MATING SYSTEMS OF CARIBBEAN CHAETODONTID
AND POMACANTHID FISHES

STEVE NEUDECKER

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

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Steve Neudecker, Principal Investigator
Institute of Ecology
Division of Environmental Studies
University of California
Davis, California 95616

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

William J. Hamilton, III
Institute of Ecology
Division of Environmental Studies
University of California
Davis, CA 95616

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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.

Mating Systems of Chaetodontid and Pomacanthid Fishes at St. Croix

INTRODUCTION

Unlike other vertebrates which are generally gonochoristic (having separate sexes), teleost fishes exhibit a complete range of hermaphroditic characteristics (protandry, protogyny, and synchronous hermaphroditism). For fishes hermaphroditism appears to be the predominant sexual mode (Atz 1964, Reinboth 1970, Smith 1975).

While reproductive behavior and mating systems of coral reef fishes, in particular, are poorly known, families on which data exist (Labridae: Robertson 1972, Warner, Robertson and Leigh 1975, and Robertson and Hoffman 1977; Pomacentridae: Moyer and Bell 1976, Ross 1978; Scaridae: Choat and Robertson 1975, and Warner and Downs 1977) reveal variable patterns of sequential hermaphroditism.

Our current knowledge of pomacanthid (angelfishes) spawning behavior comes from field observations of Centropyge species in Hawaii (Lobel 1978) and Japan (Moyer and Nakazono 1978) and from aquaria observations of Genicanthus species in Taiwan (Shen and Liu 1976) and Japan (Suzuki, Hioki, Tanaka and Iwasa 1979). That research indicates that species of Centropyge and Genicanthus spawn planktonic eggs at sunset and exhibit harem polygyny as well as protogynous hermaphroditism. The largest individual of a group is a single male, and is dominant over the females (Lobel 1978, Moyer and Nakazono 1978). Adults remain at a particular site for life where they breed and feed. Upon death or removal of the male, the largest or dominant female changes sex to take his place (Moyer and Nakazona 1978, C.F. Robertson 1972). There is no published information on reproductive behavior or mating systems of the remaining five pomacanthid genera (Apolemichtys, Chaetodontoplus, Holacanthus, Pomacanthus and Pygoplites) or of any western Atlantic pomacanthids.

Pomacanthid fishes occur as solitary individuals or in pairs and exhibit three basic foraging patterns. Large species such as those of <u>Holacanthus</u> and <u>Pomacanthus</u> are benthic carnivores and feed primarily on sponges, but sometimes take ascidians, fish eggs, gorgonians and zooantharians (Randall and Hartman 1968, Hobson 1974, pers. obs.). Smaller species, particularly of <u>Centropyge</u>, are herbivores (Hiatt and Strasbourg 1960, Hobson 1974, Randall 1967). The third foraging pattern is displayed by <u>Genicanthus</u> species which are planktivores and take pelagic ascidians in midwater, supplemented by some benthic invertebrates (Shen and Liu 1976, Allen 1980). Since food resource distribution is probably a critical parameter influencing mating systems (Verner and Willson 1966, Robertson and Hoffman 1977), and our current knowledge of pomacanthid reproduction is based on the herbivorous and planktivorous genera, it is not clear whether the larger benthic feeding genera should exhibit similar mating systems or not.

Reproductive behavior of chaetodontids (butterflyfishes) is known only from ancillary observations of three species in Hawaii (Lobel 1978) and from aquarium observations in Japan (Suzuki, Tanaka and Hioki 1980). However, considerable work has been done on chaetodontid social behavior (Reese 1973, 1975, 1977; Ehrlich, Talbot, Russell and Anderson 1977), and foraging patterns (Hiatt and Strassburg 1960, Hobson 1975, Neudecker 1977, 1979, Birkeland and Neudecker 1981). From these reports it appears that several species of butterflyfishes are monogamous and may therefore be an exception to the prevalent pattern of coral reef fish hermaphroditism.

Most chaetodontids are diurnal carnivores that exhibit three main foraging patterns: corallivores, benthic omnivores, and planktivores. Many <u>Chaetodon</u> species are corallivores (Reese 1977, Neudecker 1977) and have been further classified as grazers, browsers and corallum feeders (Neudecker 1979). It has

been suggested that chaetodontid species diversity and the relative number of corallivores increases with scleractinian coral diversity across the Pacific (Reese 1977). Remaining Chaetodon species are omnivores that prey on corals, crustaceans, fish eggs, gorgonians, polychaetes and zooanthids (Hiatt and Strasburg 1960, Hobson 1975). Dietary generalization has been compared to prey abundance for two such omnivores in the Caribbean (Birkeland and Neudecker 1981). Finally, the genera Hemitaurichtys and Heniochus feed on plankton in midwater (Hobson 1974, Allen 1980:327). Since adult chaetodontids appear to remain on one home-range reef for life (Reese 1973, Neudecker pers. obs.) and feed on benthic prey, their mates, food, and shelter are potentially defensible.

Although chaetodontids and pomacanthids were once classified as the same family, they are not close phylogenetically (Friehofer 1963, Burgess 1974). They are similar reproductively in that they spawn planktonic eggs up, away from the reef at dusk. Because of their ecological similarities as well as their potential differences in reproduction (monogamy versus polygyny), we compared the reproductive behavior and mating systems of two Caribbean chaetodontids (Chaetodon aculeatus and C. capistratus) and three pomacanthids (particularly Holacanthus tricolor, and incidentally Pomacanthus arcuatus and P. paru) at St. Croix, US Virgin Islands.

