THE ADAPTIVE SIGNIFICANCE OF COLONIALITY

AND HAREM POLYGYNY IN THE

SAND TILEFISH, <u>MALACANTHUS PLUMIERI</u>

By

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ABSTRACT

The social and reproductive biology of the sand tilefish,
Malacanthus plumieri (Malacanthidae), was studied in the field
at Glover's Reef, Belize, Central America. Discrete colonies of
tilefish were highly clumped in some sandy habitats with coral
rubble used by tilefish in burrow construction. Both females
and males each occupied one "home burrow" as a refuge from
predator attacks. Tilefish were most abundant in a channel
through the fringing reef. Smaller numbers of fish occupied
slopes adjacent to isolated patch reefs (reef slopes) inside the
lagoon.

Neither limitation of habitat nor social transfer of
foraging cues appears to explain colony formation in M.
plumieri, because unoccupied habitats were abundant and fish
forage solitarily. The proximity of unoccupied to occupied
habitats also suggests that colonies do not result because
larvae are transported only to some patches. Rather, juveniles
appear to settle preferentially near adults, perhaps because
proximity to conspecifics reduces predation risk. Contagious
reactions to predators and experimental disturbance support this
hypothesis. Tilefish disappeared more frequently in the channel
than in the reef slope, perhaps because channel fish incurred
higher predation rates.

Tilefish exhibit a harem polygynous mating system. Home
range overlap among fish of the same sex was low. Females and
males defended exclusive use of most of their home ranges
against all conspecifics except mates. Areas defended by males

overlapped the territories of up to six females. Males
maintained dominance over mates by aggression. Females spawned
as frequently as every day, with the male whose territory
encompassed their territories. Histological and behavioral
evidence indicate that M. plumieri is capable of functional
protogynous hermaphroditism.

Removal tests and observations on foraging indicated that
females defend burrows and feeding spaces. Male removals
revealed that females mate with whichever male occupies their
feeding territory, and do not position territories solely to be
near mates. Female removals confirmed that intrasexual
competition restricts use of space by some females. Colony
formation suggests, however, that competition costs are not so
high as to prevent female occupation of adjacent territories.
Instead, joining harems may promote spawning opportunities for
females that are restricted to burrows for predator avoidance.

Removal tests indicated that males position their
territories to defend female territories and acquire mates.
However, males did not prevent mates from moving to other harems
when females were removed. Males also did not abandon their
territories when mates were removed. A dichotomy between
resource and female defense does not apply to tilefish or to
other group-living fishes where females are site-restricted and
egg production occurs year-round.

Differences in tilefish density suggest that reef slope and
channel habitats may differ in quality. Channel females spawned
twice as frequently as reef slope females, but daily batch
fecundity and net yearly mating success were similar in the two

habitats. By contrast, net yearly male mating success was higher in the channel because harems were larger. Adults did not move between reef slope and channel habitats. Therefore, the dense concentration of adult M. plumieri in the channel, appears to be a consequence of larval transport by prevailing currents.

Supplemental feeding increased female fecundity and growth in both habitats. Different responses to feeding by reef slope and channel females is consistent with the hypothesis that reproductive tactics are conditional upon the type of predation risk that fish experience in local habitats.

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CHAPTER 1

GENERAL INTRODUCTION

The study of the evolution of animal social organization and reproductive behavior has blossomed in the last two decades. Undoubtedly, the concepts of individual (Williams, 1966) and inclusive fitness (Hamilton, 1964), have been fundamental to progress in this field. An even more important contribution to understanding the evolution of mating systems was Trivers' (1972) formalization of the notion that females and males maximize fitness in different ways. This set the stage for Emlen and Oring's (1977) general ecological model of the conditions under which monogamous and polygamous social organizations evolve.

Much of the research progress in the evolution of social systems has been made in birds and mammals (e.g. see Rubenstein and Wrangham, 1987 and papers cited therein), and research on the social systems of lower vertebrates lags behind that of higher vertebrates. Further study of fishes, amphibians, and reptiles is needed to expand the data base, and to test the generality of ideas from study of other taxa.

Tropical marine fishes exhibit several features that make them suitable for research on social systems. Adults are often sedentary and diurnal; this allows direct observation of most behaviors. Many of these species spawn daily throughout the year during short but predictable time periods (reviewed by Thresher, 1984; Warner, 1984a). Therefore, the distribution and

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frequency of matings can be observed directly (e.g. Warner and Hoffman, 1980a; 1980b; Hoffman, 1985). Fertilization occurs in the water column in many species, and adults do not provide parental care for the planktonic embryos and larvae (reviewed by Thresher, 1984). In fishes with this type of reproduction, factors that affect the survival of planktonic offspring are almost certainly stochastic (Barlow, 1981; Doherty et al., 1985; Victor, 1983), and not influenced by the behavior of adults. Therefore, mating frequency is an unbiased estimate of reproductive success (Warner and Hoffman, 1980a; 1980b). These features, together with the clear water in tropical marine habitats, make it possible to record much of the behavior of known individuals and relate it to fitness.

Despite the relative ease of observing tropical marine fishes, three areas of research are particularly meager relative to studies on higher vertebrates. A major focus of studies on tropical fishes has been the behavior of males in species characterized by male competition for mates, polygyny, and protogynous hermaphroditism (reviewed by Thresher, 1984; Warner, 1984a; 1988; Shapiro, 1987a). An understanding of factors that influence the fitness of females in such systems is emerging more slowly (e.g. Robertson, 1972; Robertson and Hoffman, 1977; Kuwamura, 1984; Hourigan, 1986; Shapiro, 1986). Even studies that document female behavior in detail do so to determine which mating tactics are successful for males, or to ask how females increase their chances of changing sex and mating as males in the future. Few studies have examined factors that contribute to fitness during the female life-history phase (but see Warner,

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1987).

Secondly, workers have just recently begun to examine factors that may influence the distribution and abundance of local populations of tropical marine fishes (Shapiro and Boulon, 1987; Robertson, 1988; Shapiro et al., 1988). The distribution and abundance of local populations almost certainly affect the type of adult social systems that evolve because many species are concentrated in isolated patches of habitat (Warner, 1984a). Thus, the environmental potential for polygamy (Emlen and Oring, 1977) is high. Settlement of planktonic larvae is thought to play a stronger role than habitat selection by post-larval fish in determining the distribution and abundance of adults (Doherty, 1983; Cowen, 1985; Victor, 1986; Robertson, 1988). Grouping may occur on coral reefs, because larval settlement is episodic (Victor, 1983; 1984; Robertson, 1988), and predation risk prevents settled fish from departing reef refugia to choose habitats (Robertson and Hoffman, 1977; Warner and Hoffman, 1980a; 1980b).

Alternatively, individuals may also choose from among available habitats based upon the costs of competition and the quality of resources (Fretwell and Lucas, 1969; Fretwell, 1972). Also, there may be advantages that favor individuals that settle near conspecifics (Wittenberger, 1981). The formation of discrete aggregations has now been reported in a number of reef and non reef species (Fricke, 1970; Colin, 1973; Clark, 1983; Petersen and Fischer, 1986; Victor, 1987; Shapiro, 1987). Factors that influence the distribution of local populations,

therefore, merit further investigation in a variety of species.

Finally, studies on the social behavior and life-histories of tropical marine fishes too often focus on a few individuals occupying a single type of habitat. Variation in the behavior and life histories of individuals in different habitats has not been examined in many marine fishes. A few species, however, exhibit marked differences in social behavior between separate locations (Thresher, 1979; Robertson, 1981), or among groups within one area (Warner, 1984a). Such environmental variation is a valuable tool for examining the adaptive function of behavior (Warner, 1984a), because individuals may be compared without confounding influences of different phyletic histories (Clutton-Brock and Harvey, 1984).

Objectives and Organization of the Thesis

Populations of the sand tilefish, _Malacanthus plumieri_ (Bloch), at Glover's Reef, Belize Central America (formerly British Honduras), provided me an opportunity to conduct descriptive and experimental field studies on: 1) factors that influence the fitness of females as well as males, 2) factors that influence the distribution of groups, and 3) differences in the behavior and life-history traits of females and males in different habitats. Furthermore, I could study these facets of tilefish biology under undisturbed conditions because Glover's Reef lies 26 miles off mainland Belize in a remote location, and this species is not fished commercially.

Following a general methods chapter (Chapter 2), there are five data chapters. Burrowing is the most obvious feature of

tilefish behavior. In Chapter 3, I describe the structure of burrows, burrow construction behavior, and the role of burrows as refuges from predators. I then compare sand tilefish burrows with those of other marine fishes.

In Chapter 4, I document the clustered distribution of tilefish and examine the extent to which four popular hypotheses that have been proposed to explain the evolution of group living may apply to this species. In particular, I investigate the role of predation risk in group formation by reporting on predator activity, tilefish predator avoidance behavior, and by estimating survival rates in two types of habitat occupied by M. plumieri. I also describe experiments to examine contagious reactions to threatening stimuli.

In Chapter 5, I document the social organization within tilefish groups, paying particular attention to the locations of individual females and males in relation to burrows, food resources, and mates. Also, I report on experiments to determine if M. plumieri is capable of protogynous sex reversal. In Chapter 6, I investigate the function of territory defense and the harem social organization of tilefish using a series of fish and burrow removal experiments. These tests were designed to investigate the degree to which male tilefish monopolize harems through resource defense or direct control of females.

In Chapter 7, I compare estimates of mating success in relation to predation rates in two types of habitat, and observations on fish location in relation to the physical and biotic environment. I then examine the extent to which habitat selection models (Fretwell and Lucas, 1969; Fretwell, 1972) or

larval settlement processes may explain the distribution of adult tilefish.

I conclude the thesis with a general discussion (Chapter 8), in which I examine results in relation to the general issues raised in each data chapter.

CHAPTER 2

GENERAL METHODS

Study Site

Glover's Reef (87°45' W, 16°45' N, Figure 1) is a coral
atoll with a shallow (1.5-30 m depth) lagoon that is enclosed by
a fringing coral reef (Figure 1, after Stoddart, 1962). The
lagoon contains hundreds of patch reefs of living coral isolated
from one another by expanses of deep barren sand interspersed
with beds of turtle grass (Thallasia testudinum). My studies
were conducted within a 15 km^2 area adjacent to Long and
Northeast Cays inside the lagoon and in a channel through the
fringing reef that connects the lagoon with the Caribbean Sea
(Figure 1).

General Techniques

Tilefish are diurnal and occur over flat, relatively
barren substrates where direct observation of social behavior
among individuals is unobstructed by physical features of the
environment. Tilefish habituate quickly to a diver snorkeling
quietly a few meters above and to one side. Fish foraged,
maintained burrows, interacted, and spawned nearly every day
apparently undisturbed by an observer's presence. Consequently,
I could record almost all aspects of tilefish behavior.
Individuals within social groups each occupy a specific burrow
site. It was also possible, therefore, to capture and mark fish
enabling me to measure and monitor life history components of
known individuals for prolonged periods. Finally, tilefish
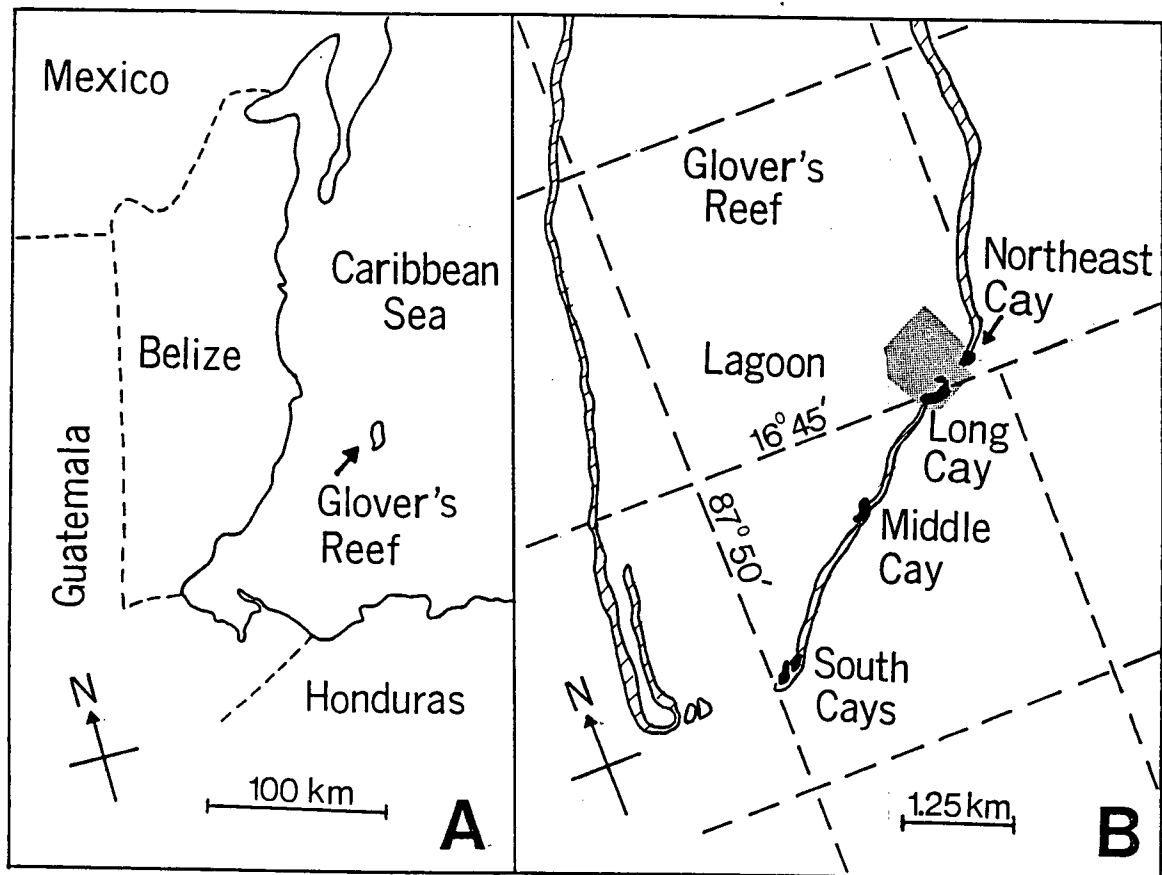
Figure 1. A. Location of Glover's Reef relative to adjacent coastal regions. B. Southern portion (65%) of Glover's Reef (after Stoddart, 1962). Hatching indicates fringing coral reef. Shading indicates study area.

occurred in two distinct habitats at Glover's Reef. This allowed comparisons of behaviors adopted under different biotic and physical environmental conditions.

