EFFECTS OF PSEUDOPREDATION ON SPAWNING BEHAVIOR OF *Hypoplectrus guttavarius* (SERRANIDAE)

STEVE NEUDECKER

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NULS Mission 80-1

Final Report

Mating Systems of Caribbean chaetodontid and pomacanthid fishes

and

Effects of pseudopredation on spawning behavior of *Hypoplectrus guttavarius* (Serranidae)

by

Steve Neudecker

Final Scientific Report 80-1

Mating systems of Caribbean chaetodontid and pomacanthid fishes

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Effects of pseudopredation on spawning behavior of *Hypoplectrus guttavarius* (Serranidae)

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Prelude

The purpose of NULS mission 80-1 was to continue investigations of social behavior and foraging patterns of chaetodontid and pomacanthid fishes (Birkeland and Neudecker NULS 78-1, 1980), and to attempt to observe and describe the previously unknown reproductive behavior of these fishes.

We were fortunate to accomplish all of our goals and also managed to conduct a novel experiment testing effects of predators on reproductive behavior of coral reef fishes which spawn planktonic zygotes at dusk. Results of our abundance, distribution, and foraging measurements were reported in Quick Look Report 80-1 (Neudecker 1980) and are not repeated here. Those results will constitute another complete manuscript (Neudecker in prep) that will be published elsewhere.

This final report contains two manuscripts which are to be published in scientific journals. The first report, "Mating systems of chaetodontid and pomacanthid fishes," is a draft of the manuscript accepted for publication by Zeitschrift für Tierpsychologie. The second paper, "Effects of pseudopredation on spawning behavior of *Hypoplectrus guttavarius* (Serranidae)," has been submitted to the Journal of Experimental Marine Biology and Ecology. Additional information on the mission, including excursion logs, are included in the appendices.

Effects of Disturbance on Spawning Behavior of the Hamlet Fish, *Hypoplectus guttavarius* (Serranidae)

ABSTRACT

The hamlet fish, *Hypoplectrus guttavarius*, spawns only during the dusk crepuscular period. Dusk is also a time of general increase in predatory activity by piscivores. Fish were observed spawning daily at St. Croix, U.S.V.I., and divers attempted to inhibit and alter reproductive behavior by acting aggressively while swimming vigorously toward mating pairs. The hamlets did not abort spawning and responded by persisting to spawn later into the night, moving sites more often, and spawning progressively nearer the substratum. These responses are sensible predator avoidance strategies. Continuation of reproduction despite overt risks may be indicative of the strong adaptive advantages for the survival of floating eggs fertilized at dusk. These advantages apparently outweigh prospective risks to adults exposed to crepuscular predators.

INTRODUCTION

For many years the mating behavior of most tropical marine fishes eluded observation. This has changed in recent years with the discovery that many species mate only during the evening crepuscular period. So far, studies on the reproductive behavior of tropical coastal marine fishes in the field have been mainly observational. The emphasis has been on documenting where, when and how various species spawn. Herein, we report an experiment which attempted to manipulate the behavior of a fish while it mated. Our goal was to see how the spawning behavior of the hamlet fish, Hypoplectrus guttavarius, might be altered. Because hamlets and many other species spawn at dusk when predation by piscivores is most likely, we evaluated the response of the hamlet when "attacked". In this experiment attacks were made by scuba-divers.

We posed the question of how much and for how long fish would risk spawning when overtly and continually threatened. Fish disrupted during the spawning act may cease all activity, move sites, depart and seek other mates, or merely continue despite the disturbance. Some species which gather in large spawning aggregations are apparently oblivious to human or natural predators even when attacked (Johannes 1978). In contrast, the mere presence of a diver-observer will disrupt the mating of some smaller species unless the fish are approached and observed with stealth (Johannes 1978, Lobel 1978).

