganus doliatus

light intensity were taken at approximately 5-minute intervals. Eight separate observations were made at dawn and eight at dusk, making a total of 16 observations over 8 days.

Light intensities were measured with a Gossen "Lunasix 3" photographic light meter. This instrument did not read in footcandles, but the appropriate conversion was made. Although this is a sensitive light meter for photographic purposes, its sensitivity to different wavelengths is probably not identical to that of the fish eye.

To arrive at a particular light intensity and time for the appearance of a given species of fish at dawn we decided to take the time and light intensity at which the first fish of that species was seen. At dusk the time and light intensity were taken when the last fish of a given species disappeared. These gave cutoff points that were easy to determine. In fact most species of fishes appeared or disappeared within a short interval of time: about 5 minutes for most fishes, although scarids took up to 15 minutes.

Certain species of fishes were seen taking shelter at dusk in the many nooks and crannies of coral surrounding the Observatory (Chaetodontidae, Pomacentridae, Scaridae, Apogonidae, and Lutjanidae). With these fishes it was possible to obtain exact information on their disappearance at dusk and appearance at dawn. Other species (e.g., Siganidae) did not seek shelter but merely became motionless and ceased active swimming. The most difficult group consisted of those that disappeared over the edge of the Observatory platform (e.g., Labridae and Acanthuridae). Because these fishes disappeared within fairly narrow time limits and in a consistent pattern, we have assumed they were taking cover for the night.

TABLE 2

THE TIME AND LIGHT INTENSITY AT WHICH THE LABRIDAE DISAPPEARED AT DUSK

FISH	MEAN TIME	STANDARD DEVIATION (MINUTES)	MEAN LIGHT (FOOT-CANDLES)	STANDARD DEVIATION (FOOT-CANDLES)	SAMPLE SIZE (N)
Lienardella fasciatus	1730	16.8	76.0	38.0	7
Hemigymnus melapterus	1745	12.2	40.0	18.0	8
Labroides dimidiatus	1751	4.4	26.4	9.3	8
Thalassoma lunare	1752	3.8	23.7	8.6	8
Epibulus insidiator	1754	4.8	22.0	9.4	8
Average time of sunset	1754				

NOTE: *Choerodon albigena* was not present at the Observatory during the late afternoon and dusk.

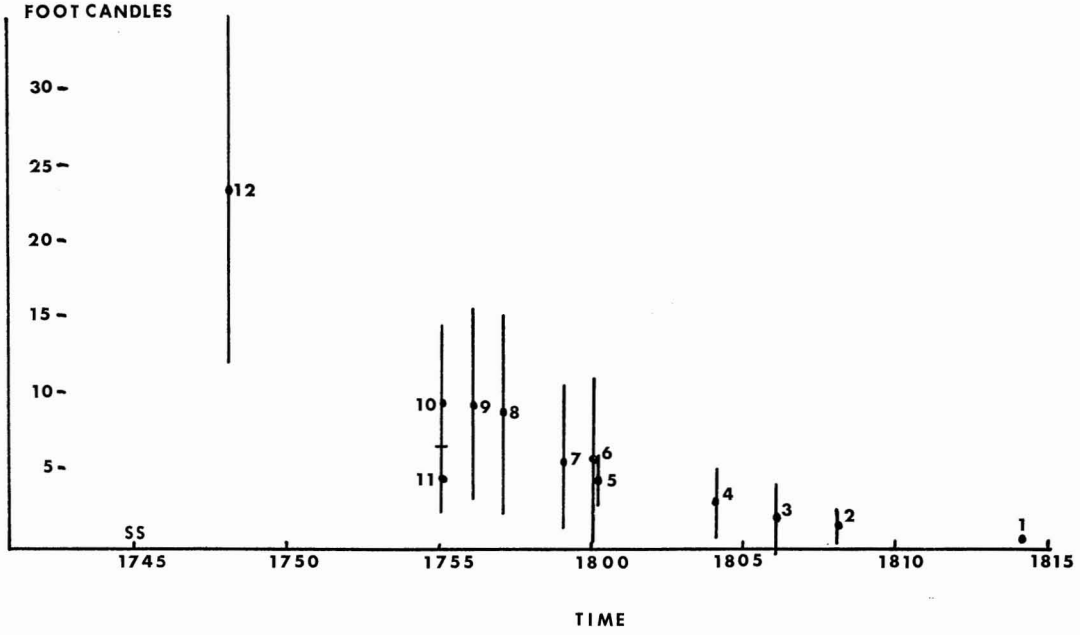

FIG. 1. The time of disappearance of fishes at dusk in relation to light intensity is shown. The vertical lines with each number represent the standard deviation (footcandles) for that species. 1, *Abudefduf palmeri*; 2, Scaridae; 3, *Siganus doliatus*; 4, *Acanthurus xanthopterus*; 5, Apogonidae; 6, *Caesio chrysozonus*; 7, Chaetodontidae; 8, *Abudefduf bankieri*; 9, *Pomacentrus sufflavus*; 10, *Chromis dimidiatus*; 11, *Chaetodontiplus personifer*; 12, *Thalassoma lunare*.

