DIURNAL PERIODICITY OF SPAWNING ACTIVITY BY THE HAMLET FISH, *HYPOPLECTRUS GUTTAVARIUS* (SERRANIDAE)

Phillip S. Lobel
Center for Earth and Plantetary Physics
Harvard University
Cambridge, Massachusetts 02138

and

Steve Neudecker
1301 Union Drive
Davis, California 95616

[Converted to electric format by Damon J. Gomez (NOAA/RSMAS) in 2002. Copy available at the NOAA Miami Regional Library. Minor editorial changes were made.]

DIURNAL PERIODICITY OF SPAWNING ACTIVITY BY THE HAMLET FISH, *HYPOPLECTRUS GUTTAVARIUS* (SERRANIDAE)

Phillip S. Lobel[1]
Center for Earth and Planetary Physics
Harvard University
Cambridge, Massachusetts 02138

and

Steve Neudecker
1301 Union Drive
Davis, California 95616

ABSTRACT

Many coral reef fishes spawn during the afternoon crepuscular period, a time of increased predatory activity by piscivores. We document the diel timing and spawning behavior of the hamlet fish, *Hypoplectrus guttavarius*, at St. Croix, U.S.V.I. This fish spawns daily during dusk in the water column above specific reef sites.

The time of spawning relative to sunset was quantified at two sites at different depths. Spawning commenced earlier at the deep reef site and continued later at the shallow reef site. A field manipulation evaluated how this species responded to disburbances during reproduction. When scuba divers attempted to alter the fish's behavior by swimming vigorously toward mating pairs, the hamlets did not abort spawning. The pair responded (1) by continuing to spawn later into the night than those not disturbed and (2) by spawning progressively nearer the substratum.

INTRODUCTION

Until the 1970s, the reproductive behavior of most tropical coastal marine fishes eluded observation. This has changed recently with the discovery that many species spawn during restricted times of ebb tide, off-reef current flow, or crepuscular periods. A majority of coral reef fishes spawn eggs that are bouyant and are advected by ocean currents. Having planktonic propagules is thought to facilitate both rapid advection/dispersal in currents and reduced predation by other reef fishes (Johannes, 1978; Lobel, 1978; Barlow, 1981). In general, fishes seek out specific reef localities and/or pinnacles over which they ascend and spawn. This behavior is particularly interesting for fishes spawning shortly before and during dusk because crepuscular periods are generally believed to be times of increased predator activity and success (e.g., Hobson, 1968, 1972, 1974). Also, to witness

---

[1] Present affiliation: Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543.

natural predation on spawning fishes or their eggs is not rare (Randall and Randall, 1963; Hobson, 1965; Moyer, 1974, 1975; Meyer, 1977; Colin, 1976, 1978; Robertson and Hoffman, 1977; Jones, 1981; Robertson, 1983). Some species gather in spawning aggregations and apparently are oblivious to human or natural piscivore predators even when disturbed or attacked (Johannes, 1978, 1981; Robertson, 1983). In contrast, the mere presence of a diver-observer will interrupt the mating of some smaller species unless the fish are approached and observed with stealth (Johannes, 1978; Lobel, 1978).

To date, studies on the reproductive behavior of tropical coastal marine fishes in the field have been primarily observational. The emphasis has been on documenting where, when, and how various species spawn. Herein we report the spawning behavior, diel timing, and a manipulation that attempted to disturb the behavior of a fish during reproduction. Our goal was to see whether and how the spawning behavior of the Caribbean hamlet, *Hypoplectrus guttavarius*, might be altered. Because hamlets and many other fishes spawn during the evening crepuscular period when predation by piscivores is most likely, we wanted to determine whether fish that were disturbed by scuba divers during the spawning act would cease all activity, move sites, depart and seek other mates, or merely continue despite the disturbance.

The Caribbean hamlet, *Hypoplectrus guttavarius* (fig. 1) was selected for study because it maintained stable, identifiable pairs which spawned almost every evening at specific sites during February 1980, at St. Croix. It was common, easily observed, and the spawning act was unmistakable and easily quantified. The diel timing of spawning is compared with that of *H. chlorurus*, *H. nigricans*, *H. puella*, and *H. unicolor*.