MATERIALS AND METHODS

Data Sources

Five sources of data are the basis for our analyses: 1) Observations during National Undersea Laboratory System (NULS) Mission 78-1 in May and June

1978 during 13 scuba excursions (38 h by SN) from underwater habitat Hydrolab at St. Croix, U.S. Virgin Islands; 2) Most observations reported herein were made during NULS Mission 80-1 (February-March 1980) in 13 scuba excursions (70 h for two aquanauts); 3) Forty hours of observations were made on Buck Island Channel Patch Reefs after Mission 80-1 at St. Croix; 4) Data on sexual dimorphism of chaetodontid and pomacanthid fishes were taken from museum specimens loaned by the Academy of Natural Sciences of Philadelphia; and 5) from data provided by the Museum of the University of Miami Rosenstiel School of Marine and Atmospheric Sciences.

Study Site Descriptions

Salt River Canyon. The Hydrolab is located on a sand bottom in 15.5 m of water about 30 m north of the barrier reef fronting Salt River Estuary and about 5 m west of the eastern slope. Salt River Submarine Canyon cuts north-northwest for 450 m across the narrow St. Croix shelf and continues downward to a depth of 3500 m, where it joins the Christiansted Canyon (West Indies Laboratory 1979).

Observations in Salt River Canyon were made at four 100 m transect lines established in 1978 along the 15 and 30 m isobaths on the east slope and west wall, described by Birkeland and Neudecker (1981), and at a submarine buttress in 18 m of water on the east slope. Sample transects began at the excursion limit line, about 215 m from the habitat, and extended 100 m seaward along each side of the canyon.

The west wall of the canyon is steep to vertical in many places, and has some overhangs and caves. Scleractinian corals are more prevalent on the west wall at both 15 and 30 m than on the eastern slope at either depth (Birkeland and Neudecker 1981). Most coral species are more abundant at 15 m at both

locations, except _Agaricia_ which is more prevalent at 30 m (Birkeland and Neudecker 1981).

The eastern slope is characterized by a gentle slope of 15-20 degrees and has more unconsolidated sediments. Rounded coral cobbles blanketed by a layer of carbonate sand are the substratum and form sediment trails running down to the canyon floor. Gorgonaceans are more common on the eastern slope at both depths and corals are less abundant than on the west wall. Most spawning observations were made on a buttress near the eastern slope tank drop and emergency way station in 18 m of water. The buttress extends up and outward from the slope and drops vertically on the seaward side to the canyon floor at about 30 m. Many species of fishes were observed spawning at or near this promontory.

Patch Reefs. The three Buck Island Channel patch reefs are located between St. Croix and Buck Island. These reefs are about 2 km north of Coakley Bay and about 700 m west of Buck Island. The reefs are between 7 and 11 m deep and are predominated by _Acropora cervicornis_ coral and _Pseudoplexaura_ gorgonians. These reefs range from 100 to 200 m^2 and are bordered by sand.

Observation Techniques

Observers positioned themselves on site about one hour before sunset so that fish were not disturbed by the sudden appearance of a diver, and the entire spawning event could be observed. For _Chaetodon capistratus_, pairs were followed within their home range to their breeding site. Individual _C. aculeatus_ were observed in their home range and followed. Males of _Holacanthus tricolor_ were observed in their territories with their females.

Times reported here are Eastern Standard Time. Configurations of the moon and times of sunset for St. Croix were obtained from the 1980 American Ephemeris and Nautical Almanac (U.S. Government 1979).

RESULTS

Chaetodon capistratus

General Ecology. Chaetodon capistratus is abundant on reefs throughout the western Atlantic, and in Salt River Canyon exhibited a mean abundance of 2.2 ± 1.6 individuals per 200 m^2. On average, this species accounted for 47 percent of all chaetodontid and pomacanthid fishes counted (Table 1a). C. capistratus is a browser of anthozoans and prefers hexacorals, especially scleractinians, over octocorals and antipatharians (Birkeland and Neudecker 1981). This butterflyfish occurs mostly in pairs (Table 1b) which forage and rest in specific home ranges.

Courtship and Mating. Reproductive behavior of C. capistratus was studied at Salt River Canyon at depths between 15 and 20 m, and at the Channel patch reefs in 10 m of water. Spawning behavior of nine C. capistratus pairs was recorded during the dusk crepuscular period of six evenings (Fig. 1a). No spawning of any chaetodontid or pomacanthid fishes was observed at any time but sunset during our observations at all times of day and night. Seven spawns of C. capistratus were within four days of the full moon, and two were witin nine days prior to the full moon. Courtship behavior did not culminate in spawning on five occasions during other phases of the moon. On nights when spawning occurred, foraging rate began decreasing about 45 min prior to sunset when

Table 1a. Abundance and distribution of chaetodontid and pomacanthid fishes and surface areas of major resource groups at Salt River Canyon in 1978. Fishes were repeatedly quantified by counting all individuals within 1 m to either side of and within 2 m above 100 m transect lines (sample area = 200 m^2 or 400 m^3). Data are presented as average percentage of total number of chaetodontid and pomacanthid fishes at each transect.

Fishes (percent of total)	West Wall		East Slope	
	15 m	30 m	15 m	30 m
Chaetodontidae				
Chaetodon aculeatus	15	38	9	31
C. capistratus	67	26	63	31
Pomacanthidae				
Holacanthus ciliaris	2	0	0	0
H. tricolor	9	30	9	0
Pomacanthus arcuatus	7	6	19	38
$\bar{X} \pm S$ Number of fishes	7.9 ± 2.4	5.9 ± 1.8	3.6 ± 1.8	3.3 ± 2.1
Resources % (N)				
Plexaurids	44 (22)	4 (4)	84 (75)	80 (75)
Scleractinians	20 (263)	33 (41)	13 (122)	>1 (16)
Sponges	1 (27)	5 (15)	>1 (7)	1 (12)
Antipatharians	29 (2)	55 (26)	0	15 (7)
Percent of Total	92	97	98	97

Figure 1a. Spawning observations of butterfly and angelfishes at St. Croix. Timing relative to sunset (solid line) and lunar phase. Spawning by all species (N = 3 spp., 19 ind.) before sunset 3 ± 8 min ($\bar{X} \pm S$).