The Caribbean hamlet, Hypoplectrus guttavarius (Figure 2a), was selected for study because it maintained stable, identifiable pairs which spawned almost every evening at specific sites. It was common, easily observed, and the spawning act was unmistakable and easily quantified.

The reproductive habits of hamlets are, however, somewhat enigmatic. It has been suggested that Hypoplectrus nigricans and other hamlets are

Figure 2a. Adult *Hypoplectrus guttavarius*.

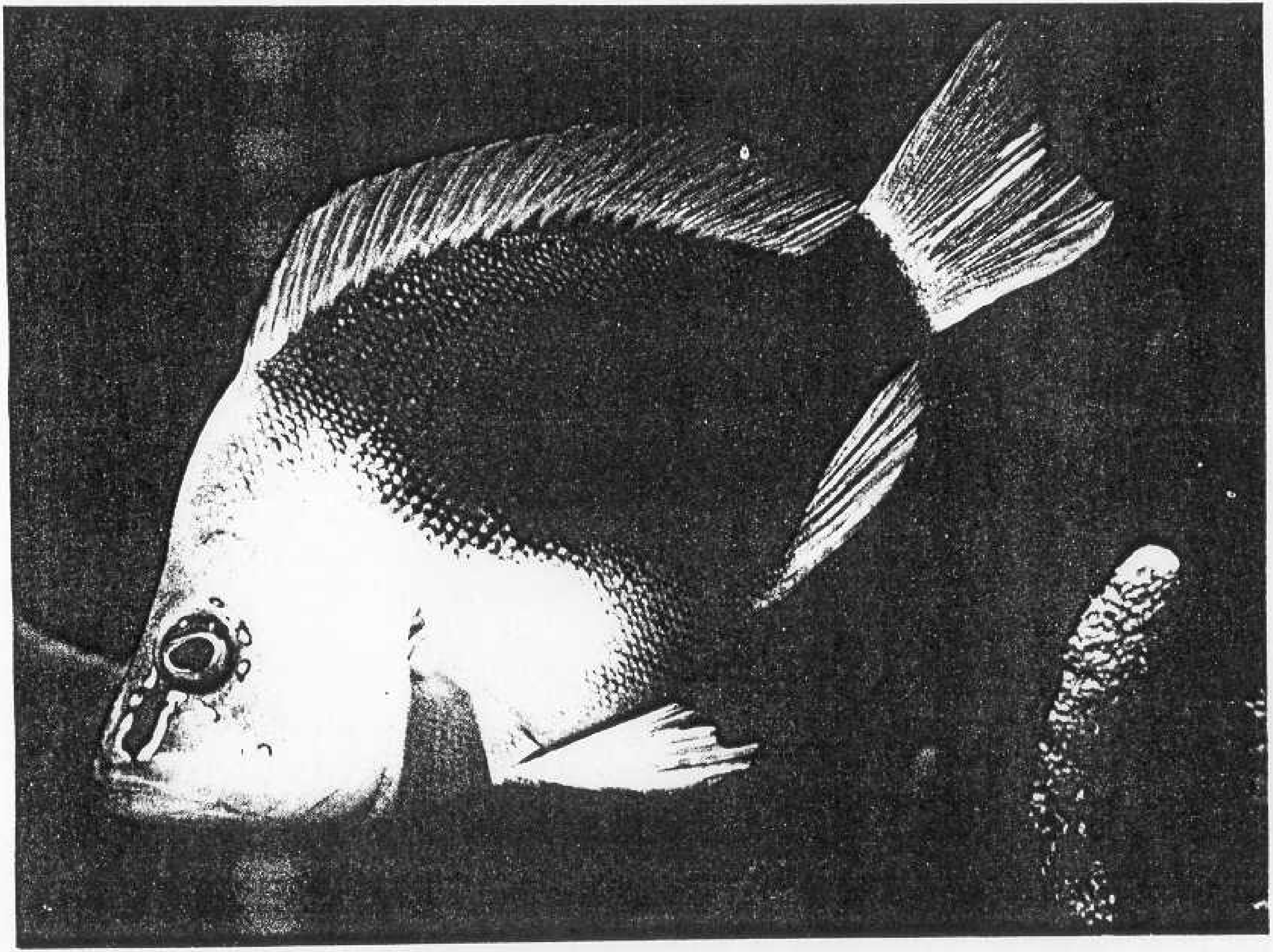

Figure 2a

simultaneous hermaphrodites, and that individuals alternate sexual roles between spawning clasps (Barlow 1975, Fischer 1980a, 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 1980b). Hamlets usually mate assortatively by color pattern, although mixed pairs have been observed, and fish found which exhibit color markings characteristic of two or more color forms (Barlow 1975, Thresher 1978, Graves and Rosenblatt 1980, Fischer 1980a). Thus, the reproductive behavior of hamlets is interesting from several perspectives.

We examined the reproductive behavior of H. guttavarius and its response during spawning to scuba-divers acting like predators. We also compared its spawning behavior with congeners H. chlorurus, H. nigricans, H. pullea, and H. unicolor. To maintain simplicity and clarity, we refer to the various hamlet morphs 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). Fish at this site were observed at 20-30 m depths and since we were saturated, extensive time (approximately 35 hours each) was spent by us here from February 11 to 15, 1980. The second site was located on a few patch reefs in the Buck Island Channel outside the reef at the West Indies Laboratory. Depth here was about 10 m. Observations were made from February

20 to March 3, 1980. Detailed site descriptions are given by Neudecker and Lobel, 1981.

METHODS

Specific H. guttavarius pairs were identified and details of their spawning behavior recorded before, during and after the experiment. Observers selected one pair each evening and positioned themselves unobtrusively on site at least 15 minutes before fish initiated courtship. The baseline spawning behavior of each pair was determined during one or two evenings prior to the disturbance experiment (3 of 7 pairs were observed for two consecutive days previous). 