The reproductive ecology of hamlets is somewhat enigmatic. It has been suggested that *Hypoplectrus nigricans* and other hamlets are simultaneous hermaphrodites, and that individuals alternate sexual roles between spawning clasps (Barlow, 1975; Fischer, 1980*a*, 1980*b*, 1981). It is also controversial whether different morphological variants of hamlets represent aggressive-mimetic morphs of the single species, *Hypoplectrus unicolor*, or are reproductively isolated incipient species (Thresher, 1978; Graves and Rosenblatt, 1980; Fischer, 1980*b*). Hamlets usually mate assortatively by color patterns, although mixed pairs have been observed, and individuals which exhibit color markings characteristic of two or more color forms are known (Barlow, 1975; Thresher, 1978; Graves and Rosenblatt, 1980; Fischer, 1980*a*). Thus, the reproductive behavior of hamlets is interesting from several perspectives. To maintain simplicity and clarity, we refer to the various hamlets by their established species names (cf. Randall, 1968).

STUDY SITES

Fish were examined at two locations on St. Croix, U.S. Virgin Islands (64°35'W, 17°45'N). The first site was the east slope of Salt River canyon within the excursion limits of the NOAA National Undersea Laboratory System habitat (HYDROLAB). Since we were saturated, we spent approximately 53 hours per person observing fish at 20-30 m depths from February 11 to 15, 1980. The second site was located on several patch reefs at about 10 m depths in

Figure 1.--Adult Hypoplectrus guttavarius (the shy hamlet) approximately 11 cm in length.

the Buck Island Channel outside Teague Bay Reef on the northeast coast of St. Croix. Observations were made from February 20 to March 3, 1980. Further site descriptions are given by Neudecker and Lobel, 1982.

METHODS

Specific pairs of H. guttavarius were identified and details of their spawning behavior were recorded before, during, and after the manipulation. Observers selected one pair each evening and positioned themselves unobtrusively on site at least 15 min before the fish initiated courtship. The baseline spawning behavior of each pair was determined during one or two evenings prior to the disturbance manipulation (3 of 7 pairs were observed for 2 consecutive days before the manipulations; the other 4 pairs were observed the day before the manipulations). In cases where sites lacked distinguishing natural features, the specific site at which each pair spawned was marked with small floats. We spent several days diving at all hours, including sunrise, and saw hamlets spawn only during dusk (total observation 158.7 man-hours during the 7 days in HYDROLAB). Data recorded each time a pair spawned included the time, height in the water relative to the bottom and the coral/gorgonian structure over which spawning took place, approximate distance moved between spawning sites, and general notes on the pair's response to observers and other species.

Figure 2.--A pair of Hypoplectrus guttavarius engaged in courtship at a typical spawning site (Deep Reef at East Wall of Salt River Canyon, HYDROLAB site).

The disturbance manipulations were conducted the day after baseline spawning behavior was determined. The manipulation was to disrupt the spawning act each time the fish attempted it. As the pair began to enter the spawning clasp, the observer swam rapidly toward the pair (in an attempt to mimic a predator's behavior). The pair was harassed repeatedly this way for as long as spawning was attempted. When mates parted, close watch was maintained until it was certain that spawning had ceased for the night. Occasionally, a pair would separate, swim several meters apart, return several minutes later, rejoin and attempt to spawn again. Follow-up observations were made on the same pair the day after the manipulation. Data analysis of treatments used the nonparametric Mann-Whitney U test statistic.

On any given day, at least three diver/observers were engaged in various phases of the manipulation. To provide control observations, a diver watched a spawning pair without interfering while other divers were either harassing a spawning pair or conducting follow-up observations.

Figure 3.--Hypoplectrus guttavarius embraced in the spawning clasp. The individual facing head-down has bent body in an S-shape.

RESULTS

Typical Spawning Behavior

Our observations provided the following general picture of spawning in H. guttavarius. Hamlets mate only in pairs. Fertilization is external and zygotes are planktonic. During the daytime, mates appear loosely associated in adjacent or nearby home ranges. They begin to interact within 2 hr of sunset. They first rendezvous, remain close together, and engage in occasional short chases. The spawning act begins when one fish presents a lateral display while flicking its pelvic fins (fig. 2). The displaying individual slowly rises while continuing its display. The bright blue flank of this individual fades to a pastel shade. The other fish follows. The two then rise together about 1 m above some towering reef structure. At St. Croix, these structures were vertical colonies of the gorgonian, Pseudoplexaura sp., or the coral, Acropora cervicornis.

Once the proper height (about 1-2 m) is attained over a tall reef structure, the following fish folds around the pale colored leader, who poses head down in an S-shaped position (fig. 3). Release of eggs and sperm occurs

Figure 4.--Hypoplectrus guttavarius embraced in the spawning clasp. The individual folded around the other one facing head-down opens its mouth while quivering and spawning.

as both fish quiver. Quivering lasts for 2-3 sec. The individual folded around the other often opens its mouth while quivering (fig. 4). Following consummation, the fish cease embracing and quickly descend to the bottom. The embracing behavior of hamlets when spawning has been termed the spawning clasp (Fischer, 1980a) and occurs many times throughout an evening. Infrequently, fish would embrace but not quiver, and the release of gametes was not evident. Fischer (1980a) has described the similar spawning behavior and sexual role of H. nigricans.