Initial observations on social and reproductive behavior were carried out from May 14 to June 20, 1983. All other studies were conducted from February 7 through July 8, 1984 and from April 1 through August 10 in both 1985 and 1986. Data were collected while snorkeling 5-10 m from study fish. Horizontal underwater visibility is usually 20 m or more at Glover's Reef (measured by sighting a submerged marker). Data were recorded on slates by the author and one other experienced observer.

To facilitate identification of individuals, fish were tagged by sewing colored plastic beads strung on monofilament line through the epaxial musculature 1-3 mm below the anterior portion of the dorsal fin. Individuals were captured by chasing them into their burrows (described in Chapter 3) and placing a cage (constructed from 1.5 cm mesh wire cloth) with a vertical funnel opening through the bottom over the burrow entrance. Fish left burrows within 1 h and ascended through the funnel into the cage. When tagging subjects of studies on social behavior, cages were monitored continuously so that fish could be removed immediately to minimize injury and trauma. Trapped fish were immediately taken to a boat, measured (SL to the nearest mm), tagged, and then carefully placed inside their home burrow. Tagging required only 5-10 min. All of these fish were behaving normally in my presence within a few hours of tagging.

Some fish whose locations were monitored for census purposes (Chapter 4) and for removal tests (Chapter 6) were not

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tagged. Untagged fish were identified by making detailed
drawings of the unique patterns of spots and patches of black
skin. These spots result from deposition of melanin around
trematodes encysted in the dermis (see Figure 8, Chapter 5).
The size, location and arrangement of spots was unique on each
individual and did not change rapidly. Therefore spots could be
used to identify individuals for several months.

Mapping Techniques and Collection of Behavioral Data

Most data were recorded on scale maps (1cm=1m, or
0.8cm=1m). Study areas were mapped by recording distances and
compass readings between reference points that consisted of
prominent features on the substrate (e.g., tilefish burrows,
gorgonian corals) or stakes, which were marked for easy
visibility. Reference markers were located such that the
position of study fish could be determined in relation to a
minimum of three known points. Collection of spatial data
involved tracing the swimming path of a fish onto a map for a 20
min period. The location of burrowing behaviors, responses to
potential predators, and social interactions were recorded
directly on these traces. A minimum of four (and in most
instances five) replicate traces, each recorded between 900 and
1200h on separate days was obtained for a total of 54 females
and 25 males. In addition, traces (4-5 replicates/fish) were
recorded from 1630-1730h for these same 25 males and 16 others.
Overall, behavioral data recorded on maps totaled 130 h of focal
observations. Additional focal observations on males during
which social and reproductive behavior was recorded totalled 415 h.

Statistical Treatment of Data

All behavioral frequencies presented below are average values for individuals calculated by dividing the total number of observed acts by the total focal observation time on that fish. Data for other results are explained in methods for each data chapter. I used standard statistical techniques throughout (Sokal and Rohlf, 1969; Zar, 1974). Two-tailed probabilities were used except in a few instances where a priori predictions justified use of 1-tailed probabilities. Some data were log-transformed to homogenize sample variances and improve the fit to normality. The Mann-Whitney statistic was used in one instance where the variances of log-transformed data were heterogeneous as determined by an F test.

Some questions required statistical examination of the degree of spatial clumping of fish, prey organisms, or foraging bites (Chapters 4 and 6). Spatial clumping was examined by recording the frequencies of fish or foraging bites, or the quantity of prey in sampling quadrats and calculating the variance to mean ratio of the resultant distribution. This analysis is based on the Poisson distribution which requires that the average density of objects or events being sampled is low relative to densities that could potentially occur given the amount of available area (Cox, 1976; Grieg-Smith, 1983). In clustered distributions this ratio is statistically greater than 1.0 (tested using the t statistic), in a random distribution it equals 1.0, and is less than 1.0 in uniform distributions (Cox, 1976; Grieg-Smith, 1983).

CHAPTER 3

BURROWS AND BURROWING BEHAVIOR

INTRODUCTION

Many tropical marine fishes live on reefs that provide an abundance of holes that can be used as nocturnal shelters or to evade predator attacks (Thresher, 1984). In contrast, there are relatively few structures that can be used as refugia on the flat open substrates juxtaposed with reefs. Therefore, species that occur in non-reef habitats exclusively, such as M. plumieri (see Chapter 4), may require an alternate means of taking refuge.

The most conspicuous aspect of sand tilefish behavior is its use of large mounded burrows as shelters. Burrowing behavior has been described previously for M. plumieri in the U.S. Virgin Islands (Clifton and Hunter, 1972), and in the Bahamas (Colin, 1973; Clarke et al., 1977). These authors reported that fish retreat to burrows when disturbed by divers. However, the design, maintenance, and use of burrows for predator avoidance has not been examined in detail. In this chapter, I describe the design and maintenance of tilefish burrows, and examine the possible anti-predator function of burrowing behavior.

METHODS

Sixteen burrows were dismantled to examine their internal structure. The extent to which each fish uses one or more

burrows was examined by recording the frequency, type, and location of burrow-related activities on maps during spatial traces. Burrows were marked with plastic tags fixed to pvc poles pounded into the substrate. The burrow sites occupied at dusk were recorded on a minimum of five days/fish. Three study sites were examined with a light between 2000 and 2200 h to determine if tilefish remain in their burrows at night. Initial observations suggested that approach by large piscivores, primarily the barracuda (Sphyraena barracuda), sometimes caused one or more tilefish to retreat abruptly to burrows. The occurrence of such avoidance reactions to barracuda was recorded during focal observations, and the greatest distance ventured from burrows was estimated from mapped traces of fish movements.

RESULTS

Use of Burrows

Individuals of either sex occupied a single home burrow (Figure 2). Fish sealed the entrance to their home burrow about 1 h before sunset and later pushed their way inside (see below). Tilefish were not sighted during night examination of study areas, and burrow entrances were closed.

Home burrows were used during the day as refuges from predators. Females responded to the approach of barracuda by retreating to and entering or hovering above their home burrows. Males also usually retreated to their home burrows. However, if a male was far from its home site when a predator approached the male sometimes swam to a burrow occupied by another fish,

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Figure 2. Sand tilefish burrows. a. Cross-sectional diagram showing cavern (c), foundation rock (f), mounded roof of coral rubble (r), and sand pit (p) leading into tunnel entrance (t). b. Photograph of roof mound. c. Close-up of tunnel entrance with elongate coral pieces that the occupant has positioned as supporting struts (s).

a

30cm

t

s

r

p

f

c

15

b

R

P

c

S

P
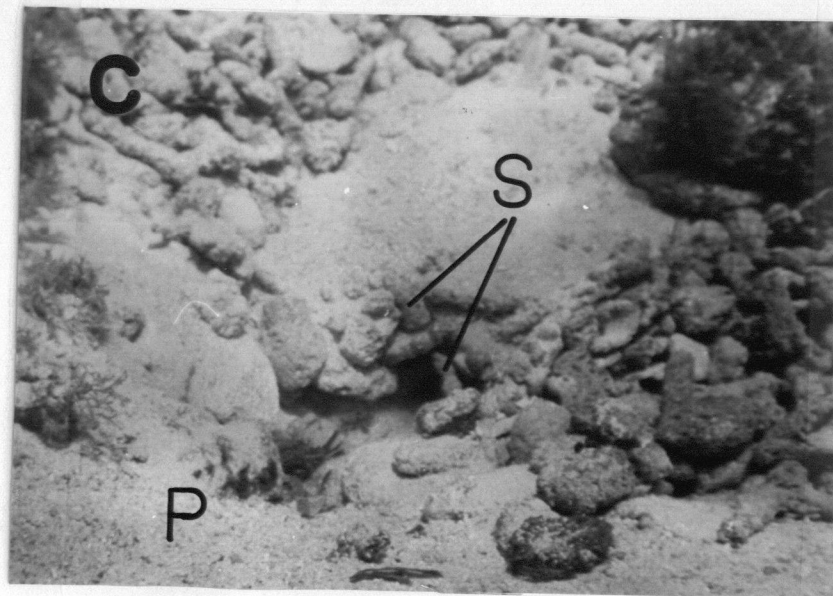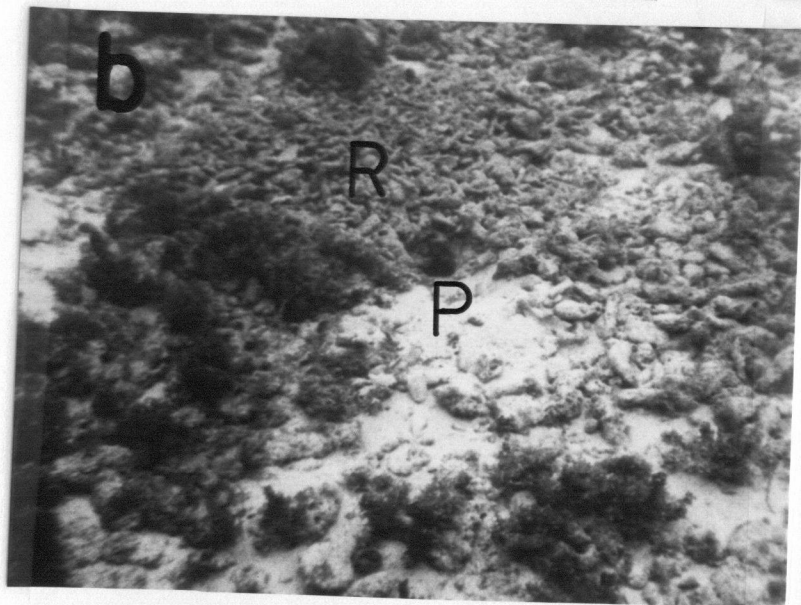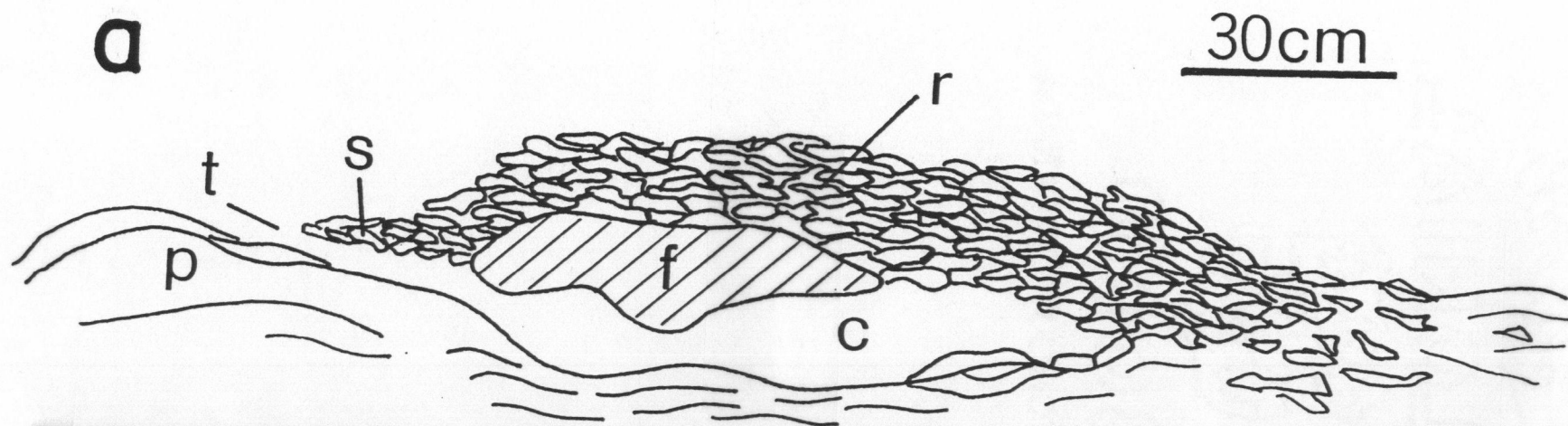
usually that of a female mate. For fish in all study areas pooled, females retreated to their burrows in response to approach by barracuda, an average of 0.25 times/h (N=54 females, SE=0.10), while the average frequency of retreats by males was 0.13/h (N=39 males, SE=0.04). Although the mean frequency of retreats by females was almost double that for males, frequencies among females were sufficiently variable that the difference between males and females is not statistically significant (t=0.67, p>0.05).