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. Data recorded each time a pair spawned included the time, height in the water relative to the bottom and coral/gorgonian structure over which spawning took place, approximate distance moved between spawning sites and general notes on the pair's response to divers and other species encountered.

The disturbance experiment was conducted the day after baseline spawning behavior was determined. The experiment was to disrupt the spawning act each time fish attempted it. As the pair began to enter into the spawning clasp, the observer swam hard and fast directly at the pair (as one might expect a predator to do). The pair was repeatedly harassed this way for as long as spawning was attempted. When mates parted, close watch was maintained until it was certain spawning had ceased for the night. Follow-up observations were made on the same pair the day after the experiment.

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

RESULTS

Typical Spawning Behavior

Hamlets mate only in pairs. Fertilization is external and zygotes are released into the plankton. During the daytime, mates appear loosely associated in adjacent or nearby home ranges. They begin to interact within 2 hours 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. The displaying individual slowly rises while continuing its display. This individual fades its bright blue flank to a pastel shade. The other fish follows. The two rise together about 1 m above some towering reef structure. At St. Croix, these structures were vertical colonies or the gorgonian, *Pseudoplexura* sp., or the coral *Acropora cervicornis*.

Once the proper height 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. Release of eggs and sperm happens as the fish quiver. Quivering lasts for 2-3 seconds. The individual folded around the other often opens its mouth while quivering (Figure 2b). Following consummation the fish cease embracing and quickly descend to the bottom. The behavior of hamlets embracing when spawning is termed the spawning clasp (Fischer 1980a) and occurs

Figure 2b. *Hypoplectrus guttavarius* embraced in a spawning clasp.