Each pair of hamlets initiated spawning at a specific reef location each evening. Pairs showed strong spawning site specificity. They moved between a few (from 1 to 4) particular sites each evening, and frequently a pair returned to their original site. When some pairs moved between spawning sites, other individuals occasionally interfered and attempted to steal a mate. These 'floater' individuals were seldom successful. Out of all hamlet spawnings observed (N = 314 of 5 spp.), only once was a floater successful in stealing a mate by breaking up an existing pair (the pair and floater species was H. unicolor).

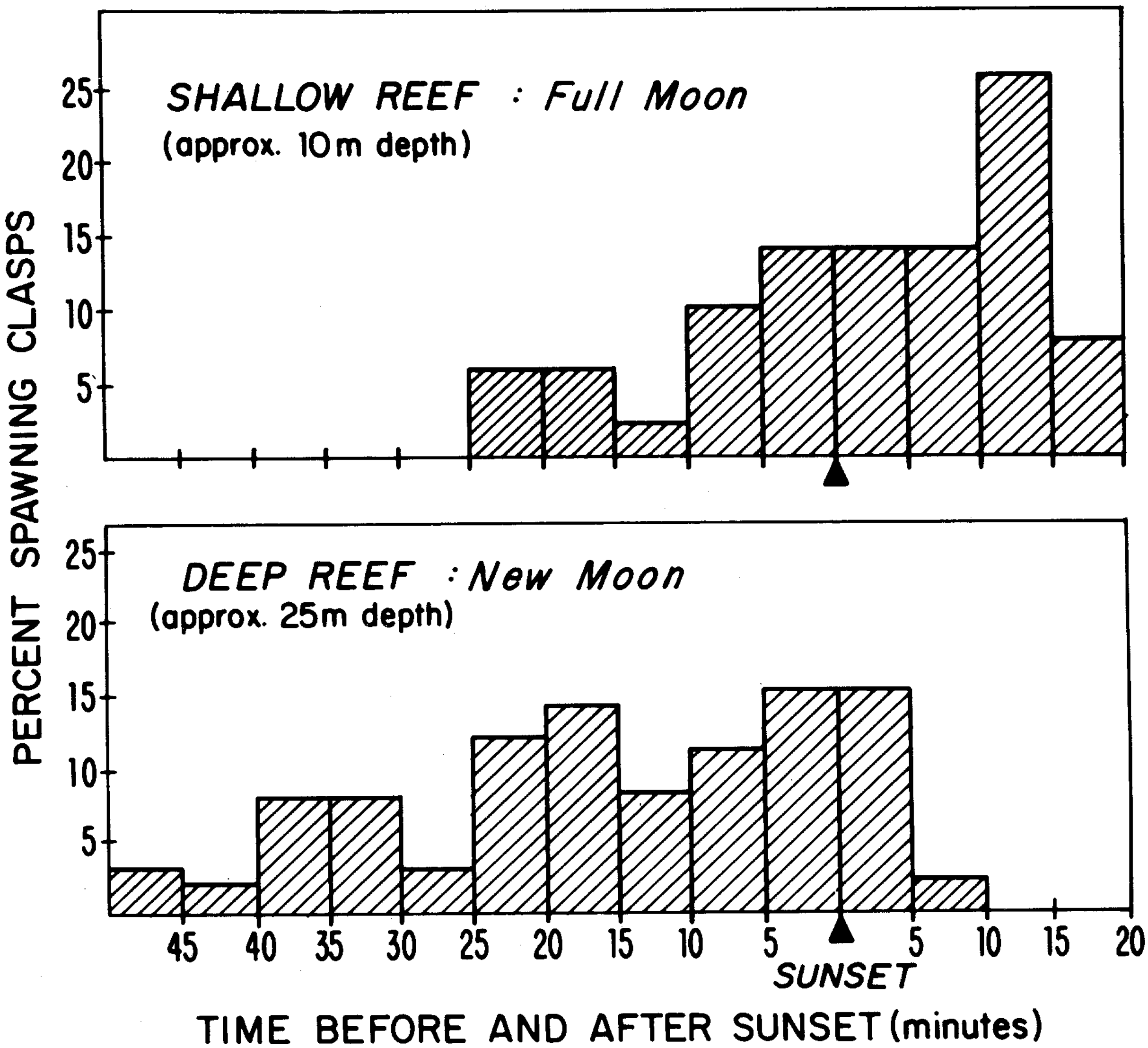

Figure 5.--Diel reproductive timing of Hypoplectrus guttavarius at two depths. The shallow site (10 m depth) was occupied during the full moon phase (Feb. 24-27, 1980), while the deep site (22-30 m depth) was occupied during the new moon (Feb. 11-13, 1980). The shallow group consisted of 4 pairs observed over 4 days for a total of 67 spawning clasps. The deep group consisted of 7 pairs observed over 4 days for a total of 210 spawning clasps. Time is in minutes before and after sunset. See text for discussion.