LUNAR PHASE
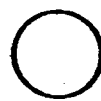
SPAWNINGS :
CHAETODON ACULEATUS △
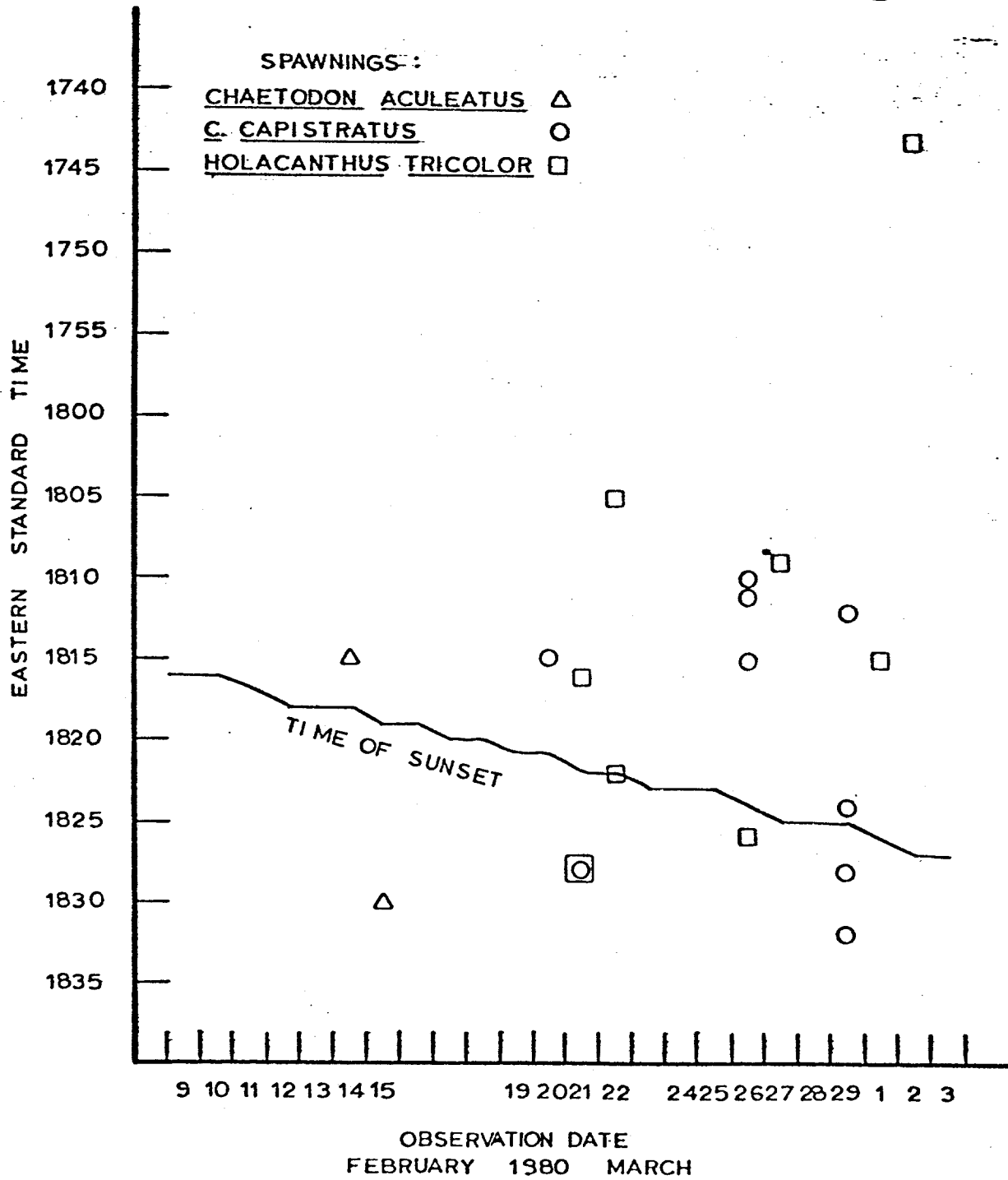C. CAPISTRATUS ○
HOLACANTHUS TRICOLOR ☐

EASTERN STANDARD TIME

1740
1745
1750
1755
1800
1805
1810
1815
1820
1825
1830
1835

TIME OF SUNSET

9 10 11 12 13 14 15   19 20 21 22   24 25 26 27 28 29 1 2 3

OBSERVATION DATE
FEBRUARY   1980   MARCH

males began swimming closely behind their females. Periodically, the pair swam up from the bottom and presented a coordination display by orienting parallel to one another while erecting all fins as if to increase apparent size.

All observations of spawning were above a tall, conspicuous reef feature such as the gorgonian Pseudoplexaura, or the coral Acropora cervicornis. Close circling, or carrouselling (Reese 1975) began as soon as the female swam above the spawning structure. The male nudged the female's anal/abdominal region with his snout which led to almost instantaneous positioning of her above him. The female's head was pointed upward at about a 20° angle and sometimes she listed to the side. Males remained below and/or to the side of the female while both fish quivered as gametes were released. Depending upon the observer's orientation to light, sperm could be seen as a small white cloud. A pair spawned only once per evening. Immediately after spawning, the pair darted back down to the reef substratum. Combined duration of courtship and spawning was 2-6 min. Both sexes varied the intensity of their coloration while courting and mating. On three occasions, changes into nocturnal coloration occurred within 10 min after sunset. This coloration included a blanching of the eye mask, a white ring around the eye, and a dark dorso-ventral band about 1.5 cm wide just behind the pectoral fins.