Burrow Design and Maintenance

A burrow consists of a cavern excavated beneath and adjacent to a flat foundation rock (Figure 2a). Tilefish excavate the cavern by lying prone on the substrate and undulating laterally in the sediment. When digging in this manner, a fish sometimes grasps part of the substrate with its mouth, presumably for leverage. Such movements of the ventral part of the body, the elongate anal fin, and the caudal fin push sand backward and outward removing it from the cavern. Fish moved rubble out of the cavern by grasping pieces in the mouth and carrying or dragging them away. Coral rubble, particularly staghorn, Acropora cervicornis, is arranged adjacent to the foundation rock in a latticework of inter-locking pieces that covers the cavern (Figure 2a). Additional rubble is piled upon the roof, forming a raised mound (Figures 2a and b). The diameter of burrow mounds ranged from 0.75 to 2.0 m. At least one tunnel, through which the fish enters and exits the cavern head first, penetrates each mound at a downward (10-20°) angle.

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Tunnel entrances are characterized by elongate pieces of rubble that the fish positions as horizontal and vertical struts supporting the opening (Figures 2a and c). An area of loose sand is usually found directly in front of and leading into burrow entrances (Figure 2c).

Tilefish gathered new rubble from throughout their territories (see Chapter 5) and added it to the burrow or rearranged existing parts of the burrow by grasping and carrying pieces in their mouths. Fish sometimes carried pieces of rubble as large as one-fourth of their body length up to 12 m to their burrows. Burrow maintenance was a continuing process. Caverns were maintained by removing pieces of rubble and by digging while inside the burrow such that sand was pushed out of the entrance. The bed of loose sand and the struts supporting the entrance were maintained meticulously. Fish maintained the tunnel entrances by removing debris that obstructed the opening or the sand pit, and by loosening the sand by digging while lying prone. Females and males performed these burrow maintenance acts at similar rates ($\bar{X}$ maintenance acts/h=10.5, N=54 females, SE=1.9; males $\bar{X}$=11.3, N=39, SE=1.7).

About 1 h before sunset, fish began pushing loose sand from the pit backward into the entrance by digging with their anal and caudal fins. Sometimes fish also gathered benthic algae in their mouths and placed it in burrow entrances. Fish later dived head first through the sand filled tunnel to enter the burrow for the night.

DISCUSSION

Function of Burrows

Results show clearly that each individual of both sexes occupies a particular "home burrow." Burrows are used as refuges at night and to evade attacks by predators during the day. Burrows are not used either as nests for laying eggs or as lairs from which to ambush prey, as implied previously (Clifton and Hunter, 1972; Dooley, 1978). Burrows do not serve either of these purposes because foraging occurs outside of refuges, and gametes are broadcast pelagically (Chapter 5).

Even though each fish occupied one home refuge, burrows or the clastic materials used to construct them are common throughout Glover's Reef. Old, unoccupied burrow mounds and coral rock of the type used in construction of burrows were abundant on all sites (Chapter 4).

Why should individuals rely on a single burrow for refuge when clastic materials and unused burrows are abundant? One possibility is that reliance on one burrow facilitates predator avoidance because individuals become highly familiar with their home refuge site. Potential predators such as mutton snapper (Lutjanus analis) are abundant at Glover's Reef. Stomach contents confirm that this snapper preys on tilefish as large as 32.0 cm SL (Randall, 1967). The barracuda, however, is probably the major predator on tilefish at Glover's Reef. Tilefish exhibited obvious escape responses when barracuda approached, and numerous unsuccessful attacks were observed. Moreover, I witnessed one successful attack, and recorded

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several instances where known individuals acquired wounds of the type likely to be produced by the sharp conical teeth of this predator.

Barracuda, as well as other large piscivores strike their prey suddenly. Escape from such predators may be enhanced by reliance on one familiar refuge. Frequent and meticulous maintenance of home burrows suggests also that the condition of these structures is important with regard to their suitability as refuges. The time and energy required to maintain burrows may limit use to one site. Particular attention is directed to the maintenance of tunnel entrances. A tunnel entrance that can be entered readily from several angles may increase the chance of escape. Also, frequent maintenance and defense (see Chapter 5) of one burrow ensures that the refuge is suitable for immediate occupancy when rapid access is crucial.

The function of sealing burrow entrances at night is not obvious because known tilefish predators are much too large to enter burrows. One possibility is that filling the opening with sand and algae camouflages the exact location of the tunnel. Disguising the opening could make it difficult for predators to lurk near the entrance to attack tilefish when they emerge in the morning. The design and maintenance of mounded burrow roofs probably also deters predators. Mounds of abrasive coral fragments built up around a sturdy foundation rock would certainly deter most piscivores from digging into the burrow.

Comparison With Other Tropical Burrowing Marine Fishes

Burrowing occurs in several other marine fishes that occupy flat open seabeds. Other malacanthid and branchiostegid tilefishes construct burrows, but large mounded shelters are unique to malacanthids (Dooley, 1978; Able et al., 1982; 1987). Three congeners construct mounded burrows similar in size and design to those of M. plumieri (Clark and Ben-Tuvia, 1973; Fricke and Kacher, 1982). In some locations the pearly razorfish, Hemipteronotus novacula, piles coral fragments on the roof of its burrows (Bohlke and Chaplin, 1968), but this species does not build mounded burrows at Glover's Reef (pers. observations). Burrows of the yellow-headed jawfish, Opistognathus aurifrons, lack mounded roofs but otherwise rival those of tilefish in complexity. Jawfish excavate a subterranean chamber that is connected with the surface by a narrow vertical tunnel lined with stones (Colin, 1973). Some garden eels (Heterocongridae), also construct vertical tube-like burrows in which the sides are cemented with mucous to prevent caving-in (Fricke, 1970). Burrows that are little more than a hole under a rock are characteristic of toadfishes (Batrachoididae, Hoffman and Robertson, 1983). Perhaps the simplest burrow design is that of the straight-tailed razorfish, Xyrichtys martinicensis. Burrows in this species appear to consist of only a shallow depression in the sand bed that fish maintain by removing debris and churning in the sand (Victor, 1987; Baird, 1988). The mounded burrows of M. plumieri and other malacanthids, therefore, appear to be the largest and among the most elaborate burrow structures built by marine fishes.

CHAPTER SUMMARY

1. Individuals of each sex occupy home burrows that serve as nocturnal retreats and as refuges from predator attacks.

2. Individuals meticulously maintained the condition of home burrows, paying particular attention to keeping tunnel entrances unobstructed.

3. Tilefish burrows are among the largest and most elaborate structures constructed by marine fishes.

CHAPTER 4

COLONIALITY AND PREDATOR AVOIDANCE

INTRODUCTION

Four non-exclusive hypotheses have been proposed to explain why some vertebrates form social groups (reviewed by Wittenberger, 1981). 1) Groups result because individuals passively accumulate in certain areas as a result of currents in air or water: 2) Suitable habitat and/or resources are limited and occur in discrete patches; 3) Proximity to conspecifics allows some individuals to utilize social cues to locate food resources (Ward and Zahavi, 1973; Emlen and Demong, 1975); 4) Living in groups reduces the threat of predation by enabling individuals to utilize cues from conspecifics to detect potential predators and/or confuse or distract predators (reviewed by Pulliam and Caraco, 1984).

Schooling is a common form of grouping behavior among mobile fishes, and protection from predators is one well-known function of such behavior (Brock and Riffenberg, 1960; Shaw, 1970; 1978; Partridge, 1982). The function of group living in sedentary bottom dwelling fishes such as M. plumieri, however, is understood less well. Clarke et al., (1977) reported that populations of M. plumieri in the Bahamas were aggregated, and tilefish also appeared to be concentrated in certain habitats at Glover's Reef. The purpose of this chapter is to document the distribution of tilefish at Glover's Reef, and to examine the adaptive significance of group formation in this species.

Social facilitation of feeding (hypothesis 3) does not appear to explain the clustered distribution of M. plumieri, because individuals forage solitarily (Chapter 5). Even though adult tilefish can swim against currents, their distribution may be influenced by patterns of oceanic currents because larvae float passively in the plankton. Under this hypothesis, adult tilefish may be most abundant in areas where oceanic currents flow onto suitable habitats because the largest numbers of larvae would be transported to these locations. I estimated densities of juveniles and adults in relation to proximity to prevailing oceanic currents to examine this possibility. To examine the hypothesis that groups may result because suitable habitat is patchy and limited, I characterized the substrates(s) occupied by M. plumieri, and determined the distribution of fish in relation to these areas.

It seemed likely that living near conspecifics might confer anti-predator advantages in tilefish because this species occupies flat, two-dimensional substrates with few natural hiding places. Since I did not find isolated individuals, I could not compare the behavior of solitary fish with those living in groups to examine this possibility. For some group-living species, however, individuals in large or dense groups are less vulnerable then those in smaller less dense groups (reviewed by Wittenberger, 1981). I examined this possibility in tilefish by comparing reactions to natural potential predators and the frequencies of disappearance of fish in small (8-25 fish) groups with fish in a single large (>300 fish) group. I also compare the influence of simulated predator

attacks on the burrowing behavior of fish in large and small groups.

METHODS

Distribution of Tilefish at Glover's Reef

Tilefish appeared to occur exclusively on sandy terrain with exposed coral base rock and loose clastic material (referred to below as sand-rubble substrate). An apron of sand-rubble substrate surrounds all patch reefs located in the lagoon and also parallels the fringing reef. Aprons decline gradually (10-20 degrees) outward from the bases of reefs. I refer to these sand-rubble aprons as "reef slopes." Water depth on reef slopes inhabited by tilefish ranges from 1.5 to 3 m. Reef slopes vary in size, but all are demarcated by an abrupt transition to deep sand and turtle grass bed, (Thallassia testudinum, where exposed coral rock and rubble are absent. Areas of deep sand and grass are not inhabited by tilefish. Sand-rubble substrate is also present throughout the channel between Long and Northeast Cays that connects the lagoon with the Caribbean Sea (Figure 1). The main body of this channel is 4-8 m deep.

In 1986 the number of fish present in each patch of sand-rubble substrate within the study area was recorded on maps to determine the distribution of tilefish in more detail. Boundaries of this study area were determined arbitrarily by the amount of terrain that I could survey. The relative location of reef slopes was estimated by sighting patch reefs from a boat.

Areas between reef slopes were surveyed thoroughly for tilefish. Distances separating adjacent sand rubble aprons were estimated (within 20 m) from maps drawn while swimming around and between separate reefs. Some patch reefs were sufficiently close to others that the surrounding sand-rubble aprons were continuous. Continuous reef-slopes were considered single sites for census purposes, as was the large continuous expanse of sand-rubble substrate in the channel (Figure 3). Between June 15 and August 10, 1986, the number of fish on reef slope sites and in a subsection of the channel was censused at least once per week. At each census, spot patterns were noted to monitor individuals.