Diel Reproductive Timing

Hypoplectrus guttavarius spawned almost every evening during the study period. Fish were studied at two sites which differed in depth. The deep reef site (20-30 m depth) was occupied by us February 11-15, and the shallow site (10 m depth) from February 20-March 3. We did not see hamlets spawn on two evenings, February 21-22. Observations at the deep site corresponded to the presence of a new moon (February 15). We were at the shallow site during the full moon (March 1). The dates on which hamlets were not seen spawning coincided with the last quarter moon phase (February 22).

The diel timing of reproduction, relative to sunset, differed for *H. guttavarius* at the two sites (depths) and lunar phases. The first spawnings at the deep reef site began 50 min before sunset (with a mean, $\bar{X}$, and standard deviation, S.D., of 33 $\pm$ 1 min) and the last spawnings ended 10 min ($\bar{X}$ $\pm$ S.D. = 2 $\pm$ 9 min) after sunset; most spawnings occurred just prior to sunset. Spawning at the shallow reef site commenced later, 25 min ($\bar{X}$ $\pm$ S.D. = 16 $\pm$ 7 min) before sunset, and ended later, 20 min ($\bar{X}$ $\pm$ S.D. = 3 $\pm$ 6 min) after sunset; here most spawnings occurred just past sunset (fig. 5). Reproduction by fish at the two sites did not differ in any other aspect.

We did not observe any strong lunar periodicity in the daily spawning behavior of *H. guttavarius*. However, our data do not allow distinguishing between the possible effects of 1) different phases of the moon during the times that each group was observed vs. 2) the difference in depth and corresponding changes in light levels during dusk.

Effects of Disturbance on Spawning Behavior

All *H. guttavarius* persisted in spawning in spite of overt and constant harassment. Harassed pairs attempted twice as many spawning clasps and continued for about 25 min later than nonharassed (day before and day after) pairs (tables 1, 2). However, the frequency of spawning clasps attempted per 5 min remained the same (about 2 $\pm$ 1 clasps; tables 1b, 2b). The number of times a pair changed spawning sites relative to the number of spawning clasps also did not vary significantly (tables 1c, 2c). One particularly striking effect of disturbance on these spawning fish was that, as spawning was continuously disrupted, a pair attempted to spawn progressively nearer the substratum (based on our qualitative observations). At the end of the disturbance period, several pairs were trying to spawn next to the bottom while hidden among coral/gorgonian branches. This result simply may indicate that once ovulation has begun, the fish must spawn.

Overall, the fish persisted in spawning despite the aggressive behavior of the scuba divers. However, we have no estimate of the fate of zygotes when released next to the bottom and in between coral/gorgonian branches as compared to those normally dispersed about a meter above reef structures. The experience of the disturbance had no apparent lasting effects on the fish. The fish's behavior did not differ markedly on the day after compared to the day before the disturbance (tables 1, 2).

Table 1.--Effect of disturbance on the spawning behavior of *Hypoplectrus guttavarius*. Data for shallow and deep water groups were pooled except when related to sunset time. In addition to the above changes, when fish were disturbed, they would attempt to spawn closer to the substrate until they were on the bottom. Notations in last rows (e, f) indicate before (-) or after (+) sunset.