Although C. capistratus is usually seen in pairs (Table 1b) we observed pairs break up and reform with other individuals one evening when there was no spawning. At the full moon on 1 March 1980, two observers devoted the entire observation period to following two particular pairs and recording all reproductive behavior. Lights were not needed since the reef was well illuminated by the full moon. Neither observer was able to stay with both pair members since they split up and reformed several times. Pairs began courtship with the coordination display but no carouselling or spawning occurred.

Table 1b. Grouping patterns of chaetodontid and pomacanthid fishes in Salt River Canyon. Chaetodontid group status was recorded with foraging observations whereas pomacanthid patterns were noted during transect counts. Groups are composed of three or more individuals.

	Solitary (N)	Paired (N)	Grouped (N)
Chaetodontidae			
Chaetodon aculeatus	91% (61)	8% (6)	0
C. capistratus	15% (13)	75% (64)	10% (8)
Pomacanthidae			
Holacanthus ciliaris	100% (5)	0	0
H. tricolor	100% (46)	0	0
Pomacanthus arcuatus	43% (6)	57% (8)	0
P. paru	0	100% (4)	0

Solitary individuals would display to a paired female and several times the female left her mate and joined the interloper. In other instances, the intruder was chased away (see Agonistic Behavior).

Agonistic Behavior. Three times unpaired males attempted to court a paired female and were invariably chased away by the paired male. Some attacks were preceded by the paired male returning the parallel display. A more typical agonistic encounter occurred between two pairs during the spawning period on five occasions. As a pair moved about their home range prior to spawning they encountered conspecific pairs, presumably near range boundaries, but also at specific spawning sites near towering structures. Since females usually lead the pair, she would be the first to encounter the second pair. Fin-erect lateral displays would be exchanged before members of the pair attempted to chase away the interloper(s). It appeared that, generally, the pair with the largest individuals won these fights.

Size Dimorphism. Specimens collected from both sides of Salt River Canyon in 1978 for stomach content analyses (Birkeland and Neudecker 1981) were also sexed and measured. Size dimorphism was calculated and additional data were acquired from museum specimens collected throughout the western Atlantic (Table 3).

Males of C. capistratus tend to be slightly larger than females (Table 1c). Chaetodon species occur mostly as male-female pairs of individuals of approximately equal size (Reese 1975, pers. obs.). Because pairs appear to be permanent and remain in one area of the reef for life (Reese 1973, 1975), we suspect that individuals pair while small and grow at similar rates. Consequently, when fishes are collected indiscriminately, and not in pairs, some females are larger than males, resulting from different ages or growth rates

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Table 1c. Size dimorphism of Caribbean chaetodontid and pomacanthid fishes. Since pairs or harems were seldom collected together, we lumped individuals by sex and compared mean sizes for local dimorphism. Mean species dimorphism was calculated as the average of local populations. Salt River Canyon collections were made in 1978. Other data was taken from museum collections provided by (1) James E. Böhlke, Chairman and Curator of Icthyology, Academy of Natural Sciences of Philadelphia and (2) David J. Gordon, University of Miami, School of Marine and Atmospheric Sciences.

	Collection Sites	Males $\bar{X} \pm S$ (N) SL (mm)	Females $\bar{X} \pm S$ (N) SL	Local Size Dimorphism	Species $\bar{X} \pm S$ Size Dimorphism
Chaetodontidae					
Chaetodon aculeatus	Salt River	67 ± 2 (8)	64 ± 2 (4)	1.05	
	Bermuda, Grand Cayman, Jamaica[1]	73 ± 6 (3)	72 ± 9 (3)	1.01	1.07 ± 0.07
	Florida, Bahamas, Columbia[2]	57 ± 11 (6)	50 ± 4 (9)	1.14	
C. capistratus	Salt River	91 ± 6 (3)	86 ± 9 (4)	1.06	
	Santa Catalina, Columbia Fortune Island, Bahamas[1]	55 (1)	57 ± 13 (2)	0.96	1.03 ± 0.06
	Florida, St. John, British Honduras, Bahamas, Puerto Rico[2]	78 ± 3 (4)	76 ± 7 (10)	1.06	
Pomacanthidae					
Holacanthus tricolor	Salt River	152 ± 32 (2)	111 ± 10 (4)	1.37	
	St. Lucia, St. Vincent, Bahamas, Cuba, Bermuda[1]	156 ± 32 (3)	104 ± 21 (10)	1.50	1.44 ± 0.07
	Florida, St. John[2]	135 ± 23 (10)	92 ± 27 (13)	1.44	

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between pairs. Growth rates and pair size may also be related to habitat food abundance and quality which is partly reflected by geographical variance in size dimorphism (Table 1c).

Chaetodon aculeatus

General Ecology. Foraging patterns and behavior of Chaetodon (Prognathodes) aculeatus in Salt River Canyon are reported elsewhere (Birkeland and Neudecker 1981). This species is a predator of polychaetes, especially serpulid worms, crustaceans, and fish eggs for which they forage on the undersurfaces of corals, on sponges, and from algal turf. C. aculeatus occurs solitarily (Table 1b) which forage and remain inactive at night in a specific home range. The mean abundance of C. aculeatus for counts taken in 1978 was 1.2 ± 0.8 individuals per 200 m^2, which accounted for 23 ± 14 percent of chaetodontid and pomacanthid fishes.