To examine whether or not the distribution of tilefish was statistically clumped, a grid of 78 quadrats (600 m^2) was randomly superimposed over the study area map and the number of fish per quadrat was tallied. The variance to mean ratio of fish/quadrat was then determined as an index of clumping (Grieg-Smith, 1983). Because inclusion of quadrats that did not contain sand-rubble habitat would bias this analysis towards clumping, these (N=14 quadrats) were eliminated. Bias towards clumping could also result because more fish might occur in quadrats with large habitat patches. Up to four tilefish occupied even the smallest habitat patches. Therefore, to eliminate this source of bias, quadrats were tallied as containing 0 to 4 fish even though some quadrats contained many more than four fish.
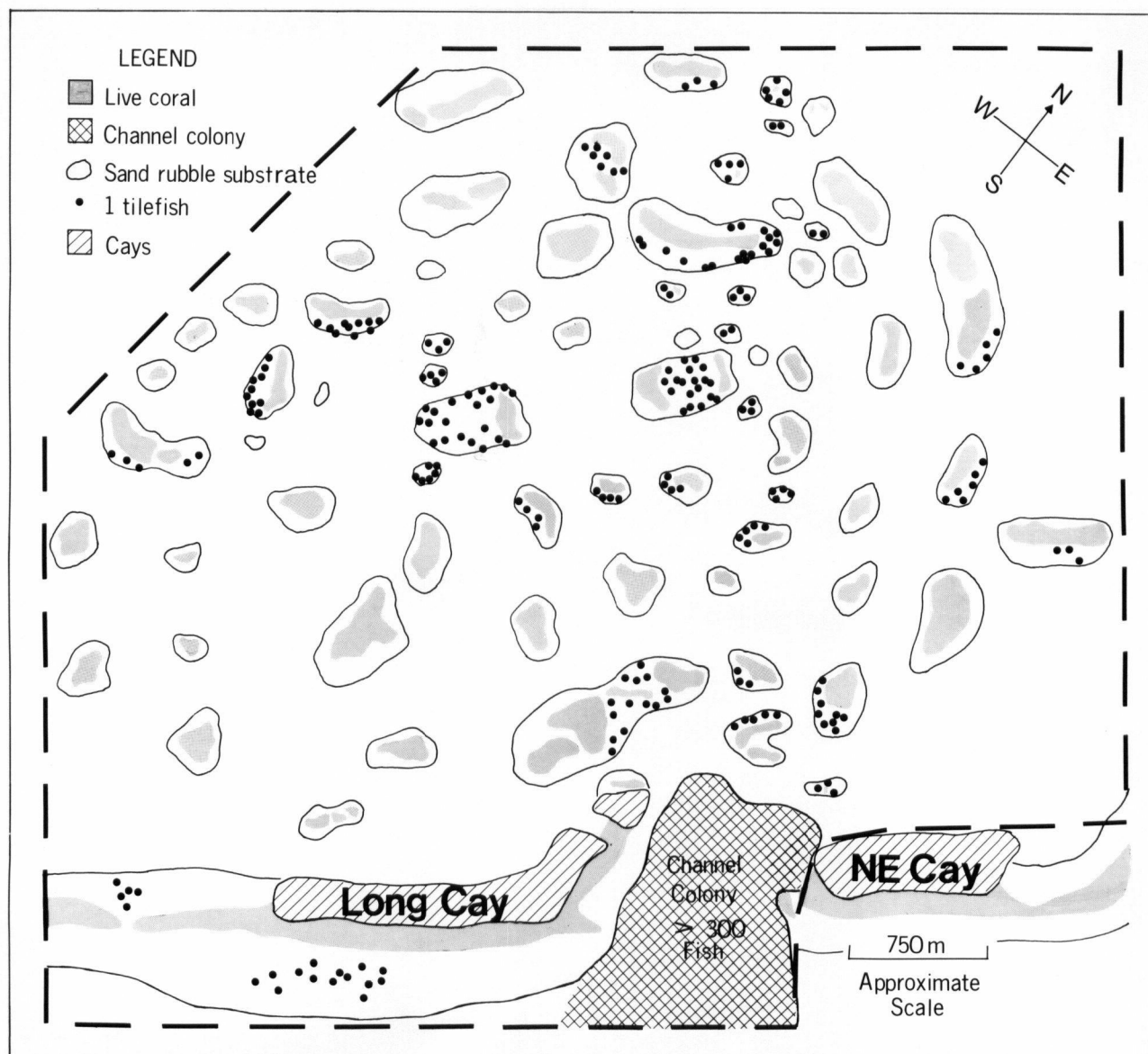
Figure 3. Map of study area showing approximate location and size of sand-rubble patches and tilefish censused in 1986.

Density of Tilefish and Burrows Within Sites

Because the inhabited area in the channel was too large to map completely, densities of adults (>15.0 cm) and burrows were estimated along thirteen transects (50X20 m, LXW) taken across the channel. Density of juveniles (<15.0 cm) was estimated along eight transects (30X20 m, LXW). Reef slopes were sufficiently small to draw scale maps of each site, tag all adults, and monitor the number of juveniles.

Diver Approach Experiments

Two types of tests were conducted to examine responses of fish in the large channel group and those in smaller reef slope groups to the approach of a submerged diver. Fish used in these tests had not been handled or observed previously, except to note their location. Tests conducted on reef slope fish were on sites that had not been used previously. Tests conducted on channel fish were in areas separated by at least 50 m from study areas.

In 1985, "gradual approach" tests were conducted. These consisted of a submerged scuba diver approaching a fish along the bottom. The test individual's initial reaction was recorded, and the location of the diver was marked when the fish entered its burrow. The distance between the diver and the burrow when the fish entered its refuge (diver approach distance) could then be measured. The occurrence of abrupt retreats to burrows by one or more tilefish within 10 m of the test fish was also noted. When test subjects did not retreat to their burrows, the fish was pursued, and the amount of time

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until it entered its burrow was recorded. Gradual approach tests were conducted on 15 reef slope and 15 channel fish ranging from 20.0 to 30.0 cm SL.

In 1986, tests involved a more rapidly approaching stimulus. Naive subjects were observed from the surface for a 20 min acclimation period during which the location of the home burrow was determined. Following acclimation, the total amount of time spent inside the burrow was recorded and the distance of the fish from its burrow was estimated at 10, one-minute intervals and summed (cumulative distance). Upon completion of this control period, the diver submerged and swam rapidly toward the test fish for 15 seconds. The diver then surfaced and recorded whether the test fish had burrowed or fled, its distance from burrows at ten, 1 min intervals, and time spent inside burrows. Rapid approach tests were conducted on 15 medium sized (200-275 mm SL) fish in both the channel and reef slope study sites.

Estimation of Survival Rates

Between April 1 and August 10 in both 1985 and 1986, disappearance of tagged fish was monitored to estimate survival of adults in the channel and reef slope sites. Survival was monitored for 30 days after tagging by censusing individuals every three to five days. Fish that were behaving normally (i.e., foraging, defending territories, see Chapter 5) in my presence at least one week after tagging were assumed to have recovered from tagging trauma. Only these fish were included in survival studies. When a tagged fish was absent from its burrow

and territory, adjacent areas for at least 50 m in all directions were surveyed for several days to determine if the fish had moved. I assumed that fish which were absent from their original burrows and home ranges, and did not reappear in surrounding areas, were victims of predation. One-hundred twenty channel fish and 121 fish in five reef-slope sites were monitored. Observations were limited to a 30 day period by the requirements of other experiments involving removal of tagged fish (see Chapters 6 and 7). Fish almost always retained tags for 60 to 90 days. Fish that lost tags were not mistakenly counted as predation victims because they could be distinguished by distinct tagging scars.

Fish were tagged throughout my study; therefore, censuses of tagged fish were not conducted over a single concurrent period. Sub-samples of channel and reef slope fish were monitored concurrently to reduce bias in between habitat comparisons that might result from sporadic intense predation in certain sites. I did not expect intense episodic predation, because large piscivores were active on all sites throughout all study seasons.

RESULTS

Distribution and Abundance of Tilefish and Burrows

Figure 3 maps the locations of all tilefish censused within the study area in 1986. M. plumieri was found only where coral base rock was exposed above the sand and where loose coral rubble was abundant. Substrates of deep sand and grass were not

inhabited. The variance to mean ratio of fish per quadrat

($S^2/\bar{X}$=1.71) was statistically greater than 1.0 (t=3.99, N=64,

p<0.001), indicating that the distribution of fish within the

study area was statistically clumped. Numerous tilefish

occurred in some patches of this habitat while others were not

occupied. Even on inhabited sites, individuals were often

clumped in part of the available substrate rather than being

dispersed over entire patches. Remnants of tilefish burrows on

some unoccupied sites indicated that they had been inhabited

previously, suggesting that these areas were suitable for burrow

construction. In both reef slopes and the channel, neighboring

tilefish were always near enough to one another (< 12 m) that

they were in visual range of at least one conspecific.

Juveniles (<150 mm SL) were also observed only in areas adjacent

to those occupied by adults.

Tilefish occurred continuously across the width of the

channel (500 m), and seaward for as far as I could survey (at

least 700 m seaward from the edge of the lagoon, Figure 3). The

substrate occupied by M. plumieri in the channel was demarcated

on the lagoon side by a dense grass bed. The areas of reef

slope sites that were mapped ranged from 0.03 to 0.44 ha.

Density of adults in the channel was about 1.6 times (t=5.43,

p<0.01) that in reef slope sites (N=12) and juveniles were over

15 times more abundant in the channel (t=14.35, p<0.01, Figure

4). Burrow density exceeded density of adults in both reef

slopes and the channel (Figure 4), and abandoned burrow mounds

were numerous on all sites. The mean density of burrows in the

channel was also higher (t=2.95, p<0.01) than that on reef

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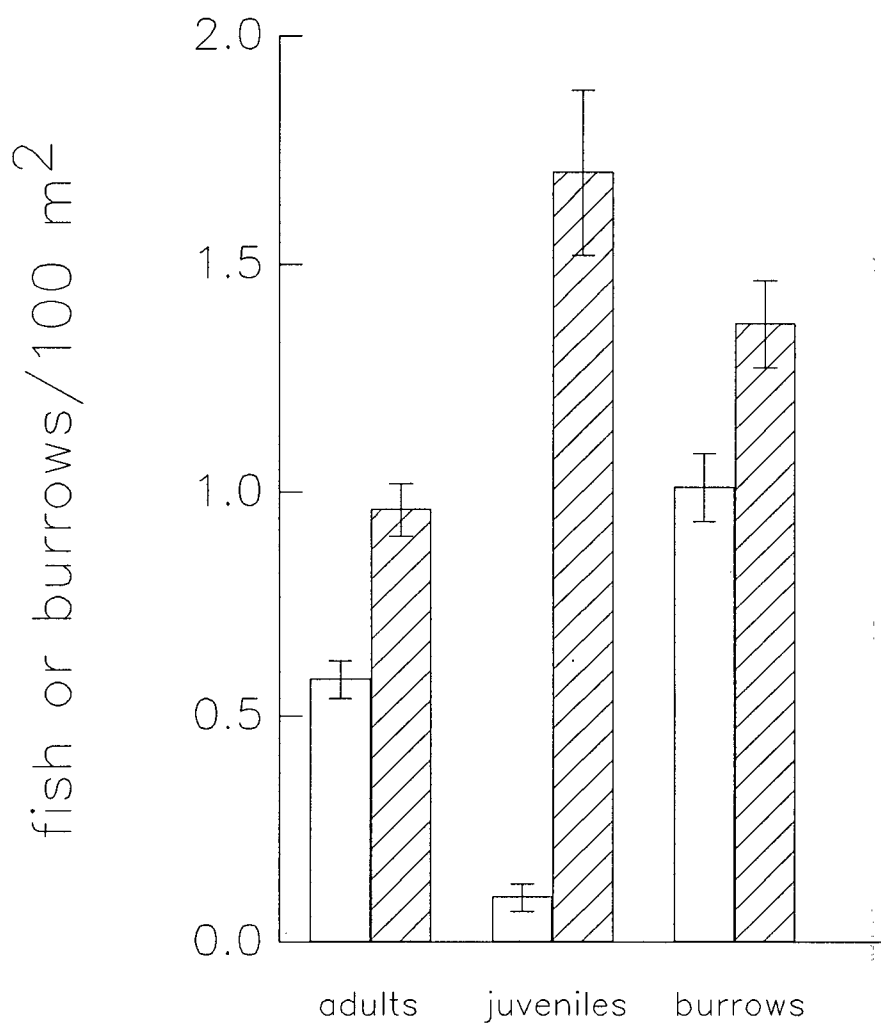
Figure 4. Tilefish and burrow density estimates ($\overline{X}$ ± SEM) in the reef slope (open bars) and the channel (hatched bars).

slopes. Rubble of the type used to construct burrows (3-15 cm long) was abundant on all occupied and unoccupied sites.

The locations of colonies censused weekly did not change throughout the 1986 study season. Although systematic weekly censuses were limited to 1986, colonies were also recorded in most of these same locations from 1984 through 1986. Extinction of known colonies was not observed within or between seasons, nor did new colonies appear in areas that were unoccupied during previous surveys.

Predator Behavior and Tilefish Avoidance Responses

The hunting behavior of barracuda differed markedly in reef slope and channel habitats. On reef slopes, barracuda were frequently seen, prone on the substrate, stalking or lying in wait for tilefish. Stalking barracuda swam slowly, to within a few meters of burrows where they waited for and lunged at tilefish. Repeated sightings of barracuda with unique markings suggested that they sometimes remained near particular reef slopes for several hours before moving to other areas. Barracuda were also common in the channel, but they were not observed to stalk tilefish in this area. Instead, barracuda almost always swam high in the water column. The few retreats that were observed in the channel occurred when a barracuda dived abruptly toward tilefish from above.

Retreats in response to approaching barracuda were very obvious in reef slope sites. In several instances, tilefish descended to the substrate abruptly and swam rapidly along the bottom to their burrows in response to the approach or an attack

by a barracuda.   Even though barracuda were abundant in the channel, such retreats by channel fish were uncommon.   Channel tilefish usually responded to barracuda swimming overhead by hovering motionless, but sometimes did not even stop their activities if barracuda continued to swim past.   The frequency of retreats observed in reef slope fish ($\bar{X}$ retreats/h= 0.09, N=52, SE=0.02) was about four times higher (t=15.24, p<0.01) than in channel fish ($\bar{X}$=0.02, N=41, SE=0.01).   The distance travelled away from burrows in the two habitats was compared separately for each sex because males had larger territories than females (see Chapter 5).   The mean greatest distance that channel females travelled from burrows was 2.4 m farther (t=7.73, p<0.01) than that of reef slope females.   The mean distance that channel males swam from burrows was 6.2 m farther (t=7.00, p<0.01) than that of reef slope males (Figure 5).