When the results from the first set of observations were analyzed, the data for the disappearance of the labrids at dusk, with the exception of those for *Thalassoma lunare*, did not give a clear picture. A shorter, more detailed study was conducted, therefore, on the disappearance of labrids. This study dated from 26 September 1970 to 8 October 1970. As conditions and time of year differ slightly, these results cannot be compared directly with the first set of data and are included in Table 2.

RESULTS

The results indicate that the appearance and disappearance of the fish species relative to each other are not random but follow a certain sequence at dusk that approximately reverses it-

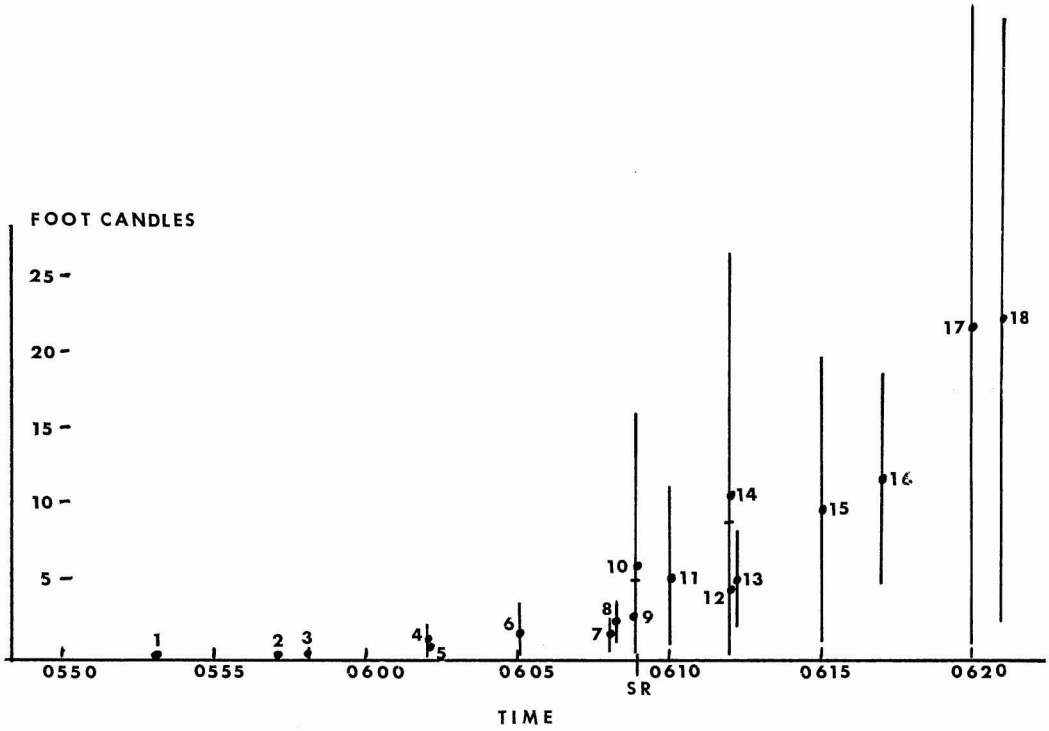

Fig. 2. The time of appearance of fishes at dawn in relation to light intensity is shown. The vertical lines with each number represent the standard deviation (footcandles) for that species. 1, *Abudefduf palmeri*; 2, *Caesio chrysozonus*; 3, Scaridae; 4, Chaetodontidae; 5, *Acanthurus xanthopterus*; 6, *Abudefduf melas*; 7, Apogonidae; 8, *Pomacentrus sufflavus*; 9, *Choerodon albigena*; 10, *Epibulus insidiator*; 11, *Lienardella fasciatus*; 12, *Chromis dimidiatus*; 13, *Abudefduf bankieri*; 14, *Siganus doliatus*; 15, *Thalassoma lunare*; 16, *Chaetodontiplus personifer*; 17, *Labroides dimidiatus*; 18, *Hemigymnus melapterus*.

self at dawn. Each species has a characteristic position in the sequence (see Fig. 1 and 2).