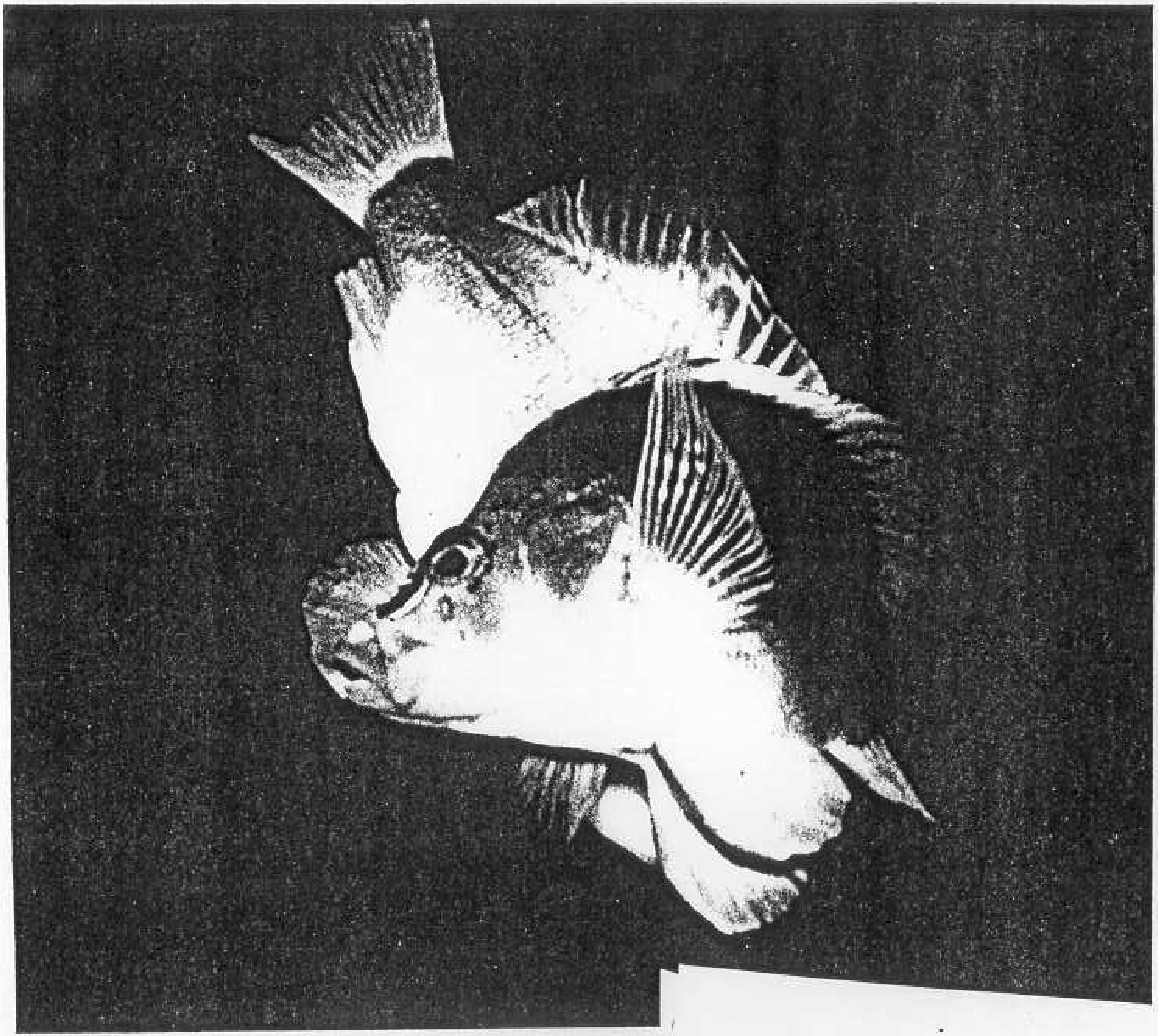

Figure 26

many times an evening. Infrequently, fish would embrace but not quiver and the release of gametes was not evident. Fisher (1980a) has described well the spawning behavior and sexual roles of H. nigricans.