Courtship and Mating. Spawning behavior of Chaetodon aculeatus was observed twice in Salt River Submarine Canyon and courtship without spawning was observed on three occasions. Both spawning events climaxed within 15 min of sunset during a new moon period (Fig. 1a). Spawning was observed on 13 and 15 February 1980, a period of new moon, and did not occur on 20-22 February, during the moon's first quarter, nor after the full moon on 3 March 1980. Mates maintained adjacent home ranges and met at the same spawning site each evening before sunset. We judged the sexes of individuals by their reproductive role.

The male swam into his mate's home range about 40 min before sunset. All spawning activity began and climaxed above a large black coral (Antipathes) colony which grew up and outward over a large buttress at 18 m on the eastern

slope. Upon meeting each evening, the pair performed a coordination display by orienting side-by-side and erecting all fins. This was followed by parallel swimming for one to two minutes. This same coordination display occurred on several nights when reproduction did not occur. One evening the pair sporadically fed upon the Antipathes colony while swimming around it. Whenever the pair was separated by more than two meters, they displayed when they rejoined. On evenings when spawning occurred, the female was noticeably swollen with roe.

Courtship lasted between 10 and 15 min and parallel swimming gradually escalated into carouselling, with the female in front and the male close behind. The male approached the female from below and nudged her abdomen with his snout and, while carrouselling, the pair ascended to less than a meter above the Antipathes colony. The female stopped in the water column and oriented her head upward at about a 20° angle. The male swam underneath her at a similar angle and both fish quivered for about one second while releasing eggs and sperm. On each occasion the pair spawned only once. The pair separated after releasing gametes and returned to their respective home ranges. The female rested in her area near the bottom among Montasrea corals.

Size Dimorphism. Males of C. aculeatus tend to be seven percent larger than females (Table 1c). The greater dimorphism of C. aculeatus than C. capistratus may partly result from the weaker association of pair members. Males initiate courtship and larger size may be critical for this function.

Holacanthus tricolor

General Ecology. H. tricolor is the most abundant pomacanthid in Salt River Canyon (1.2 ± 0.8 individuals/200 m^2) and accounted for 12 ± 13 percent

of sampled fishes. Dispersed groups of individuals remained in a specific territory for the duration of each of our observations. Groups consisted of one large individual and 3-4 smaller ones, but individuals foraged solitarily (Table 1a) primarily on sponges (Randall and Hartman 1968) in territories which are defended by a large male. During 5-min foraging observations (1978), H. tricolor fed on sponges (e.g. Callyspongia, Verongia, 76 percent of all bites) and in the algal turf (21 percent of bites) at a mean foraging rate of 10 ± 5 bites/ 5 min (range 5-19, N = 6). Stomach content analysis showed mean percent of diet volumes as 98.25% sponge and 1.75% algae (N = 6).

Courtship and Mating. Spawning of H. tricolor was observed four times at Salt River Canyon and four times at patch reefs. All spawns occurred within eight days prior to full moon (Fig. 1a). H. tricolor is polygynous, as are some Pacific pomacanthids (Lobel 1978, Moyer and Nakazona 1978). Entire spawning sequences (dominant male and all females) were observed twice. As a result our data tend to underestimate total spawns per evening per male. Six spawns climaxed less than 16 min before sunset ($\overline{X}$ = 11 ± 7 min), and the remainder climaxed less than 7 min after sunset.

Males of H. tricolor are significantly larger than females (Fig. 1b) and during spawning one male was accompanied by 2-4 females which lived in his territory.

About 35 min prior to sunset the large male began to swim around his territory and display to females. The male approached females in an undulating manner by rolling back and forth on his side and presenting lateral displays with erect fins. One male appeared to visit all females in his territory while making his way to a spawning site. In many cases these towers were the largest colonies of the gorgonian Pseudoplexaura in the territory. The male then began to court a single female with additional listing and lateral displays and by

Figure 1b. <u>Holacanthus</u> <u>tricolor</u> mating. The male is the larger fish on the right. The male nudges the female with his snout against her lower abdomen. The male's head color darkens during spawning.

swimming in ascending circles above her. If the female did not ascend up over the tower, the male returned to her and continued to display. Usually this courtship included false spawns, in which the female moved up over the tower but then darted back to the substratum when the male attempted to position himself beneath her. In these cases the male followed the female and continued his courting. Once above the structure, and ready to spawn, the female allowed the male below her and he nudged her in the anal and abdominal regions with his mouth and forehead while pushing her upward until the pair was 0.5-1 m above the tower. While spawning, the female remained nearly perpendicular to the bottom, and the male stayed below her with his head upward at about a 50° angle (Fig. 1b). Both fish quivered while releasing their gametes. Immediately after spawning the fish darted back to the bottom; sometimes the female then chased the male. Females spawned only once but the male spawned with two or more females each evening.

Sexual Dimorphism. Males of H. tricolor average 44 percent larger than females (Fig. 1b, Table 1c). Within any single harem the male was the largest individual. There were no males smaller than 93 mm and most were larger than 120 mm. A few females were larger than 120 mm (5 of 37) but the vast majority (32 of 37) were smaller than 100 mm.

Pomacanthus arcuatus and P. paru

Courtship. Our observations of P. arcuatus and P. paru in Salt River Canyon (Table 1a) show that both species sometimes occur as pairs although more strongly for P. paru. The fewer number of P. arcuatus pairs is probably a reflection of the distance paired individuals maintain and the resolution of our transect counts (> 2 m would be scored as solitary). However, our

observations throughout the Caribbean indicate that adults of both species occur as pairs which are closely matched in size.