Diver Approach Experiments

Approach by a submerged diver elicited tilefish escape responses in both habitats.   Initial responses to disturbance differed, (p<0.01, Fisher's Exact test), however, between habitats.   In reef slopes, test subjects and one or more neighboring fish retreated immediately to and hovered above their burrow entrances in all trials.   Instead of retreating immediately to their burrows, in 9 of 15 tests channel fish swam erratically for up to 5 minutes ($\bar{X}$ time=1.55 min, range=0.5-5 min) before entering their burrows.   Erratic swimming elicited One or more nearby conspecifics also responded with erratic swimming in these nine tests.   The average diver approach

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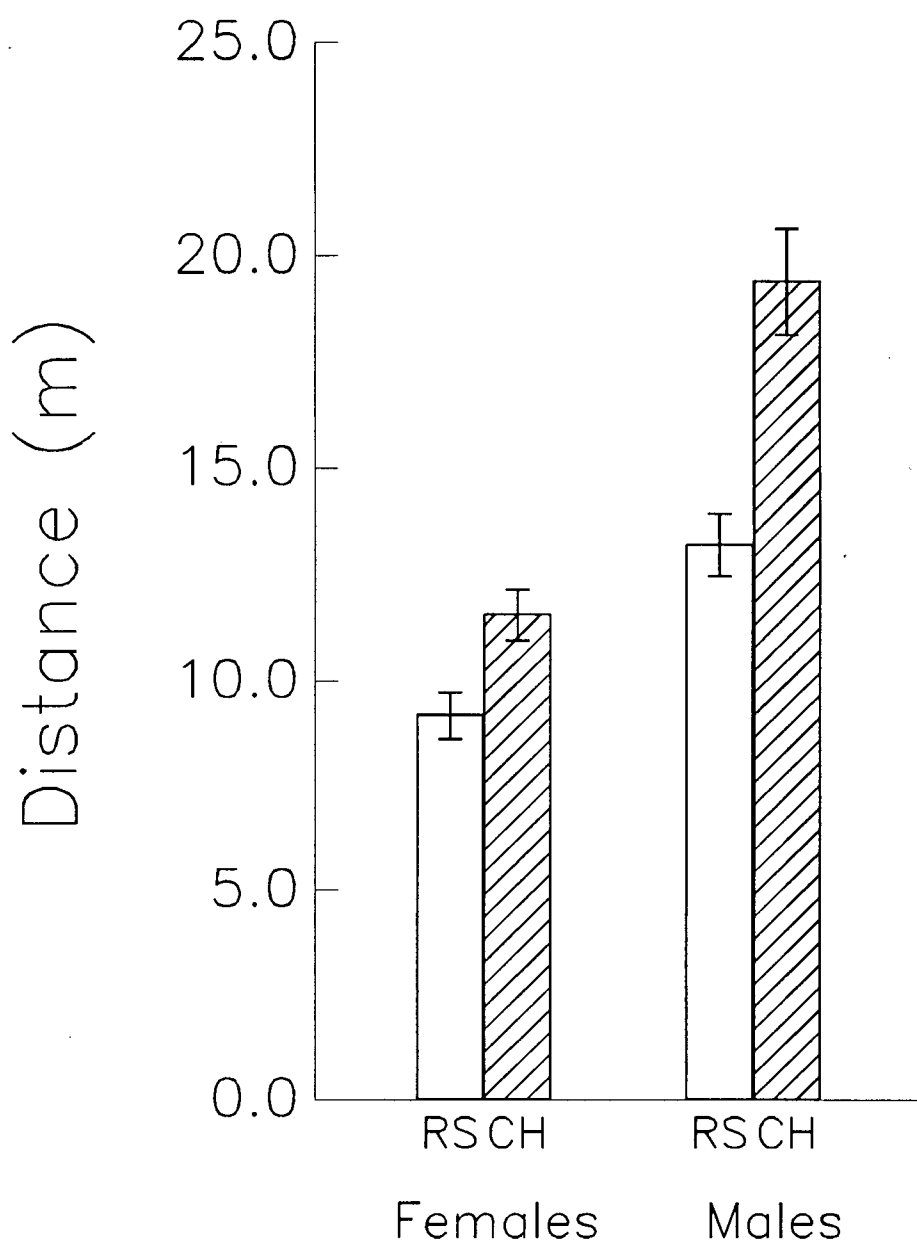
Figure 5. Greatest distance travelled ($\bar{X} \pm$ SEM) from home burrows in channel (CH) and reef slope (RS) fish.

distance at burrowing in reef slope fish ($\bar{X}$=7.6 m, SE=0.76) was considerably greater (t=5.67, p<0.01) than in channel fish ($\bar{X}$=2.5, SE=0.53).

The initial responses of fish in rapid approach tests was also different (p<0.01, Fisher's Exact Test) in the two habitats. Reef slope fish immediately entered their burrows in 14 of 15 tests. In contrast, channel fish initially fled away from the diver in 9 of 15 tests. Two-way analysis of variance revealed that cumulative distance from burrows was lower (F=14.14, p<0.01, 2-tailed) and time spent in burrows was higher (F=11.27, p<0.01, 2-tailed) in reef slope fish than in channel fish both before and after disturbance (Figure 6). Disturbance increased time spent in burrows (F=23.50, p<0.01, 1-tailed) and decreased cumulative distance (F=10.52,<0.01, 1-tailed) in both habitats (Figure 6). Statistically significant interactions between habitat and both cumulative distance (F=4.49, p<0.05 1-tailed) and percent time in burrows (F=7.19, p<0.01 1-tailed) indicate further that disturbance caused reef slope fish to remain closer and spend more time inside burrows than channel fish.

Disappearance of Tagged Fish

Only two tagged fish disappeared from reef slope sites while 19 disappeared in the channel (Table 1). The number of fish disappearing was not significantly different (p>0.05, Fisher's Exact or Chi-Square tests) among sites or years for reef slopes, or between years in the channel (Table 1). Therefore, data were pooled to compare the number of fish
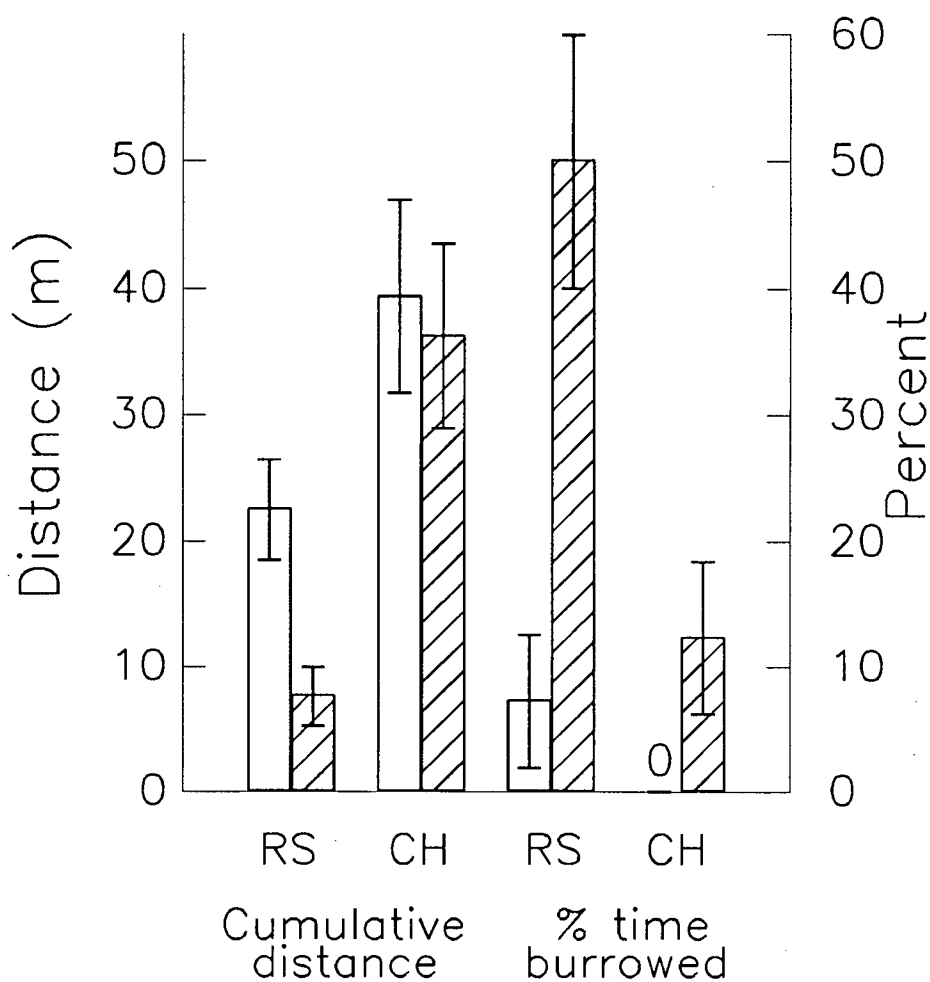
Figure 6. Behavior ($\overline{X} \pm$ SEM) of reef slope (RS) and channel
(CH) fish before (open bars) and after (hatched bars) rapid
approach by a submerged diver.

Table 1. Percentage of tilefish present 30 days after tagging in reef slope and channel habitats.

Site	Number of fish tagged	Number of fish present at 30 days	Percent disappearance
Reef Slope Sites			
1985 C	20	19	5
1986 C	10	10	0
1985 D	20	20	0
1986 D	10	10	0
1986 E	30	30	0
1986 G	18	17	5.5
1986 I	10	10	0
Total Reef Slope	120	118	1.67
1985 Channel	40	36	10.0
1986 Channel	81	66	18.5
Total Channel	121	102	15.7*

* $p < 0.01$ that percent disappearance is independent of habitat for all fish tagged in the channel and all reef slope sites combined, Chi-square test of association.

disappearing in the channel with that of all reef slope sites combined. Overall, the frequency of disappearance was nearly nine times higher (p<0.05, X^2=15.25) in the channel than in reef slope sites (Table 1).

DISCUSSION

Distribution in Relation to Available Habitat

At Glover's Reef, tilefish occur only on sand rubble flats where the exposed coral rock and rubble used for burrow construction are available. Further, tilefish were concentrated into some of these habitats, while other areas were not occupied. No solitary individuals were encountered. Wittenberger (1981) defined coloniality as the occurrence of discrete and site-attached groups, within which individuals maintain a well-defined and relatively fixed spatial organization. Tilefish occur in site-attached groups. Within groups each individual occupies a fixed home burrow site and a territory around the burrow (Chapter 5). Tilefish at Glover's Reef, therefore, are colonial according to this definition.

Functional Significance of Coloniality in Tilefish

1) Transfer of foraging information: It is unlikely that tilefish occur in colonies because proximity to conspecifics enhances the transfer of information concerning the location of food patches (Ward and Zahavi, 1973). Since both female and male tilefish forage solitarily within exclusive territories (see Chapter 5), there is little opportunity to gain foraging information from conspecifics.

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2) Limited availability of suitable habitat: Coloniality
may also evolve because suitable habitat is limited. Clarke et
al., (1977) suggested that a shortage of clastic material
explained the clumped distribution of <u>M. plumieri</u> in the
Bahamas. Sand rubble substrate, however, is not limited at
Glover's Reef. Unoccupied reef slope sites were common in the
lagoon. Some unused substrate was available even within the
channel where the largest and most dense concentration of
tilefish was located. Old burrow mounds on both unoccupied
reef slopes, and in unoccupied areas of the channel confirmed
that these habitats were suitable for construction of burrows.

I did not measure the availability of tilefish prey
(benthic invertebrates, see Chapter 5) on unoccupied sites
quantitatively. However, observations suggested that food was
available on sites not occupied by <u>M. plumieri</u>. Tilefish
sometimes chase goatfishes, <u>Pseudupeneus maculatus</u>; wrasses,
<u>Halichores spp.</u>; jacks, <u>Caranx spp.</u> away from their territories,
and pilfer food items from them. These species also feed on
benthic invertebrates, and may compete with tilefish for food
resources. These probable competitors foraged on sites that
were not occupied by tilefish, suggesting that benthic
invertebrates were available on these locations. Thus, it seems
unlikely that the distribution of tilefish is exclusively a
response to the distribution of potential prey.

3) Concentration by currents: Prevailing currents may play
a role in colony location and density. The prevailing oceanic
currents flow north-westwardly across the Caribbean towards

Glover's Reef (Stoddart, 1962). The channel site is one of two east-west passages on the eastern side of the atoll that connects the lagoon with the Caribbean (Figure 2). As a consequence of the prevailing currents, a large volume of oceanic water passes through the channel and the direction of flow across Glover's Reef is usually from the east to west (Stoddart, 1962). The high densities of adults and juveniles in the channel relative to reef slopes, therefore, are consistent with the hypothesis that large scale current patterns may influence the relative abundance of M. plumieri in different habitats. I did not measure smaller scale current patterns within the lagoon. Shallow lagoons like the one at Glover's Reef are flushed frequently, particularly in areas adjacent to passages, and current patterns change with wind direction (Shapiro et al., 1988). Thus, it seems unlikely that tilefish colonies occur merely because local currents concentrate planktonic larvae on some reef slopes while recruits do not reach adjacent sites within 30 m.

4) Predator avoidance: Contagious alarm responses to both natural predators and experimental stimuli suggest that living within visual range of conspecifics enhances detection and evasion of predators. In reef slope habitats, an abrupt retreat to the burrow usually elicited similar behavior by at least one neighbor. In the channel colony, erratic flight behavior by test fish before retreating to their burrows caused several nearby conspecifics to react similarly. Early detection of would-be predators would almost certainly facilitate evasion of attacks either by an immediate escape or by fleeing initially

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and then retreating into a burrow. Natural hiding places are scarce on sand rubble flats relative to those available on reefs. Furthermore, predators can strike from several directions. Under these conditions, settlement in colonies very likely enhances escape from attacks, and selection may favor individuals that settle near conspecifics.