Each hamlet pair initiated spawning at a specific reef location each evening. Pairs had strong spawning site specificity as they moved between a few particular sites each evening. Frequently during an evening, a pair returned to their original site. While 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 spawning observed, only one time was a floater successful in stealing a mate by breaking up another pair (hamlet was H. unicolor).

Diel Reproductive Timing

The hamlet, Hypoplectrus guttavarius, spawned almost every evening. Fish were studied at two sites which differed in depth and timing of spawning. The deep reef site (20-30 m depth) was occupied by us February 11-15, and the shallow site (10 m) during February 20 to March 3. Only on two dates, February 21-22, hamlets did not spawn. 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 did not spawn 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). The first spawning at the deep reef site began 50 min ($\bar{X}$ 33 ± 1) before sunset and the last spawn ended 10 min ($\bar{X}$ 2 ± 9) after sunset with most spawns occurring just prior to sunset. Spawning at the shallow reef site commenced later, 25 min ($\bar{X}$ 16 ± 7) before sunset, and ended later, 20 min ($\bar{X}$ 3 ± 6) after sunset, with most spawns occurring just post sunset (Figure 2c). Reproduction by fish at the two sites did not differ in any other aspect.

Differences in diel reproductive timing at the two depths could be related to 1) different moon phases during the times each group was observed, and/or 2) the difference in depth and corresponding changes in light levels during dusk. Our data do not allow distinguishing between these possible effects.

Effect of Disturbance on Spawning Behavior

The experiment consisted of harassing a hamlet pair by a scuba-diver swimming fast at the fish when they began their spawning clasp. Harassment was repeated throughout the evening spawning period until the fish ceased spawning for the night. When a pair separated, close watch was maintained until it was certain no further spawning would occur that night. Occasionally, a pair would split, swim several meters apart, return several minutes later, rejoin and attempt to spawn again. Each hamlet pair was observed the day prior to the experiment (3 of 7 pairs observed for 2 days prior). All pairs, except one which vanished from site, were also watched on the day after the experiment. As one control, experiments were staggered so that on any given day, different pairs were being watched without interaction or being harassed by pseudopredators.

Unexpectedly, all H. guttavarius persisted in spawning in spite of overt and constant harassment. Pairs attempted twice as many spawning clasps, moved more often between spawning sites and continued for about 25 minutes later than normal (Table 2a). However, the frequency of spawning clasps attempted while harassed and under normal circumstances remained the same at 2 ± 1 per 5 minutes (Table 2a). Two particularly striking effects of pseudopredation on spawning fish were 1) that the pairs changed spawning sites more frequently,

Figure 2c. Diel reproductive timing of *Hypoplectrus guttavarius* at two depths.

and 2) as spawning was continuously disrupted a pair attempted to spawn progressively nearer the substratum. In the end, several pairs were trying to spawn next to the bottom while hidden among coral/gorgonian branches.

Overall, the fish persisted in spawning despite the aggressive behavior of the scuba-divers. However, we have no estimate on 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 pseudopredation experiment had no apparent lasting effects on the fish. The fish's behavior did not markedly differ on the day after the experiment from the day before it (Table 2a).

Other Hamlets Spawning

Four other hamlet species were also observed at the shallow reef site: *H. puella*, *H. chlorurus*, *H. nigricans*, and *H. unicolor*. We never saw mixed mating among hamlet species. Data contrasting aspects of these fishes' reproduction to *H. guttavarius* are presented in Table 2b. Inspection of these data offers some suggestion of differences and similarities in timing and behavior among the hamlets (see Barlow 1975 and Fischer 1980a for more data). 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 hamlet congeners.