On several occasions during dusk in Salt River Canyon, when chaetodontids and Holcanthus tricolor were spawning, courtship behavior of Pomacanthus arcuatus and P. paru was also observed, although spawning was not. The same general pattern of courtship behavior was exhibited by both species.

Between 30 min before and 10 min after sunset, on several nights, a pair of each species was observed as they swam back and forth along our 100 m transect at 20 m. Individuals of these pairs were nearly equal in size and remained close together as they swam parallel to each other. Several times one of the pair listed over to one side and swam nearly perpendicular to its mate, exposing its ventral surface. These courting passes took place about 5 m above the bottom and were not oriented above any particular topographical feature. The distance covered during these swims was greater than 100 m, the length of our transect. As a result of these observations, we suspect that Pomacanthus arcuatus and P. paru spawn near sunset during evenings preceding the full moon.

DISCUSSION

Abundance and distribution of fishes and their prey

Abundance of C. capistratus is positively correlated with relative coral cover (Table 1a, r^2 = 0.95, p < 0.05) and that of H. tricolor is positively correlated with amount of sponge surface area (r^2 = 0.90, p < 0.05). Abundance of C. aculeatus is also probably related to prey availability but is not demonstrated by our data because their small, elusive prey were not adequately sampled (Birkeland and Neudecker 1981). However, it seems possible that more

prey and shelter sites were available to C. aculeatus on the west wall as a result of its greater structural complexity; significantly more fish of this species occurred on the west wall than on the east slope.

Throughout Salt River Canyon corals are much more abundant in colony number and surface area than sponges (Table 1a). The most abundant coral, Agaricia, forms continuous tabular colonies, whereas sponges occur as large, discrete colonies such as the tubular Callyspongia or the vasiform Verongia. C. capistratus, a corralivore, is the most abundant species of chaetodontid and pomacanthid fishes, and is much more abundant than the sponge feeder H. tricolor (Table 1a). The relationships of abundance suggest that H. tricolor territories could vary in quality and that they should be larger than home ranges maintained by C. capistratus. As a result of relative scarcity of sponges and their discontinuous distribution, H. tricolor males can defend these limited food resources. This facilitates polygyny because it makes it advantageous for females to share high quality territories (Orians 1969).

Disclaimer

In the following discussions we consider the evolution of monogamy and polygyny in these fishes, which spawn planktonic eggs and exhibit no parental care. We feel that a different set of selective pressures are responsible for mating system evolution in fishes which are viviparous or lay benthic eggs. Patterns of parental care influences development of mating systems (Perrone and Zaret 1979, Wittenberger and Tilson 1980) and we divorce our arguments from theirs. Relative comparisons can be made with acanthurids, labrids, and scarids.

Social Groups

We call <u>C</u>. <u>aculeatus</u> and <u>C</u>. <u>capistratus</u> home ranging species (Reese 1973, 1975) because we have seen no defense of their feeding areas during the day. Observations of <u>C</u>. <u>capistratus</u> attacked and chased by damselfishes are abundant, but the butterflyfish simply moves on. In fact, territorial behavior is atypical for chaetodontids since it has been reported in only 4 of 93 extant species. The territorial species, <u>C</u>. <u>baronessa</u> and <u>C</u>. <u>trifascialis</u> (Reese 1973, 1975), <u>C</u>. <u>fascialis</u> (Fricke 1966), and <u>C</u>. <u>larvatus</u> (Allen 1980:193), defend small reef areas, often a single coral head (Reese 1975). We did observe conspecific aggression during spawning and over resting sites (cf. Ehrlich <u>et al</u>. 1977). Pomacanthids are more typically aggressive and territorial (Lobel 1978, Moyer and Nakazona 1978, Allen 1980:246).

Foraging patterns, prey distribution and abundance exert considerable influence on social behavior in these fishes. <u>C</u>. <u>capistratus</u> forms permanent pairs as suggested by the fact that 75 percent of all individuals observed were paired (Table 1b). Pairs fed only within their respective home ranges, generally remained within 0.5 m of each other, but rarely fed upon the same coral simultaneously. Foraging in pairs has less effect on feeding efficiency when sessile organisms are browsed because escape from predators is more difficult. In contrast, 91 percent of <u>C</u>. <u>aculeatus</u> foraged solitarily (Table 1b). Increased efficiency from solitary hunting of cryptic, motile crustaceans and prey with effective predator avoidance mechanisms may outweigh benefits of permanent pairing. An analogy can be made to the foraging group patterns of two bushbabies, <u>Galago</u> <u>senegalensis</u> and <u>G</u>. <u>crassicaudatus</u>, which are determined by prey types. <u>G</u>. <u>senegalensis</u> rests diurnally in pairs and hunts solitarily at night for elusive insects, whereas <u>G</u>. <u>crassicaudatus</u>

maintains permanent family groups diurnally and while nocturnally foraging for fruit and gum (Bearder and Doyle 1974, Clutton-Brock and Harvey 1977).

Evolution of Chaetodontid Monogamy

We have related foraging patterns and fish abundance to resource abundance and distribution. Reproduction would not be possible without adequate food, consequently considerations of the biology and distribution of prey may supercede reproductive concerns. Thus the lack of diurnal pair formation by C. aculeatus results from foraging constraints imposed by elusive prey. However, relaxation of this constraint does not, in itself, explain permanent pair formation in C. capistratus.

Acanthurids which defend permanent feeding territories form long term pairs, whereas species exhibiting weak, intermittent territoriality do not (Robertson, Polunin and Leighton 1979). Caribbean chaetodontids are not territorial, perhaps partly because there are few other piscine corallivores. However, most Caribbean species of Chaetodon do form permanent pairs and maintain exclusive use of home ranges, even though they seldom aggressively defend them.