Influence of Predator Behavior on Tilefish Avoidance Responses

The safety of individual prey may increase with the absolute size or density of groups (e.g., Brock and Riffenburg, 1960; Hoogland, 1979, 1980). On the other hand, large concentrations of prey may actually attract more predators (reviewed by Wittenberger, 1981; Alcock, 1984) to the extent that this counters potential benefits of group living. My results do not support the proposed positive relationship between individual safety and either colony size or density. The percentage of fish disappearing was much greater in the channel, even though reef slope colonies are smaller and fish are less dense. Although I cannot be certain of the fates of fish that disappeared, it is very likely that these individuals were taken by predators. Tilefish are strongly attached to their home sites (Chapter 5). Fish rarely change locations unless neighbors are removed, and even then move only into adjacent territories (Chapter 6). None of the tagged fish that disappeared from their original locations subsequently appeared in adjacent areas. Higher disappearance rates suggest, therefore, that the intensity of predation is higher in the channel than in reef slope habitats.

Responses by tilefish to both natural predators and
simulated attacks indicate that fish in reef slope and channel
colonies adopt different behavior with regard to avoidance of
predators. Furthermore, differences in tilefish behavior and
frequencies of disappearance may be related to differences in
predator activity. The channel is a primary route for daily
fish migrations including large piscivores that follow prey
swimming through this passage. Piscivores are particularly
active in the channel at dusk when tilefish are courting and
spawning (Chapter 5) and hence conspicuous. Channel tilefish,
therefore, are exposed to large numbers of mobile piscivores.
By contrast, the primary threat to tilefish on reef slopes
appears to be solitary barracuda utilizing stalking type
hunting techniques.

Tilefish might be expected to remain closer and retreat
more readily to their burrows where activity by predators is
high. My results show, however, that this was not the case.
Even though both channel and reef slope fish relied on home
burrows, channel fish were less closely attached to and
retreated less readily. One possible explanation of this
behavior is that channel tilefish do not readily detect
predators swimming high above them. Perhaps as a result,
retreats occur infrequently, and, as the high frequency of
disappearance suggests, threat of predation to channel fish is
high.

An alternative explanation is that immediate retreat to
burrows may not be an effective defense given the hunting

techniques employed by barracuda in the channel. The channel is deep relative to reef slopes, and barracuda usually swim high above. A tilefish that is undetected by a predator swimming high above might be conspicuous if it retreated abruptly. To avoid detection by predators overhead, it may be most effective to remain motionless. When attacked, erratic swimming that evokes similar behavior by nearby conspecifics may then become the best means of escape if such reactions distract or confuse a would-be predator. By contrast, remaining closer to the burrow and maintaining a high level of vigilance should be a more effective means of avoiding attacks where predators stalk tilefish along the substrate. Infrequent disappearance suggests that these tactics may be more effective than those adopted by channel fish.

CHAPTER SUMMARY

1. Tilefish are highly clumped on sand-rubble flats adjacent to isolated patch reefs (reef slopes) and in a single large aggregation within the channel.

2. The fixed locations of tilefish groups and of individuals within groups is consistent with Wittenberger's (1981) definition of coloniality.

3. Tilefish colonies do not result because habitat is limited, or because individuals benefit from social transfer of foraging information. The relative abundance of fish in reef slope and channel habitats may be a consequence of the influence on larval transport of large-scale water circulation patterns. However, it is unlikely that reef slope colonies result merely because localized currents concentrate planktonic larvae only in some patches.

4. Contagious reactions to barracuda and experimental disturbances suggest that proximity to conspecifics may reduce predation risk to individuals.

5. Barracuda hunt tilefish on reef slopes by stalking along the substrate, whereas in the channel barracuda attack from above. Perhaps as a result, reef slope fish remain closer to burrows, burrow more readily, and disappear less frequently than channel fish. By contrast, channel fish venture farther from burrows, retreat less readily and disappeared more frequently.

CHAPTER 5

REPRODUCTIVE BIOLOGY AND SOCIAL ORGANIZATION WITHIN COLONIES

INTRODUCTION

Polygynous mating systems are well documented in tropical marine fishes that inhabit coral or rocky reefs (reviewed by Thresher, 1984; Warner, 1984a). Because reef fishes are often sedentary and spawning is iterated, spacing of individuals in relation to food resources, potential mates, spawning and refuge sites, or all of these, may influence the type of mating system that evolves (e.g., Robertson and Hoffman, 1977; Moyer and Nakazono, 1978; Jones, 1981; Robertson, 1981; Thresher, 1984; Warner, 1984a; Shapiro, 1986). In particular, the behavior and distribution of females during spawning periods may influence the mating tactics that are successful for males. For example, in some species females leave their feeding ranges and congregate in favorable spawning sites where a few males are able to garner numerous matings by defending temporary territories (e.g., Warner, 1984a; 1987; Hoffman, 1985).

In contrast, polygyny may also involve male defense of permanent, all-purpose territories and monopolization of spawnings with a small group of the same females (i.e., harem-polygyny). Male defense of permanent territories and harem polygyny sometimes evolves when females do not migrate away from their usual feeding ranges in order to spawn (e.g., Robertson and Hoffman, 1977; Robertson, 1981; Hoffman, et al., 1985). Protogynous hermaphroditism is common in species with both types

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of polygynous mating system (reviewed by Thresher, 1984; Warner, 1984a; Shapiro, 1987a).

Although the importance of female behavior in the evolution of tropical marine fish mating systems seems evident, behavior of females has been studied much less than that of males (but see Shapiro, 1986; Warner, 1987). Kuwamura (1984) points out for harem species in particular, that few studies have examined in detail the spacing and social organization of females. Fishes that occupy flat open areas are particularly well suited for study of the use of space because these habitats allow unobstructed observation of the location of spawning activities, refuge sites, resources, and mates.

In M. plumieri, the potential for the evolution of polygamy is high because individuals aggregate in colonies. Intraspecific agonistic behavior and displays given to models led Clifton and Hunter (1972) and Clarke et al. (1977) to suggest that M. plumieri is territorial. The only other information on the social biology of this species are observations that tilefish sometimes spawn in pairs and release pelagic gametes (Colin and Clavijo, in press).

The objective of this chapter is to describe the social organization within tilefish colonies. In particular, I investigate the extent to which females and males defend territories, and the social and mating relationships among individuals. Because the distribution of necessary resources may have an important influence on spacing and mating behavior of pelagically spawning fishes, the locations of foraging and mating activities were examined in detail. Lastly, because

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hermaphroditism is an important component of the reproductive biology of many tropical marine species, and has been suggested for other tilefishes (Dooley, 1978; Ross and Merriner, 1982), the sexual ontogeny of M. plumieri was also investigated.

METHODS

Individual Use of Space

The use of space by individuals was investigated by continuously tracing the swimming path of a fish onto a map for 20 min. The slow rate of movement (5-13m/min) and strong affinity of individuals for home burrows facilitated recording of movements. Replicate traces were then overlayed, and the maximum perimeter of combined traces was drawn to estimate the home range of each individual. The composite trace of each fish was then drawn on a master map of the entire study site. Initial collection of ten replicate traces per individual (N=4 females and 4 males) indicated that four, 20 min traces taken on separate days yielded a reliable estimate of the size and location of an individual's home range. Additional traces changed the composite estimate of home range by less than 5%.

To determine if individuals occupied the same home ranges for long periods, I recorded the locations of fish for which spatial traces were mapped, as well as other tagged fish (N=73 females, 16 males) every few days for 1-4 months. Most fish lost tags from one season to the next, therefore, observations were terminated at the end of each field season on

all but a few fish. The duration of periods over which location was monitored varied because fish were tagged throughout my stay. Disappearance of fish due to predation and removal for other studies (Chapter 6) also contributed to variation in the length of observation periods.

To determine if tilefish defend part or all of their home range as a territory, I recorded the location-dependent social behavior of individuals. I used "exclusive occupancy of space by individuals (excepting mates, see below) by means of overt aggression and/or advertisement" (Brown, 1975; Wilson, 1975) as my working definition of territoriality. The locations, identity of participants, and outcomes of agonistic social interactions (see below) were recorded during spatial traces. These were then plotted onto the master map of the study site to examine whether or not individuals repelled or yielded to conspecifics depending on their locations.

Agonistic interactions occurred primarily near borders of neighboring home ranges. However, fish occasionally ventured into areas defended by neighbors. Such forays elicited aggression from neighbors, causing intruders to retreat. Therefore, area travelled over during such intrusions was not considered part of the territory of the fish that was chased away by a conspecific. Only the space that each individual occupied without evoking aggression from its neighbors, and from which it consistently repelled all intruders, was considered its territory.

Where the maximum perimeter of one home range was adjacent

to or overlapped that of a neighbor, defended borders were
estimated using the location-dependent outcome of agonistic
social interactions between neighboring fish. Borders of
neighboring territories were determined by plotting the
outermost segments of traces from where each fish chased away
its neighbors, and by excluding portions of swimming paths from
which that fish was itself chased away. On sides where there
were no neighboring conspecifics, territory borders were
considered to be the maximum perimeter of the home range. A map
of each territory was then constructed using these criteria, and
the areas of both home ranges and territories were measured
using a planimeter. Areas were measured in the horizontal plane
because tilefish live near the bottom (Chapter 4). However,
tilefish home ranges and territories include the water column
between the substrate and the surface.

Diet and Location of Foraging Activities

Diets were estimated by examining the preserved gut
contents of 25 females and 25 males. I could also observe
the prey eaten by M. plumieri because tilefish often repeatedly
grasped and spat out prey prior to ingesting them, apparently
to break prey apart. To examine the extent to which tilefish
foraged within their home ranges, the locations of bites were
recorded during spatial traces.

Agonistic Interactions

Agonistic interactions in which the focal individuals
participated were recorded during spatial traces. Interactions
involved one or several agonistic acts (see results) directed

toward and eliciting a response from a nearby conspecific. Either or both fish initiated aggressive acts during these exchanges. Interactions were recorded as "bouts," defined as agonistic exchanges between two fish that were separated by at least 1 min during which these fish did not interact with one another. Agonistic interactions by males were also recorded throughout focal observations during five spawning periods per male.

Reproductive Biology

Observations made throughout daylight hours suggested that reproductive behavior M. plumieri is restricted to a 2 h period prior to sunset. To describe courtship and mating behavior and document the distribution of daily matings within colonies, focal observations were conducted on 39 tagged males for a minimum of five spawning periods each. Throughout these periods, the frequencies of reproductive behavior and the identity of the participants were recorded. To examine whether individuals preferred certain sites for spawning, linear horizontal distance along the bottom between each female's burrow and the spawning site was also estimated for 60% of observed spawnings.

To examine the size distribution of male and female tilefish, 316 individuals ranging from 14.8 to 41.9 cm SL were sexed. Sex was determined by observations of spawning, and dissection and histology of gonads, or both. Specimens were collected by spear or trap and measured. Gonads were dissected from fresh specimens and preserved in Bouin's fixative. These

were later embedded in paraffin, sectioned (10-15 u), and stained with haematoxylin and eosin.

I attempted to induce sex change by removing individual males (N=20) that had been previously observed to spawn on successive days with at least one female. Observations were conducted during spawning periods for a minimum of three days following removal of males and intermittently thereafter to examine the behavior of females whose mate was removed.

In one test, all five males were removed from a colony on July 15, 1985. The remaining nine fish had previously spawned as females during at least five spawning periods. These individuals were marked with two tags to distinguish them from all other fish tagged at Glover's Reef. Loss of tags produced distinct scars where the skin was punctured. Therefore, even when tags were lost, these fish could be identified 8 months later when I returned in 1986 using double tag scars. Unique patterns of black skin spots were also recorded to aid in the identification of these individuals. These fish were monitored during spawning periods for 15 days following removal of males. In April 1986 this site was censused again, and the reproductive activity of fish surviving from 1985 was recorded.

RESULTS

Territorial Behavior of Females

Replicate traces of fish movements revealed that females each occupied a home range surrounding their home burrow sites. Overlap between adjacent female home ranges was low (Table 2).

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Table 2. Territoriality in female and male tilefish.

	SL(mm)	Territory area(m^2)	Percent[1] intrasexual home range overlap	Frequency of intrasexual interactions (bouts/h)
Females				
N	54	54	66	54
$\bar{X}$ (SE)	233.5 (4.37)	140 (9.7)	2.15 (0.35)	1.75 (0.67)
	*	*	*	*
Males				
N	39	41	30	39
$\bar{X}$ (SE)	333.1 (6.15)	411 (33)	7.45 (1.24)	1.06 (0.15)

[1]Intrasexual home range overlap is expressed as a percentage of the combined area of the two adjacent home ranges.

* p<0.01 Student t-test comparisons between females and males.

Ninety-one percent (96 of 106) of the agonistic interactions (see below) between females that were mapped, began within 2 m of the overlap of the maximum perimeters of two neighboring female home ranges. Each female repelled intruders aggressively from much of her home range ($\bar{X}$ percentage of home range area that was defended=90.8, SE=1.7, range=47.4-100.0, N=54 females).