DISCUSSION

Many diurnal tropical marine fishes remaining active during the evening crepuscular period risk being eaten by piscivores whose feeding activities generally increase at this time (Hobson 1968, 1972, 1974). This increased

Table 2a. Effects of disturbance on the spawning behavior of *Hypoplectrus guttavarius*

	Baseline before disturbed (7 pairs; 10 observations)	Disturbance experiment (6 pairs)	Day after disturbed (5 pairs)
$\bar{X} \pm S$ no. spawning clasps per day per pair	12 ± 3	25 ± 9	12 ± 2
$\bar{X} \pm S$ no. spawning clasps per 5 min	2 ± 1	2 ± 1	2 ± 1
$\bar{X} \pm S$ no. moves pair made between spawning sites per ten spawns	2 ± 2	5 ± 3	3 ± 2
$\bar{X} \pm S$ min duration of spawning per day	31 ± 8	57 ± 21	28 ± 8
Time ($\bar{X} \pm S$ min) relative to sunset spawning commenced			
shallow group	-16 ± 7 (N = 4)	-24 ± 18 (N = 3)	-11 ± 9 (N = 3)
deep group	-33 ± 1 (N = 6)	- 50 ± 19 (N = 3)	-40 ± 6 (N = 2)
Time ($\bar{X} \pm S$ min) relative to sunset spawning ceased			
shallow group	13 ± 6 (N = 4)	30 ± 9 (N = 3)	12 ± 11 (N = 3)
deep group	-2 ± 9 (N = 6)	10 ± 12 (N = 3)	-4 ± 4 (N = 2)

Note: Data for shallow and deep water groups pooled except when related to sunset time. In addition to above changes, when fish were disturbed they would attempt spawning closer to substrate until nearly on the bottom. Notations in last rows indicate before (-) or after (+) sunset.

Table 2b. Reproductive behavior and timing by other hamlets (*Hypoplectrus* spp.).[a]

	H. puella (N = 2)	*H. unicolor* (N = 2)	*H. chlorurus* (N = 2)	*H. nigricans*[b] (N = 1)
$\bar{X}$ (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 ten 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
Min before sunset spawning commenced	5 + 6	13 + 16	28 + 39	87
Min after sunset spawning ceased	8 + 11	1 + 24	8 + 11	14

[a]These fish observed at 25-30 ft depth, February 25 - March 2, 1980.
[b]See Fischer 1980 for comprehensive spawning data.

threat of predation is reflected in the potential prey's behavior, and most species retreat into shelter, aggregate, or forage closer to the reef (Hobson 1973, 1978). However, many species also periodically spawn at dusk (Lobel 1978, Moyer 1979, Moyer and Nakazano 1978, Pressley in press, Randall 1971, Moyer and Zaiser 1981, Zaiser and Moyer 1981, Neudecker and Lobel 1981). Spawning during the evening crepuscular period is thought to reduce the likelihood of planktonic eggs being eaten since most planktivorous fishes selecting such small prey are generally inactive by this time. Diurnal planktivores consume smaller prey, including eggs, than nocturnal planktivores which infrequently eat eggs (Hobson and Chess 1978). Most egg-eating fishes cease foraging as light levels diminish because low light levels make visual orientation difficult and because predation by piscine predators generally increases at this time (Hobson 1972, 1974, Hobson and Chess 1978). Any planktivores still actively feeding through dusk may also be quickly satiated by the simultaneous spawning of many species.

Spawning during dusk may reduce fish egg mortality by predation but it also increases the potential risk of predation for adult fishes. Hobson (1968, 1972, 1974, 1979) has documented extensive evidence suggesting increased predation by piscine predators on reef fishes exposed or otherwise vulnerable during the crepuscular periods. Fishes are also generally more vulnerable to predation when preoccupied with mating (Johannes 1978).

In this study we wanted to evaluate how a fish would alter its mating pattern when attacked. The results might then provide some insight into the selective pressures molding the reproductive tactics of coastal marine species in the tropics. The best method we could devise to test the possible effect of predation on these fishes was to simulate predator behavior using scuba-divers. Other studies have also considered a fish's response to a human diver to be indicative of reaction to a piscine predator (e.g. Coates 1980). However, the results of this manipulation should be related only tenuously to how the hamlet might respond to a real predator.