Relative costs of pair formation may be lower than those imposed on solitary individuals because of (1) ever ready sexual access, (2) less exposure to predators or increased defense, (3) maintenance of home range resources. Constant mate availability within a home range avoids increasing the risk of predation during mate location and of home range usurpation while gone. Pair formation could also socially reduce predation risk through numbers (Hamilton 1971) or defense (Vine 1971). However, these social mechanisms appear to have little effect on pair formation, since costs would be even lower with larger group sizes, which are uncommon (Table 1b).

It should be easier for two fish to maintain a home range than one. Solitary females of the acanthurid <u>Acanthurus</u> <u>leucosternon</u> were not as territorial and had a lower reproductive fitness than paired females (Robertson, Polunin and Leighton 1979). <u>C</u>. <u>capistratus</u> pairs seldom actively defend their home ranges during the day but do appear to constantly range over their area, patrol borders, and present displays to conspecifics. Reese (1975) has suggested that the low amount of agonistic behavior among chaetodontids results from fishes knowing each other as individuals in conjunction with advertisement displays, which allow them to maintain social relationships on the reef with only an occasional bout of reinforcing agonistic behavior.

Current sexual selection theory argues for mate desertion when parental care of progeny is absent (Trivers 1972). How then is long term monogamy explained for fishes who spawn planktonic eggs which receive no parental care? While it appears that male chaetodontids would benefit by deserting females after spawning, several factors increase the costs of polygamy. A major constraint is the temporal synchronization of spawning throughout local populations. In other words, mating is restricted to a narrow time window which begins to slam shut after sunset. Thus, to be successful, a male would be required to mate and desert a female, and then locate and mate another one. But since continuously paired species, such as <u>C</u>. <u>capistratus</u>, are distributed on what appear to be nonoverlapping, exclusive home ranges, the availability of unpaired females is low. If paired females were pursued they would have to be fought for, as evidenced by the chasing of interloping males by paired males. These constraints on multiple mating favor monogamy.

Evolution of Pomacanthid Polygyny

We have already suggested (Abundance and Distribution) that the relative scarcity and discontinuous distribution of sponges results in high variance in territory quality and defensibility. These resource differrences compensate females for costs of polygyny by offering superior territories and males. In other words, the polygyny threshold (Verner 1964, Orians 1969, Wittenberger and Tilson 1980) has been exceeded. This has facilitated the evolution of polygyny in H. tricolor and the exaggerated sexual characters of males.

In nonmonogamous bird species, the amount of time and energy devoted to display and associated activities is much greater than that in monogamous species, and male displays are exaggerated in both form and repertoire (Selander 1972). These effects result from both epigamic and intrasexual selection processes. Consequently, it is not surprising that the polygynist has the more involved and prolonged courtship.

If sexual selection has been operating on the mating system of H. tricolor, then we should expect to find sexual dimorphism in size, color, behavior, or any combination of these effects. Males of polygynous bird species have a greater variety of vocal signals than do females (Orians and Christmann 1968), whereas in monogamous species the number is the same in each sex (Selander 1972). The amount of sexual dimorphism in size is significantly correlated with the degree of polygyny in nonhuman mammals (Alexander, Hoogland, Howard, Noonan and Sherman 1979).

In polygynous systems with separate sexes (gonochores), including virtually all vertebrates, males acquire harems or reproductive status mainly through intrasexual competition. That is, males ascend to dominance by winning in male-male competition. In the polygynous, protogynous hermaphrodite, H. tricolor, the result is identical; harem males are winners of intrasexual

competition, but this competition occurs between females vying for the right to change sex and become the dominant male. Such competition may be more directly manifested as an arms race of escalation in size, but still females succeed by exhibiting the large size of males and their aggressive behavior. Consequently, floater males do not exist as such because the male sex only results when large, aggressive females are dominant and thereby successfully change sex. Therefore, dominant males compete for reproduction with all potential males which they maintain as females by active domination of them. There is strong pressure for potential males (females) to increase in size and aggressiveness and thereby challenge dominant males. This effect is evidenced by female hesitancy to spawn (H. tricolor) and by the daily agonistic encounters between dominant males and harem females exhibited by Centropyge interruptus (Moyer and Nakazona 1978) and some wrasses (Robertson 1972, Warner, Robertson, and Leigh 1975). The important difference between typical polygynous mating systems of gonochores and these hermaphrodites is that floater males in the former realize practically zero reproductive fitness, whereas potential males in the latter are reproductively active females. Harem master is the most fit reproductive tactic, even though it is a costly one because of time and energetic costs of territory defense and domination of females. Females can "hedge their bet" by assuring some reproductive fitness before gambling on the big payoff, sex change.

In the absence of floater males interfering with harem spawnings, what other factors would allow females to change sex besides death of the dominant male? For H. tricolor recruitment to harems is by juveniles, which are all females. There is no evidence to suggest that adults migrate within or between reefs. A male can spawn with a limited set of females a night, which places an upper boundary on harem size. Recognition of maximum harem size and solely

female immigration have led Shapiro and Lubbock (1980) to construct a theoretical model which allows female sex change and formation of subgroups when immigration to a harem exceeds a threshold number. Whereas models of sex change in sequential hermaphrodites have often been based on attaining a critical size or age (Smith 1967, Choat 1969, Fishelson 1975), and on the release of suppression (Robertson 1972), the Shapiro and Lubbock (1980) model accounts for some sex change as the result of the proximate social factors within groups. Social control of sex change has also been suggested for the pomcanthid Centropyge interruptus (Moyer and Nakazona 1978) and for labrids by Robertson (1972) and Warner et al. (1975). Therefore, attaining a certain age or size per se does not result in automatic sex change; what is important is an individual's relative size within a group. This explains why females larger than males were found in H. tricolor (Table 1c), and predicts that large females live with larger males. Conversely, small males probably control even smaller females.