	Baseline before disturbed (7 pairs; 10 observations)	During disturbance (6 pairs; 6 observations)	Day after disturbed (5 pairs; 5 observations)
a. $\bar{X}$ ± S.D. (range) no. spawning clasps per pair	12 ± 3 (7 to 16)	25 ± 9 (10 to 33)	12 ± 2 (9 to 15)
b. $\bar{X}$ ± S.D. (range) no. spawning clasps per 5 min	2 ± 1(0.6 to 3.6)	2 ± 1 (1.5 to 3.1)	2 ± 1 (1.5 to 3.2)
c. $\bar{X}$ ± S.D. (range) ratio of no. moves pair made between spawning sites to total no. spawning clasps	0.23 ± 0.16 (0 to 0.5)	0.48 ± 0.30 (0.06 to 0.86)	0.26 ± 0.19 (0 to 0.46)
d. $\bar{X}$ ± S.D. min. (range) duration of spawning period per day	31 ± 8 (11 to 91)	57 ± 21 (33 to 69)	28 ± 8 (21 to 38)
e. Time ($\bar{X}$, range) relative to sunset that spawning commenced (min)			
shallow group (full moon)	-16 (-22 to -6) (N = 4)	-24 (-44 to -8) (N = 3)	-11 (-19 to -2) (N = 3)
deep group (new moon)	-33 (-50 to -19) (N = 6)	-50 (-71 to -35) (N = 3)	-40 (-44 to -35) (N = 2)
f. Time ($\bar{X}$, range) relative to sunset that spawning ceased (min)			
shallow group (full moon)	+13 (+ 5 to +18) (N = 4)	+30 (+20 to +38) (N = 3)	+12 (+ 2 to +24) (N = 3)
deep group (new moon)	- 2 (-19 to + 5) (N = 6)	+10 (- 2 to +21) (N = 3)	- 4 (- 6 to - 1) (N = 2)

Table 2.--Statistical comparison of data from table 1. Values listed are calculated values of Z using the Mann-Whitney U test. Values marked by * are statistically different at p = 0.05 (critical value for Z = 1.960.)

	Before vs. During Disturbance	After vs. During Disturbance	Before vs. After Disturbance
a. No. spawning clasps per pair	*2.490	*2.008	0.245
b. No. spawning clasps per pair per 5 min.	1.844	0.548	1.347
c. No. moves pair made between spawning sites per total no. spawning clasps	1.627	1.278	0.367
d. Duration of spawning period	*2.169	*2.373	0.857

Spawning of Other Hamlets

Four other hamlets also were observed spawning at the shallow reef site: *H. puella*, *H. unicolor*, *H. chlorurus*, and *H. nigricans*. We did not see mixed mating among hamlets. Data contrasting aspects of reproduction in these fishes and of *H. guttavarius* are presented in table 3. However, the data set lacks sufficient detail to allow more than a general indication of how the pattern and timing of reproduction might vary among congeners of hamlets.

DISCUSSION

Many diurnal tropical marine fishes that remain active during the evening crepuscular period may risk being eated by piscivores, whose feeding activities generally are believed to increase at this time (Hobson, 1968, 1972, 1974; Domm and Domm, 1973; Major, 1977). This increased threat of predation is reflected in the potential prey's behavior, and most species retreat to shelter, aggregate, or forage closer to the reef (Hobson, 19783, 1978; Robertson and Sheldon, 1979). However, many species also periodically spawn during dusk (e.g., Randall, 1961; Lobel, 1978; Moyer and Nakazano, 1978; Moyer, 1979; Moyer and Zaiser, 1981; Zaiser and Moyer, 1981; Neudecker and Lobel, 1982; Moyer, *et al.*, 1983). Spawning during the evening crepuscular period is thought to reduce the likelihood of predation on planktonic eggs, since most planktivorous fishes that select such small prey are inactive by this time. It is noteworthy that the eggs of nestbuilding, demersal-spawning balistid and pomacentrid fishes hatch after dark, whereupon the larvae become planktonic (Allen, 1972; Moyer and Bell, 1976; Ross, 1978; Fricke, 1980; Lobel and Johannes, 1980; Doherty, 1983). Diurnal planktivores consume smaller prey, including eggs, than nocturnal planktivores which infrequently

Table 3.--Reproductive behavior by other hamlets (*Hypoplectrus* spp.). These fish were observed at 25-30 ft. depth, February 25-March 2, 1980. For *H. nigricans* (*), see Fischer, 1980, for comprehensive spawning data.

	H. puella (N = 2 pairs)	*H. unicolor* (N = 2 pairs)	*H. chlorurus* (N = 2 pairs)	*H. nigricans** (N = 1 pair)
$\bar{X}$ (range) no. spawning clasps per day	10 (8-12)	12 (6-17)	17 (16-18)	27
$\bar{X}$ (range) no. spawning clasps per 5 min.	3 (3-4)	2 (2-2)	2 (-2-2)	1
$\bar{X}$ (range) no. moves pair made between spawning sites per 10 spawns	5 (4-6)	7 (7-7)	7 (7-7)	7
$\bar{X}$ (range) min. duration of spawning per day	15 (14-16)	27 (16-38)	42 (38-45)	101
Minutes before sunset that spawning commenced	5 + 6	13 + 16	28 + 39	87
Minutes after sunset that spawning ceased	8 + 11	1 + 24	8 + 11	14

eat eggs (Hobson and Chess, 1978). Most egg-eating fishes cease foraging as light levels diminish, since low light levels make visual orientation difficult and also predation by piscine predators generally increases at this time (Hobson, 1972, 1974; Hobson and Chess, 1978). Additionally, any planktivores still actively feeding through dusk may be quickly satiated by the simultaneous spawning of many fishes.