The hamlet, Hypoplectrus guttavarius, altered its normal mating behavior when harassed by 1) moving more often to another spawning site, 2) spawning progressively nearer to the bottom in among shelter, and 3) attempting more clasps longer into the night. In no case was spawning terminated early; in fact, the opposite occurred with fish attempting to spawn later. The spawning sites to which the fish moved were all reef structures (gorgonian and coral) taller than the surrounding terrain. It was only after a pair had moved repeatedly that they commenced to spawn nearer the bottom/shelter. Differences in survivorship of the free-floating zygotes when released next to the bottom versus high above the reef were not determinable. Fish which were harassed one day showed no indication of lasting effects the next day.

Spawning above a tall reef structure provides safety for the adults, allowing the fish to mate relatively high in the water column while remaining as close as possible to shelter (Lobel 1978). Spawning high in the water places the free-floating eggs beyond the reach 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 reef fishes have been shaped by the threat of crepuscular predators. If his hypothesis is correct, then it would seem that fishes spawning during evening twilight are not overtly deterred by the potential threat of predation. Put another way, the adaptive advantages favoring zygote survival have been more influential in molding the behavior and timing of reproduction than factors (e.g. predation) affecting survival of the parents during the evening crepuscular period.

ACKNOWLEDGEMENTS

We are grateful for the stimulating conversation and help received from our fellow aquanaut, Williom 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 aided in the field observations. We also received generous support from the West Indies Laboratory, which greatly enhanced this work. This research was funded by a NOAA Hydrolab (NULS 80-1) grant to S. Neudecker and by OPER grant from the Institute of Ecology, U.C. Davis, to Wm. Hamilton, S. Neudecker, and P. Ward.

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APPENDIX A

Personnel

Aquanauts

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Neudecker proposed, organized, and directed the scientific investigations. He sampled the abundance and distribution of chaetodontid and pomacanthid fishes, their foraging patterns, and reproductive behavior. Neudecker also aided in the design and execution of the pseudopredation experiment.

Lobel directed the pseudopredation experiment on *Hypoplectrus guttavarius* and studies of reproductive behavior of other *Hypoplectrus* species.

Hamilton participated in the pseudopredation experiment and was responsible for intra-habitat operations.

Surface Support Crew

Scott Grace
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Denver, Colorado 80218

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Chronology

1 February 1980	Arrived St. Croix, West Indies Lab. Dived Buck Island, and Tague Bay. Practiced research methods.
4 February 1980	Moved to Fell Estate and began NULS training.
9 February 1980	Mission began. Made 37 man-dives.
16 February 1980	End saturation.
18 February 1980	Moved back to WIL. Continued observations and experiments on Buck Island Patch Reefs and at Salt River Canyon.
4 March 1980	Departed St. Croix.

Facilities

Water conditions (general and extremes) and impact on operations:
Water temperature averaged 79°F.
Visibility changed almost hourly from 20 to 130 feet but never hampered our observations.

Biomedical problems during or after operations:
Some foot sores due to fin chafing (Lobel).
Some internal chest and stomach pain on days two and three (Hamilton and Lobel).
Some biogas (Hamilton).

Safety problems or concerns during operations:
Surface support voiced some concern over the closeness of buddies. When three aquanauts dive, this problem is somewhat unavoidable, especially when behavioral follows are being done. We tried hard to always have a buddy close to the least experienced diver.

Management or personnel problems:
None. This mission went very smoothly.

Logistics or support problems:
None. All tank and camera drops were well executed and on time.

Recommendations:

After aquanauts have been trained they should be allowed two or three days diving before saturation in order to survey study sites and test equipment and methods. Our mission was delayed a few days for several reasons, but we found this to be helpful.