The location, size, and shape of female territories is shown for one colony in Figure 7. Borders of abutting territories were defined clearly by the location-dependent outcome of agonistic interactions. In 87% of interactions observed, intruders were intercepted and repulsed before they had encroached farther than 1 m inside the border of a neighbor's territory. Less often (13% of interactions), intruders had penetrated deeper than 1 m (range=1.5-8 m) into a neighbor's territory, whereupon they were intercepted and repelled by the owner. Disputes were usually terminated when the intruder was chased or escorted off the territory. Intruder/occupant roles were reversed if, while escorting an intruder, the occupant encroached onto its opponent's territory. Agonistic encounters, therefore, ended between neighboring borders or on borders that were contiguous, and invariably ended in a "stand-off" without the participants acquiring space currently occupied by the other fish.

During agonistic interactions between females, each fish performed one or more of the following behaviors: displays, involving erection of the medial or pelvic fins; abrupt upward "jumps" while the pelvic and medial fins were held erect; short (<1 m) displacements of the opponent; long (>1m) chases; and

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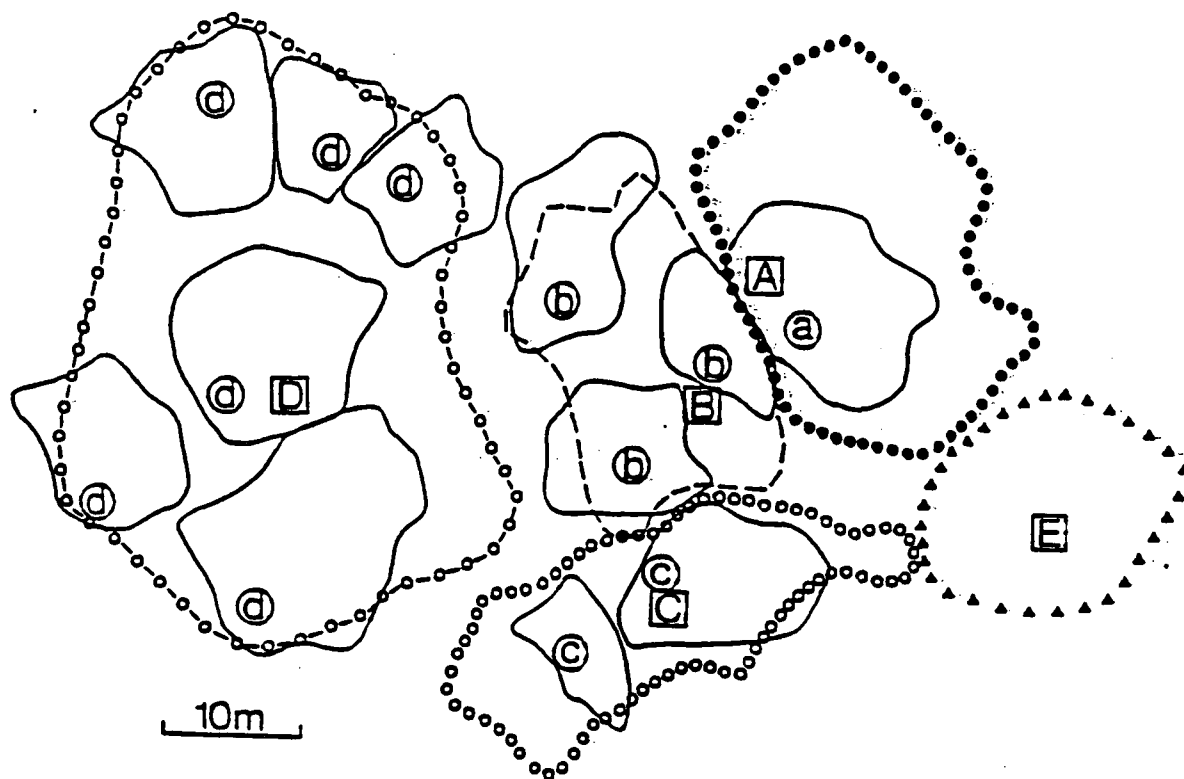
Figure 7. Map of one tilefish colony consisting of four harems ranging in size from 1 to 6 females. Female territories are enclosed by solid lines, and male territories are distinguished by lines composed of different symbols. Male burrows are indicated by squares containing capital letters. Burrows occupied by each female are circles labeled with lower case letters that correspond to their male mate. Burrows are not drawn to scale. Male E was unmated.

violent bites on the opponent's tail and fins. Interactions also included "circle displays" in which two opponents positioned themselves laterally to one another, head-to-tail, with medial and pelvic fins flared and mouths and opercula held stiffly open (Figure 8a). While in this position, each fish swam rapidly in the same direction in a small (~1 body length diameter) circle. Territorial disputes varied both in their intensity and duration. Some involved only the exchange of fin displays, while others escalated into longer and more violent exchanges.

Females participated in intrasexual aggression at different rates (Table 2). Frequencies of aggression were not correlated with female body size (r=-0.25, N=54 females, NS), and territory occupants repelled intruders regardless of their relative size. Females also reacted aggressively toward intruder males other than their mates (see below). These occurred more than 12 times less frequently, (t=7.87, p<0.01, $\bar{X}$=0.14/h, N=54 females, SE=0.04) than intrasexual disputes, perhaps because male intruders were usually intercepted by male territory occupants (see below).

The size of female territories was highly variable (range= 43-309 m^2. There was no correlation between female size and territory area (r=-0.04, N=54 females, NS), nor was the size of female defended areas related to the total number of females that were spawning with the same male (r=0.16, N=54 females, NS). The positions of female territories remained stable, providing that adjacent females were not removed (see Chapter 6). None of the females whose location was monitored (total N=127), shifted
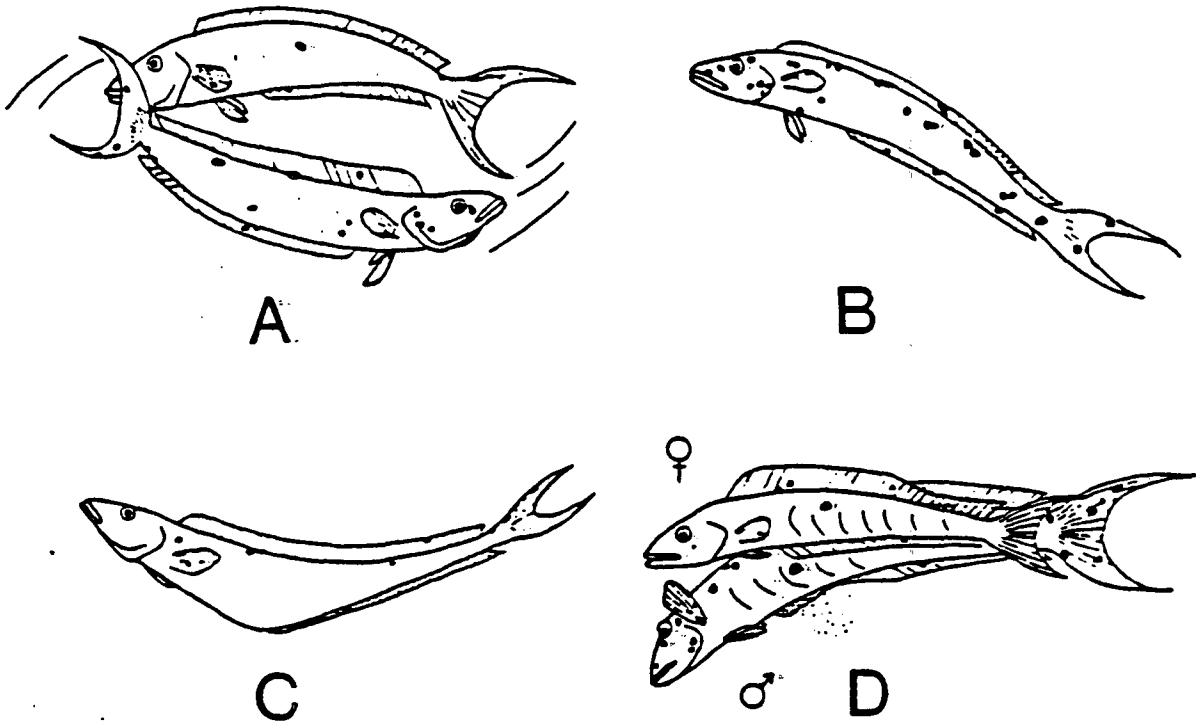
Figure 8. Aspects of social and reproductive behavior in sand
tilefish. A. circle display. B. Male advertisement display.
C. Female arc display. D. Male and female at apex of
spawning ascent. Black spots on fish are melanization of
encysted trematodes.

their burrows or territories spontaneously over periods ranging from one to four months. Moreover, three females that retained tags over two study seasons occupied the same territory for at least nine months.

Territorial Behavior of Males

Traces of fish movements also revealed that males each occupied a stable home range around their home burrow. Intrasexual overlap between adjacent male home ranges was about 3.5 times (t=3.65, p<0.01) larger than that of females (Table 2). Ninety-three percent (84 of 90) of agonistic encounters between males began within 2 m of where the maximum perimeters of two neighboring male home ranges overlapped. Male-male agonistic interactions involved the same behaviors described above for females. Males also each defended exclusive occupancy (excepting their mates, see below) of most of their home ranges ($\bar{X}$ % of home range that was defended=80.3, SE=4.2, range=50-100%, N=39 males) from intruder males. In 80% of all agonistic interactions, male intruders were repulsed within 1 m of territory borders, while in 20% of encounters an intruder penetrated 2-10 m before he was detected and chased. The frequency with which males participated in agonistic disputes was not correlated with male size (r=0.09, N=39, NS). Male disputes with neighboring females (i.e., females mating with adjacent males) also occurred, but were less frequent ($\bar{X}$=0.32 interactions/h, SE=0.08, t=3.29, p<0.001, N=39 males) than with neighbor males. The size of male territories was also highly variable (range=73-950 m^2), but territory area was not

correlated with male size (r=-o.18, N=39 males, NS). Though males occasionally went on extra-territorial excursions (see below), only 1 of 57 males shifted the location of his territory over one to four month observation periods. Furthermore, six males that retained tags between two study seasons occupied the same areas nine months later.

Although male territories were larger (t=6.69, p<0.01) than those of females, females participated in intrasexual aggression more frequently than males (t=2.68, p<0.01, Table 2). Home range overlap between adjacent males was greater than that of females, because males sometimes swam farther than 5 m beyond their defended borders without being elicited by an intruding conspecific. Extra-territorial excursions were rapid forays into territories defended by adjacent males, and occasionally across more than one neighboring territory. Such excursions were infrequent ($\bar{X}$ excursions/h=0.26, N=39 males, SE=0.05), and accounted for less than 1% of the total observation time. Behavior of males was clearly different during these excursions. Males either swam very fast or swam more slowly on the bottom as if to avoid detection. However, intruding males were almost always detected and chased away by territory occupants of both sexes. Although escalated border disputes sometimes took females onto neighbor territories, they did not make long extra-territorial excursions like those of males.

Tilefish foraged within their territories primarily on benthic invertebrates. At least 60% of the stomachs of both females and males contained gastropod and bivalve mollusks, crustaceans, and polychaete annelids (Table 3). I also observed both sexes capturing and eating these invertebrates. Maps of foraging bites revealed that an average of 97.5% of foraging bites by females (N=54, SE=0.57) and 97.0% of foraging bites by males (N=25, SE=1.24) were taken within the boundaries of their defended areas. Both sexes also chased other fish species that were feeding on benthic invertebrates within their territories, although these species were too numerous to be excluded completely. Females attacked heterospecifics more frequently (t=3.46, p<0.01, $\bar{X}$=1.28 chases/h, N=54 females, SE=0.23) than males ($\bar{X}$=0.32 chases/h, N=23 males, SE=0.07).

Reproductive Behavior

Sand tilefish spawned during all months that I was present at Glover's Reef (February through August). Spawning has been reported from October to April in Puerto Rico (Colin and Clavijo, in press), suggesting that M. plumieri may reproduce throughout the year. Observations conducted throughout the day confirmed that spawning occurred exclusively from 1630 to 1830h. All 541 spawnings observed in unmanipulated fish occurred during this time period, as did an additional 150 spawns observed in various experiments (see Chapters 6 and 7). Spawning males were larger than their mates and almost always larger than other

Table 3. Stomach contents of female and male sand tilefish.

	Percentage of Total Guts Containing		
	Crustaceans	Mollusks	Polychaetes
Females (N=25)	60	76	80
Males (N=25)	67	76	67

females within the colony. Female and male tilefish are
otherwise monomorphic.

Tilefish mating was exclusively pair-spawning involving a
single male and female. The reproductive period was
characterized by males swimming about their territories
performing "advertisement" displays. This consisted of a series
of upward jumps at a 30-45 degree angle (Figure 8b), each
followed by a downward glide. The white pelvic fins were
alternately held erect and outward from the body while
ascending, and relaxed during downward glides. Males performed
advertisement displays throughout their territories, whether or
not females were nearby.