Only the most abundant fishes have been treated in this study. With the exception of the Apogonidae, all are diurnal. There were very few nocturnal fishes present at the Observatory. Of these, only two species were present in any number: *Holocentrus* sp. (Holocentridae) and *Psammoperca melanopus* (Centropomidae). Both of these fishes commenced activity at dusk after all the diurnal fishes had disappeared and either became inactive (*Psammoperca*) or disappeared (*Holocentrus*) at dawn before the diurnal fishes emerged. The only common diurnal fishes not considered were the Serranidae which, although abundant by day, were rarely present during the dawn and dusk observations.

DISCUSSION

It is apparent particularly at dusk that fishes of the same family tend to disappear together within relatively narrow time limits (Tables 3 and 4). For example, all the labrids disappear first (Table 2). These are followed by the three species of small schooling pomacentrids. The chaetodontids retire next, followed by the acanthurids and siganids. The scarids all disappear together. The large solitary pomacentrids are more variable in their behavior and tend to disappear last of all. At dawn the family groupings are not so clearly seen.

The division of coral reef fishes into diurnal and nocturnal guilds has been suggested by other workers: Schroeder and Starck (1964), Starck and Davis (1966), and Hobson (1965). Hobson separates most of the fishes studied into diurnal, nocturnal, and crepuscular groups and

TABLE 3

THE TIME OF DISAPPEARANCE OF FISHES AT DUSK

FISH	MEAN TIME	STANDARD DEVIATION IN MINUTES	SAMPLE SIZE (N)
Thalassoma lunare	1748	7.2	8
Chromis dimidiatus	1755	4.6	8
Chaetodontiplus personifer	1755	7.6	5
Pomacentrus sufflavus	1756	4.9	8
Abudefduf bankieri	1757	4.6	8
Chaetodontidae	1759	6.9	8
Caesio chrysozonus	1800	5.6	8
Apogonidae	1800	4.6	7
Acanthurus xanthopterus	1804	5.6	8
Siganus doliatus	1806	6.3	7
Scaridae	1808	5.3	8
Abudefduf palmeri	1814	4.9	4*

* *Abudefduf palmeri* remained active on four of the eight observations after nightfall which prevented our recording the time of its disappearance.

TABLE 4

THE TIME OF APPEARANCE OF FISHES AT DAWN

FISH	MEAN TIME	STANDARD DEVIATION IN MINUTES	SAMPLE SIZE (N)
Abudefduf palmeri	0553	6.1	8
Caesio chrysozonus	0557	5.9	8
Scaridae	0558	7.1	8
Acanthurus xanthopterus	0602	4.3	8
Chaetodontidae	0602	6.6	8
Abudefduf melas	0605	6.8	8
Apogonidae	0608	5.0	5
Pomacentrus sufflavus	0608	7.0	8
Choerodon albigena	0609	5.0	8
Epibulus insidiator	0609	6.4	8
Lienardella fasciatus	0610	8.7	7
Chromis dimidiatus	0612	6.5	8
Abudefduf bankieri	0612	6.6	8
Siganus doliatus	0612	12.1	7
Thalassoma lunare	0615	6.5	8
Chaetodontiplus personifer	0617	4.5	5
Labroides dimidiatus	0620	5.3	7
Hemigymnus melapterus	0621	6.7	7

notes that "the time of major activity tends to be consistent within most of the families of fishes." Our data suggest that within most families of fishes there is also a consistent time of appearance at dawn and disappearance at dusk. This may break down when the family is large and diverse as in the Pomacentridae, where the small schooling species are separated in time from the large solitary species.

As mentioned under "Methods," fishes belonging to some families simply disappeared over the platform of the Observatory at dusk, and we had to assume that they were retiring for the night at that time. The same problem in interpretation occurred at dawn. Randall (1961), discussing the night behavior of the acanthurid *Acanthurus triostegus sandvicensis*, mentioned that this species commonly rests on the bottom in

TABLE 5

Comparison of Results from Collette and Domm

DOMM	COLLETTE
DAWN	
Pomacentridae (large solitary)	Pomacentridae
Scaridae	Acanthuridae
Chaetodontidae and Acanthuridae	Scaridae
Pomacentridae (small schooling) and some Labridae	Labridae
Labridae	
DUSK	
Labridae	Labridae
Pomacentridae (small schooling)	Chaetodontidae
Chaetodontidae	Acanthuridae
Acanthuridae	Pomacentridae
Scaridae	
Pomacentridae (large solitary)	

Note: The families above are listed in order of appearance at dawn and disappearance at dusk. Only families common to both studies are listed. One or more species were not considered representative of a family unless separated from the next species by a reasonable interval of time.

what appears to be sleep during the hours of darkness. Starck and Davis (1966) and Hobson (1965) reported that many labrids seek shelter for the night in cracks and crevices, whereas others bury themselves in the sand.