Spawning during dusk may reduce mortality of fish eggs by predation, but it also may increase the potential risk of predation for adult fishes. Hobson (1968, 1972, 1974, 1978; Hobson, et al., 1981) has documented extensive evidence suggesting increased predation by fish predators on tropical reef fishes exposed or otherwise vulnerable during the crepuscular periods. Fishes also are thought to be more vulnerable to predation when preoccupied with mating (Johannes, 1978, 1981; Robertson, 1983). Furthermore, it must be noted that there are many fishes, particularly labrids and scarids, which spawn throughout the day, appearing more in phase with tidal currents than crepuscular periods (Barlow, 1981; Kuwamura, 1981; Robertson, 1983).

In this study, we wanted to evaluate how a fish would alter its mating pattern when disturbed or attacked. The results might then provide some insight into the selective pressures molding the reproductive tactics of coastal marine species in the tropics. At the time, the best arrangement we could devise to test the possible effect of predation was by simulating predator behavior using scuba divers. Other studies also have considered a fish's response to a human diver as indicative of reaction to a piscine predator (e.g., Coates, 1980). Nevertheless, results of this manipulation should be related only tenuously to how the hamlet might respond to a fish predator. A fish predator probably would not continue to attack the same prey throughout dusk.

The hamlet, Hypoplectrus guttavarius, altered its normal mating behavior when harassed by 1) attempting more clasps longer into the night and 2) spawning progressively nearer to the bottom in and among shelter. In no case was spawning terminated early; in fact, the opposite occurred, and fish prolonged spawning attempts. This result simply may indicate that once ovulation has begun, the fish must spawn. The spawning sites were all reef structures (gorgonian and coral) taller than the surrounding terrain. Only after a pair had shifted sites repeatedly did they commence spawning nearer the bottom or in shelter. Difference in survivorship of the free-floating zygotes when released high above the reef vs. near the bottom was not determinable. Fish which were attacked and harassed one day showed no indication of lasting behavioral affects the next day.

The importance attributed to spawning above a tall reef structure is that it provides a degree of safety for the adults. It allows the fish to mate relatively high in the water column while remaining as close as possible to shelter. Spawning high in the water places the free-floating eggs beyond the grasp of benthic planktivores and in a position most favorable to advection by currents.

Hobson (1972, 1974) has suggested that the well defined twilight activities of tropical reef fishes have been shaped by the threat of crepuscular predators (Hobson, et al., 1981). If this hypothesis is correct, then it would seem that fishes spawning during evening crepuscular periods have not been overtly deterred by the potential threat of predation. Alternatively, the adaptive pressures favoring zygote survival may have been more influential in molding the diel timing of reproduction than factors affecting survival of the parents (e.g., predation) while spawning during the evening crepuscular period.

ACKNOWLEDGMENTS

We are grateful for the stimulating conversation and help received from our fellow aquanaut, William Hamilton III, both underwater and topside. The study was made possible by the tireless support of the HYDROLAB personnel, Bill and Joan Schane, Barry Walden, Rod Catanach, and Joe Langersdorf, and support divers, Scott Grace and Don Morris. Valerie Paul, Stacy Tighe, and Nancy Wolf greatly aided in the field observations. We also received generous support from the West Indies Laboratory, for which we are grateful. We thank Marjorie Reaka and William McFarland for their thoughtful reviews of this paper. This research was funded by a NOAA HYDROLAB (NULS 80-1) grant to S. Neudecker and by an OPER grant from the Institute of Ecology, University of California at Davis, to William Hamilton, S. Neudecker, and P. Ward.

LITERATURE CITED

Allen, G. R. 1972. Anemonefishes. T. F. H. Publ., Neptune City, N.J. 288 pp.

Barlow, G. W. 1975. "On the Sociobiology of Some Hermaphroditic Serranid Fishes, the Hamlets in Puerto Rico." Mar. Biol. 33:295-300.

Barlow, G. W. 1981. "Patterns of Parental Investment, Dispersal and Size Among Coral-Reef Fishes." Environ. Biol. Fish. 6:65-85.

Colin, P. L. 1976. "Filter-Feeding and Predation on the Eggs of *Thalassoma* sp. by the Scombrid Fish *Rastrelliger kanagurta*." Copeia 1976:596-597.