Refurbishing the habitat, including the addition of shelves above the counter, has greatly improved space utilization. Still, there is a lot of unused space in the habitat because of its cylindrical shape and in the submarine escape tube. Consequently, we suggest providing four to five expanding storage nets that are commonly used in sailboats. They could be attached with shock cords and small carabiners (clips).

It would also be useful to string a curtain line on the ceiling parallel to the bunks, so that sleeping aquanauts could be isolated from the person on watch.

We suggest installation of a stereo cassette system, with headphones, in part d (below). Aquanauts could bring a few favorite tapes and find habitat life more pleasant and productive.

Information on Scientific and Diver Equipment

Scientific and/or Diver Equipment	General Suitability (P,F,G,VG)	Limitations, Failures, or Operational Problems Noted During Mission	Recommendations for Corrective Action or Improvement
Underwater slates	G	Dulls pencil points quickly.	Provide Ogden slates to researchers who need them.
Ogden slate	VG	None	
Manni-hose	VG	Not a run	Add additional warmth and make it easier to don wetsuits.
Danskin leotards	VG	None	Same as above.
Coverall style wetsuit w/o zippers in sleever or legs	VG	None	None
Conventional jacket, pants	F	Zipper problems	Teflon or plastic zippers.
Cassette tape deck and headphone music system	VG	None	We feel that music is essential for happiness in the habitat and to allow the person on watch to stay awake. NOAA should install such a system in the habitat.
NULS Hydro 35 camera housing, Nikon F, 2003 strobe serviced and delivered by surface	Excellent	None	Keep up the good work. This system allowed us much more more time to concentrate on science, not cameras.

Scientific and/or Diver Equipment	General Suitability (P,F,G,VG)	Limitations, Failures, or Operational Problems Noted During Mission	Recommendations for Corrective Action or Improvement
Nikon F with motor drive	Excellent	None	Exposure rate is limited to flash rate, but lack of rewinding facilitates concentration and yields better photos.
ACR Signal Strobes	VG	None	See below.

During a night dive early in our mission, we made an impromptu measure of emergency response time. Neudecker and Lobel completed photographic work well beyond the excursion limit line and wished to surface the bulky gear. A single ACR strobe was activated and a support diver reached the aquanaut in less than two minutes. That experience was reassuring to both the aquanauts and surface support and helped to bolster team spirit.

APPENDIX B

Excursion Log -- All Aquanauts

	Divers	Date	Out	In	Neudecker	Δ	Δ-Neudecker	Max	Y Depth	Location
1	S.P.B	09F80	1653	1955	1955	182	192	105'	65'	W
2	S,P,B	10F80	0600	0726	0741	86	101	110'	65'	W
3	S,P,B	10F80	1701	1920	1930	139	149	110'	65'	W
4	S,P,B	11F80	0530	0750	0800	140	150	110'	60'	E
5	S,P,B	11F80	1615	1957	2007	222	232	120'	60'	E
6	S,P,B	12F80	0530	0841	0856	191	206	135'	80'	E
7	S,P,B	12F80	1710	1928	1936	138	148	110'	60'	E
8	S,P	13F80	1002	1217	1224	149	156	150'	80'	E
9	S,P,B	13F80	1706	1911	1931	136	145	110'	70'	E
10	S,P,B	14F80	0947	1217	1227	140	150	110'	65'	W
11	S,P,B	14F80	1637	1917	1937	160	180	90'	60'	E
12	S,P	15F80	0954	1157	1200	123	126	125'	70'	W
13	S,P,B	15F80	1615	1905	1915	180	180	110'	65'	E

Summary of Aquanaut Excursions

	Hamilton	Lobel	Neudecker
Number of excursions	11	13	13
Total Time			
(min)	1704	2060	2115
(hrs)	28.4	34.3	35.5
Mean excursion time			
(Y ± 5 min)	154 ± 36	158 ± 35	163 ± 35
(Y hrs)	2.58	2.64	2.71
Range of excursion time	1.43-3.70	1.60-3.75	1.68-3.87