The sequence of disappearance of fishes at dusk more or less reverses itself in their appearance at dawn (Fig. 1 and 2 and Table 5). The fishes in this study constitute only a small number of the species found on the Great Barrier Reef, and more data are needed before all family groupings become clear. The sequential appearance and disappearance of fishes may vary from one locality to another; however the principle remains the same.

The results of Collette and Talbot (in press) tend to be in agreement with the present study. Comparing the same families of fishes used in this study to those observed by Collette and Talbot (Table 5), we find that both show a reversal of dawn and dusk sequence and a tendency for species of the same family to be grouped together.

From observation to observation the time of appearance at dawn and disappearance at dusk is fairly consistent for each species. Most standard deviations for time are relatively small, approximately 5 to 6 minutes (see Tables 3 and 4), suggesting a rather narrow threshold of response. It seems that, whatever the stimulus is that triggers the seeking of shelter and leaving it, the response is consistent with respect to time. However, this could occur because time was more accurately measured than light.

Initially it was thought that it was light intensity that provided the stimulus inducing fishes to retire for the night and appear at dawn. The reversal of sequence tends to suggest this. If light intensity were the critical stimulus one might expect small standard deviations for light intensity; however, our results indicate that these are generally large. But this may be because conditions of water depth and clarity and of cloud cover vary from observation to observation; factors that cannot readily be corrected for. Interpretation is also complicated by the fact that, as light intensity increases in footcandles, the standard deviation also increases. In the human eye (and probably in the eyes of most other vertebrates as well) sensitivity varies inversely with intensity (Steinhardt, 1936). Therefore, it cannot be assumed that a large standard deviation implies a less critical threshold, it may reflect merely a limitation in the sensitivity of the fish eye. Most fishes tend to appear at dawn at a lower light intensity than that at which they disappear at dusk, so that two light intensities may be involved. However, this may be because at dusk the fish eye is adapting from light to dark, whereas at dawn it is dark-adapted and so should be more light-sensitive.

During dusk and dawn the wavelengths of light penetrating seawater are changing very rapidly. The fishes could be responding to a change of light quality, that is, wavelength composition. There is also the possibility that the fishes are not responding to a particular level of light intensity so much as they are to the rate of change of light intensity. The present data do not differentiate between these various possibilities.

It seems likely that the fishes are responding to an endogenous circadian clock or rhythm, the phase of which is set by light quantity, quality, or a combination of these. Activity patterns of this type have been described for a number of fishes (Woodhead, 1966).

The conclusions drawn from this study are that the sequential disappearance at dusk and appearance at dawn of the fishes observed seem to be consistent with respect to time for each species, and that light is probably involved in triggering this response; but the mechanism is not yet understood.

In order to accommodate the large numbers of diurnal species seeking shelter at dusk, natural selection possibly may have favored the development of a sequential pattern whereby most diurnal reef fishes seek shelter for the night at slightly different times. This sequential pattern would be a mechanism enabling many species of fish to obtain shelter for the night in a relatively short time, reducing the confusion which would favor predation. It would also reduce the interspecific aggression that might develop between more than one species competing for the same shelter at the same time.

SUMMARY

1. The time and light intensity at which certain species of coral reef fishes appeared at dawn and disappeared at dusk were recorded. Observations were made from the Hook Island Underwater Observatory.
2. The fishes emerged at dawn in a definite sequence that more or less reversed itself in their disappearance at dusk. There was a tendency for species of the same family to disappear close together at dusk, but this was less apparent at dawn.
3. The possibility that light is a controlling stimulus is discussed. Whether light intensity, rate of change of light intensity, or a change in wavelength is responsible, cannot be resolved. It is suggested that the fishes may be responding to an endogenous rhythm, the phase of which is set by light.
4. It is postulated that the sequential disappearance of fishes at dusk may reduce confusion and, hence, the possibility of predation by pisciverous carnivores which are active at this time. It may also reduce interspecific aggression resulting from competition for sheltering places.

ACKNOWLEDGMENTS

We would like to thank the owners of the Hook Island Underwater Observatory for giving us the opportunity to live on Hook Island and work in the Observatory. Many thanks go to J. Randall and P. M. J. Woodhead for their very helpful comments on the manuscript and to F. Talbot for his helpful comments and for making available to the authors his unpublished manuscript.

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