Colin, P. L. 1978. "Daily and Summer-Winter Variation in Mass Spawning of the Striped Parrotfish, *Scarus croicensis*." Fish. Bull. 76:117-124.

Coates, D. 1980. "Anti-Predator Defense Via Interspecific Communication in Humbug Damselfish, *Dascyllus aruanus* (Pisces, Pomacentridae)." Z. Tierpsychol. 52:355-364.

Doherty, P. J. 1983. "Diel, Lunar and Seasonal Rhythms in the Reproduction of Two Tropical Damselfishes: *Pomacentrus flavicauda* and *P. wardi*." Mar. Biol. 75:215-224.

Domm, S. B., and A. J. Domm. 1973. "The Sequence of Appearance at Dawn and Disappearance at Dusk of Some Coral Reef Fishes." Pac. Sci. 27:128-135.

Fischer, E. A. 1980a. "The Relationship Between Mating System and Simultaneous Hermaphroditism in the Coral Reef Fish, *Hypoplectrus nigricans* (Serranidae)." Anim. Behav. 52:620-633.

Fischer, E. A. 1980b. "Speciation in the Hamlets (*Hypoplectrus*; Serranidae) - A Continuing Enigma." *Copeia* 1980:649-659.

Fischer, E. A. 1981. "Sexual Allocation in a Simultaneously Hermaphroditic Coral Reef Fish." *Amer. Nat.* 117:64-82.

Fricke, H. W. 1980. "Mating Systems, Maternal and Biparental Care in Triggerfish (Balistidae)." *Z. Tierpsych.* 53:105-222.

Graves, J. E., and R. H. Rosenblatt. 1980. "Genetic Relationships of the Color Morphs of Serranid Fish, *Hypoplectrus unicolor*." *Evolution* 34:240-245.

Hobson, E. S. 1965. "Diurnal-Nocturnal Activity of Some Inshore Fishes in the Gulf of California." *Copeia* 1965:291-302.

Hobson, E. S. 1968. *Predatory Behavior of Some Shore Fishes in the Gulf of California*. U.S. Fish Wildlife Service Res. Rept. No. 73. 92 pp.

Hobson, E. S. 1972. "Activity of Hawaiian Reef Fishes During the Evening and Morning Transitions Between Daylight and Darkness." *Fish. Bull.* 70:715-740.

Hobson, E. S. 1973. "Diel Feeding Migrations in Tropical Reef Fishes." *Helgolander wiss. Meeresunters.* 24:361-370.

Hobson, E. S. 1974. "Feeding Relationships of Teleostean Fishes on Coral Reefs in Kona, Hawaii." *Fish. Bull.* 72:915-1031.

Hobson, E. S. 1978. "Aggregating as a Defense Against Predators in Aquatic and Terrestrial Environments," pp. 219-234. *In*: E. S. Reese and F. J. Lighter (eds.), *Contrasts in Behavior*. Wiley and Sons, New York.

Hobson, E. S., and J. R. Chess. 1978. "Trophic Relationships Among Fishes and Plankton in the Lagoon at Enewetak Atoll, Marshall Islands." *Fish. Bull.* 76:133-153.

Hobson, E. S., W. N. McFarland, and J. R. Chess. 1981. "Crepuscular and Nocturnal Activities of Californian Nearshore Fishes, With Consideration of Their Scotopic Visual Pigments and the Photic Environment." *Fish. Bull.* 79:1-30.

Johannes, R. E. 1978. "Reproductive Strategies of Coastal Marine Fishes in the Tropics." *Environ. Biol. Fishes* 3:65-84.

Johannes, R. E. 1981. *Words of the Lagoon*. University of Calfornia Press, Berkeley. 245 pp.

Jones, G. P. 1981. "Spawning-Site Choice by Female *Pseudolabrus celidotus* (Pisces: Labridae) and Its Influence on the Mating System." *Behav. Ecol. Sociobiol.* 8:129-142.

Kuwamura, T. 1981. "Diurnal Periodicity of Spawning Activity in Free-Spawning Labrid Fishes." Jap. J. Ichthyol. 28:343-348.

Lobel, P. S. 1978. "Diel, Lunar and Seasonal Periodicity in the Reproductive Behavior of the Pomacanthid Fish, Centropyge potteri, and Some Other Reef Fishes in Hawaii." Pac. Sci. 32:193-207.

Lobel, P. S., and R. E. Johannes. 1980. "Nesting, Eggs and Larvae of Triggerfishes (Balistidae)." Environ. Biol. Fish. 5:251-252.