After polygyny began it is easy to comprehend how this mating system could perpetuate. Female recruits play an ascendency game to become harem master that promotes female groups which increase potential rewards. Recruits should choose harem sizes which offer the best chance to become males. In environments saturated with fish and where resource patches vary greatly in quality, harems at threshold size should be preferred. In poorer quality environments that cannot support groups, pairs should be more common. Lobel (1978) related sex ratios (pairs versus harems) of the Hawaiian angelfish, Centropyge potteri, to habitat defensibility such that harems form on discrete, defensible reef patches. Similarly, Centropyge interruptus forms harems in habitats with maximum shelter such as tunnels and crevices, and unstable mono- gamous pairs in less structurally complex boulder habitats (Moyer and Nakazono

1978). Although pairs would be preferred in unsaturated environments, the probability of a recruit encountering a solitary male is low because males result from sex change which requires interaction with other females. In the absence of other conspecifics, female recruits would probably compete through a series of behavioral interactions. The expectation being that the dominant female would change sex to male.

Sequential Hermaphroditism and Polygyny as Barriers to Adult Transfers

Extending the logic of harem size threshold (Shapiro and Lubbock 1980) with solely juvenile female recruitment, several interesting predictions can be made. When a dominant male controls a threshold size harem, he should attempt to exclude all immigrants. Females should assist all smaller recruits to expedite their own sex change. While most authors have evoked an increased risk of predation to explain the lack of adult transfer within or between reefs, we envision an additional mechanism. In sequential hermaphrodites which are polygynous, large fish attempting to join groups should be repelled by group members. Therefore, group social pressure may also be an important constraint on adult transfers.

SUMMARY

Chaetodon aculeatus foraged solitarily during the day for elusive prey and formed monogamous pairs with a nearby individual at dusk. Pair formation occurred over the same site each evening, even without spawning. Considerable amounts of time were devoted to greeting and, upon meeting, males began by exhibiting parallel lateral displays which were returned by females. Courtship

lasted between 10 and 15 min and culminated with a close carrouseling ascent, anal nudging and one gamete release per evening.

C. capistratus forms permanent pairs which forage together in home ranges in the day, breed there at dusk, and remain inactive there at night. Courtship of this monogamous fish lasted only 2-6 min but included the same display repertoire exhibited by C. aculeatus. Females played active roles in courtship. Pairs spawned only once per evening within 20 min of sunset and most gamete release occurred just before sunset.

These Chaetodontids are site-attached reef fishes that maintain exclusive use of certain resources contained within permanent home ranges. These use patterns have probably allowed the evolution of monogamy because of lower costs of home range maintenance for pairs and easy sexual access. Presumably, movements to better spawning sites, those offering multiple matings and lower zygote predation, increase the risk of loss of resourcesto usurpers.

Courtship differs for each of the three species studied. Pairs of the highly monogamous species, Chaetodon capistratus, spawn once per evening, and courtship is uninvolved and lasts only 2-6 min. C. aculeatus, which forages solitarily during the day and joins a nearby mate at sunset, exhibits a relatively prolonged courtship of 10-15 min, although the display repertoire is the same. In contrast, the polygynous species, Holacanthus tricolor, has an involved courtship consisting of a diverse display repertoire. These differences are not limited to courtship complexity. Chaetodontid males and females present and return courtship displays, whereas H. tricolor females are hesitant and often do not spawn unless a male displays repeatedly.

The monogamous species are not dimorphic in size and spend considerably less time and effort on courtship than does the polygynist. Since C. capistratus pairs are continuously together, courtship serves primarily to synchronize

gamete release. The less closely associated pairs of C. aculeatus spend considerable amounts of time on greeting and pair formation before spawning. Female chaetodontids reciprocate the displays given by their mates. Males of H. tricolor are 44 percent larger than females, exhibit more displays than chaetodontids, and present them more frequently to females. Females are hesitant to spawn, often require males to repeat their displays before spawning and seldom return displays. H. tricolor males must continuously reaffirm their dominance, especially to dominant females, because of their challenge as potential males. Females play their sex role because it is a complementary reproductive tactic which guarantees some fitness at a relatively low cost compared to the high cost, albeit high payoff, male tactic.

Overall, spatial and temporal patterns of spawning behaviors of chaetodontid and pomacanthid fishes support zygote and adult antipredation hypotheses (Jones 1968, Johannes 1978, Lobel 1978). Gametes are released above structures which place them above foraging diurnal planktivores and offer adults refuge from predators. Spawning culminates near sunset, a time when the primary zygote predators are becoming inactive and beginning an interlude of planktivore inactivity. Later, nocturnal planktivores begin to feed, but they take few of the then abundant zygotes. Spawning intensity appears to peak during the week prior to the full moon, another correlate of zygote avoidance of predators, since tidal exchanges are maximal then.

ACKNOWLEDGEMENTS

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APPENDIX A

Personnel

Aquanauts

Steve Neudecker, Principal Investigator
Ph.D. candidate, Ecology
Division of Environmental Studies
University of California
Davis, CA 95616

William J. Hamilton, III
Professor of Ecology
Division of Environmental Studies
University of California
Davis, CA 95616

Philip S. Lobel
Post Doctoral Fellow, Oceanography
Center for Earth and Planetary Physics
Harvard University
Cambridge, Massachusetts 02138

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
Environmental Protection Agency
Denver, Colorado 80218

Don Morris
Diving Officer
University of California
Davis, California 95616

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			
($Y \pm 5$ 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