Lobel, P. S., and A. R. Robinson. 1983. "Reef Fishes at Sea: Ocean Currents and the Advection of Larvae," pp. 29-38. In: M. L. Reaka (ed.), The Ecology of Deep and Shallow Coral Reefs. NOAA Symp. Ser. Undersea Res., Vol. 1(1). NOAA Undersea Res. Progr., Rockville, Md.

Major, P. F. 1977. "Predator-Prey Interactions in Schooling Fishes During Periods of Twilight: A Study of the Silverside Pranesus insulanum in Hawaii." Fish. Bull. 72:415-426.

McFarland, W. N. 1982. "Recruitment Patterns in Tropical Reef Fishes," pp. 83-91. In: G. R. Huntsman, W. R. Nicholson, and W. W. Fox (eds.), The Biological Bases for Reef Fishery Management. NOAA Tech. Mem. NMFS-SEFC-80. Nat. Mar. Fish. Serv., Beaufort, N.C.

Meyer, K. A. 1977. "Reproductive Behavior and Patterns of Sexuality in the Japanese Labrid Fish Thalassoma cupido." Jap. J. Ichthyol. 24:101-112.

Moyer, J. T. 1974. "Notes on the Reproductive Behavior of the Wrasse Thalassoma cupido." Jap. J. Ichthyol. 21:34-36.

Moyer, J. T. 1975. "Reproductive Behavior of the Damselfish Pomacentrus nagasakiensis at Miyake-jima, Japan." Jap. J. Ichthyol. 22:151-163.

Moyer, J. T. 1979. "Mating Strategies and Reproductive Behavior of ostraciid Fishes at Miyake-jima, Japan." Jap. J. Ichthyol. 26:148-160.

Moyer, J. T., and L. J. Bell. 1976. "Reproductive Behavior of the Anemonefish Anphiprion clarkii at Miyake-jima, Japan." Jap. J. Ichthyol. 23:23-32.

Moyer, J. T., and A. Nakazono. 1978. "Population Structure, Reproductive Behavior and Protogynous Hermaphroditism in the Angelfish, Centropyge interruptus at Miyake-jima, Japan." Jap. J. Ichthyol. 25:25-39.

Moyer, J. T., and M. J. Zaiser. 1981. "Social Organization and Spawning of the Pteroine Fish, Dendrochirus zebra, at Miyake-jima, Japan." Jap. J. Ichthyol. 28:52-69.

Moyer, J. T., R. E. Thresher, and P. L. Colin. 1983. "Courtship, Spawning and Inferred Social Organizations of American Angelfishes (Genera Pomacanthus, Holocanthus, and Centropyge; Pomacanthidae)." Environ. Biol. Fish. 9:25-39.

Neudecker, S., and P. S. Lobel. 1982. "Mating Systems of Chaetodontid and Pomacanthid Fishes at St. Croix." Zeit. Tierpsychol. 59:299-318.

Randall, J. E. 1961. "Observations on the Spawning of Surgeon-Fishes (Acanthuridae) in the Society Islands." Copeia 1961:237-238.

Randall, J. E. 1968. Caribbean Reef Fishes. T. F. H. Publ., Neptune City, N.J. 318 pp.

Randall, J. E., and H. A. Randall. 1963. "The Spawning and Early Development of the Atlantic Parrotfish, Sparisoma rubripinne, with notes on Other Scarid and Labrid Fishes." Zoologica 48:49-60.

Robertson, D. R. 1983. "On the Spawning Behavior and Spawning Cycles of Eight Surgeonfishes (Acanthuridae) from the Indo-Pacific." Environ. Biol. Fish. 9:193-223.

Robertson, D. R., and S. G. Hoffman. 1977. "The Roles of Female Mate Choice and Predation in the Mating Systems of Some Tropical Labrid Fishes." Zeit. Tierpsychol. 45:298-320.

Robertson, D. R., and J. M. Sheldon. 1979. "Competitive Interactions and the Availability of Sleeping Sites for a Diurnal Coral Reef Fish." J. Exp. Mar. Biol. Ecol. 40:285-298.

Ross, R. M. 1978. "Reproductive Behavior of the Anemonefish Amphiprion melanopus on Guam." Copeia 1978:103-107.

Thresher, R. E. 1978. "Polymorphism, Mimicry, and the Evolution of the Hamlets (Hypoplectrus, Serranidae)." Bull. Mar. Sci. 28:345-353.

Thresher, R. E. 1980. Reef Fish: Behavior and Ecology on the Reef and in the Aquarium. Palmetto Publ. Co., St. Petersburg, Florida. 171 pp.

Zaiser, M. J., and J. T. Moyer. 1981. "Notes on Reproductive Behavior of the Lizardfish Synodus ulae on Miyake-jima, Japan." Jap. J. Ichthyol. 28:95-98.