Pair-spawning was initiated by females. When ready to
spawn, a female ascended 1-3 m above the bottom while protruding
her abdomen in an exaggerated manner. As she ascended, the
snout and caudal fin were also pointed upward, forming her body
into a shallow inverted arc (Figure 8c). If the display
attracted her mate, the two fish "paired" side-by-side and
remained in this position often rubbing bodies for 5 to 60 sec.
Paired fish often parted and then re-paired 1 to 10 or more
times prior to a spawning ascent. An ascent began when the male
swam laterally to but slightly above and behind the female.
While in this position, the pair ascended 2-4 m at a 30 to 40
degree angle above the horizontal. During the last one-third of
the ascent, the abdomen of each fish quivered and gametes were
released externally (Figure 8d). Following gamete release, both
adults returned immediately to the bottom. Each female spawned
above her territory near to her burrow ($\bar{X}$ distance from burrow

to spawning site=3.8m, N=401 spawns, SE=1.0).

Social and Mating System

Data on social interactions, the location of male territories in relation to those of their mates, and the distribution of spawnings (Table 4) revealed that tilefish have a mating system characterized by male monopolization of one or more females (i.e., harem polygyny). Male territories encompassed the burrow and most of the territory occupied by each mate (Figure 7, Table 4) in all fish for which spatial traces were recorded. For females whose territories were not mapped, but whose mate and burrow location were known (N=73), the male's territory at least encompassed the burrows of all mates.

Males initiated aggressive interactions with each female within their territories (Table 4). Aggressive interactions by males with their mates were the same as those described for intrasexual disputes, except that they did not involve circle displays. In some instances, males attacked or chased females in response to female territorial disputes (Table 4). Such intervention was usually (86% of all interventions observed, N=39 males) elicited from a male when two of his mates entered into a dispute. The other interventions occurred when one mate was interacting with a female from a neighboring harem.

Although disputes between females were common, females did not initiate aggression with the male whose defended area encompassed their territories. In response to aggression from mates, females either fled, lowered their head and swam

Table 4. Male social and reproductive monopolization of harems.

	Male interactions/ mate/h	Percent male intervention responses/mate	Percent[1] female territory overlapped	Pair-spawns /female/day
Number of females	94	94	54	94
Mean(SE)	1.09(0.08)	13.25(2.18)	72.9(2.77)	0.91(0.05)

[1]Percentage of male intervention responses is the proportion of each male's interactions with his mates that was elicited by intrasexual aggression involving those females.

beneath the approaching male, or briefly (1-10 sec) exhibited an arc display.

Females maintained almost exclusive spawning fidelity with one male. Focal observations on 10 females for entire spawning periods revealed that these fish mated only with the males that defended areas which encompassed each of their territories. In only 3 of 691 pair-spawns (0.4%) did a female (N=94) mate with a partner other than the male whose territory overlapped her burrow and territory. In each instance of infidelity, the female's usual mate was inside his burrow for a large part of the spawning period, and she spawned with a male that occupied an adjacent territory. Females sometimes spawned as many as three times during a single daily reproductive period, but did not spawn during 22.5% of the total reproductive observation periods (see Chapter 7).

Males spawned as many as 10 times/day, and the number of mates (harem size) of males ranged from 1 to 6. There was no correlation between male size and harem size (N=39 males, r=-0.18, NS), nor did spawning frequency per female vary consistently with harem size. Because male territories encompassed much of each female's territory (Table 4), harem size was positively correlated (p<0.001) with male territory area (Figure 9).

All colonies also contained individuals that were not observed to spawn. The size of these fish ranged from 19.0 to >29.0 cm SL. Spatial traces and observations on social interactions of 10 non-mating fish showed that they each occupied a home burrow and were aggressive to nearby mating and
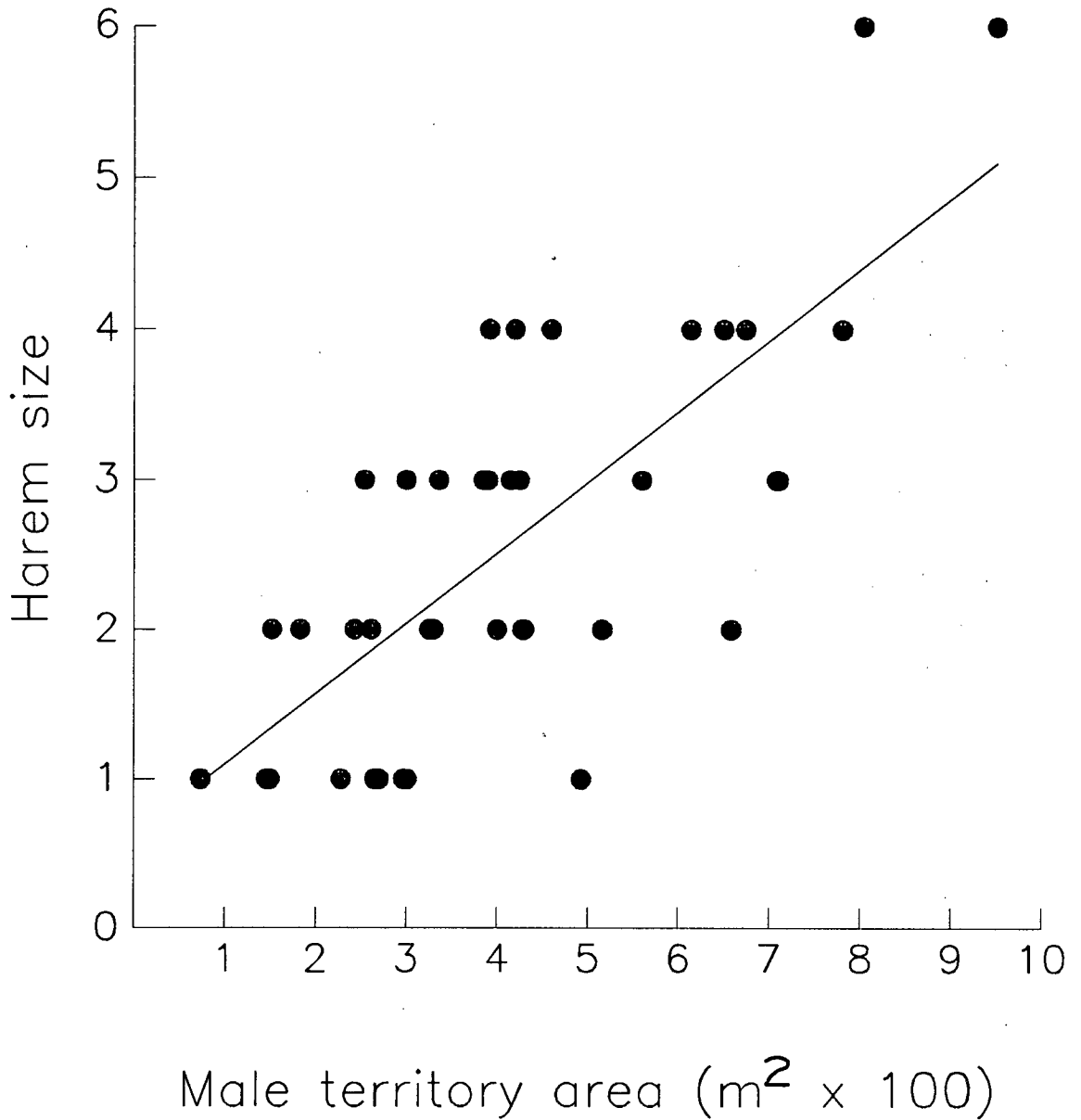
Figure 9. Male harem size (number of female mates) as a function of the territory areas (m^2 x 100) of 41 males. Line is least squares regression described by the equation, harem size = 0.626 + 0.47 territory area, r=0.75, p<0.001.

non-mating conspecifics. Histological examination of six non-spawning individuals (24.4-29.2 mm SL) revealed that these fish were males. Location and outcome of social interactions revealed that large unmated males defended territories from neighboring males. Unmated males were adjacent to one or more harems but their territories did not encompass territories occupied by females. Territories of these males usually encompassed one or more smaller non-mating fish. Dissection and histology of two small specimens revealed that they had immature gonads. Although I mapped interactions of only four small non-mating fish, they did not appear to defend exclusive territories. Areas occupied by these fish overlapped considerably (20 to 70%) with one or more similarly sized conspecifics, and the outcome of social interactions was not clearly related to location.

Evidence of Protogynous Sex Reversal

Figure 10 shows the size distribution of the sexes for 316 fish collected from 20 colonies. There is a large size overlap between the sexes, however, females and males predominate in small and large size classes respectively. Several aspects of gonad microstructure indicate that M. plumieri is a protogynous hermaphrodite. Twelve specimens ranging from 19.1 to 24.3 cm SL had gonads that appeared to be transforming from ovary to testis. Transitional gonads contained spermatogenic crypts adjacent to degenerating ova (Figure 11a & b). Although late stage transitional gonads are similar to testes, they are distinguished from functional testes by the absence of free
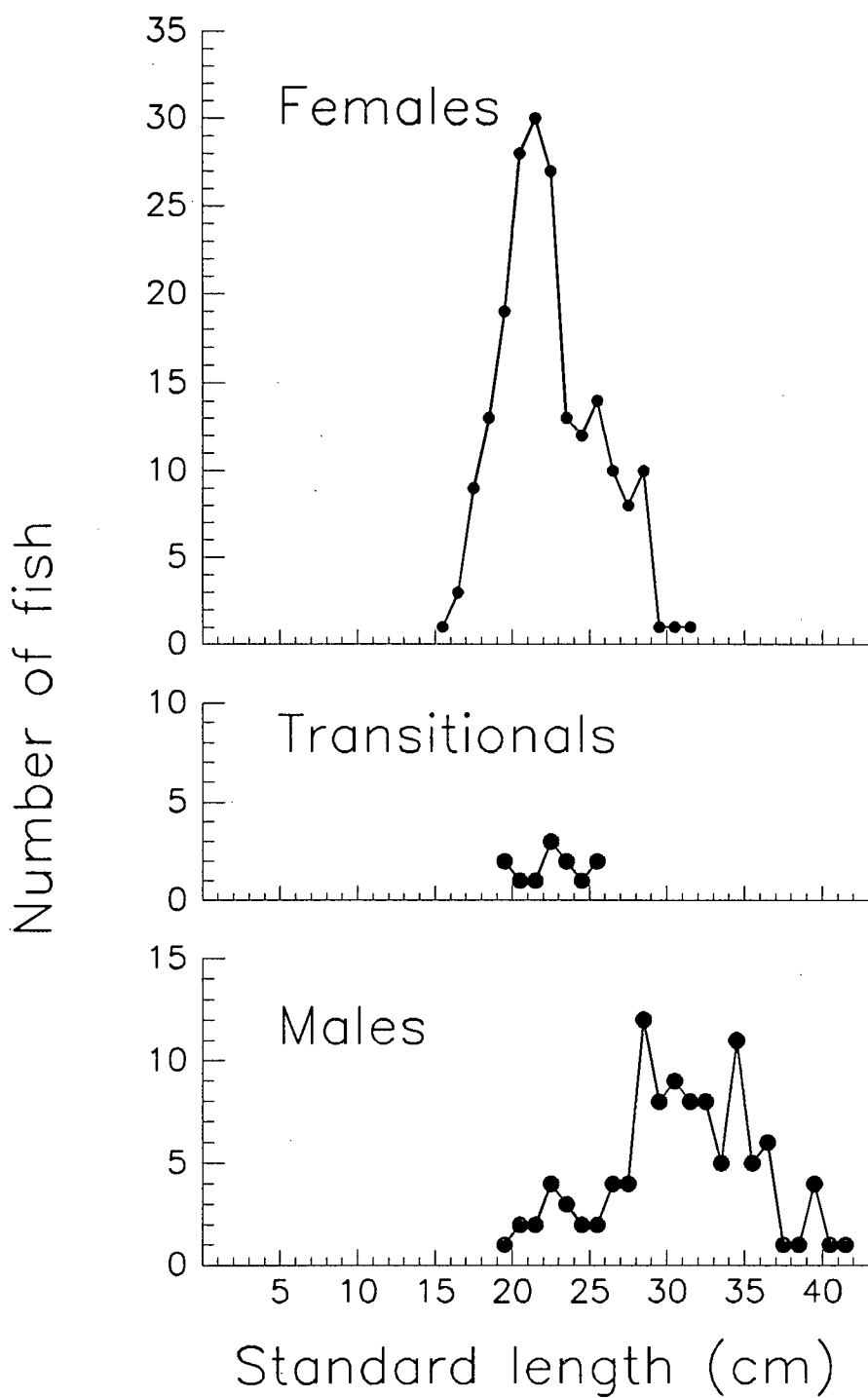
Figure 10. Body size distribution of males (N=104), transitionals (N=12) and mature females (N=200).

Figure 11. Photomicrographs of transverse sections of tilefish gonads. Black bars give scale for each panel. a. and b. Transitional gonads showing developing spermatogenic crypts adjacent to several degenerating ova. c. and d. Male testes showing sperm sinuses containing spermatozoa, atretic ova in c, and a narrow cavity that may be a remnant of the ovarian lumen in d. SC-spermatogenic crypts, DO-degenerating ova, SS-sperm sinuses, SZ-spermatozoa, OL-remnant of ovarian lumen.
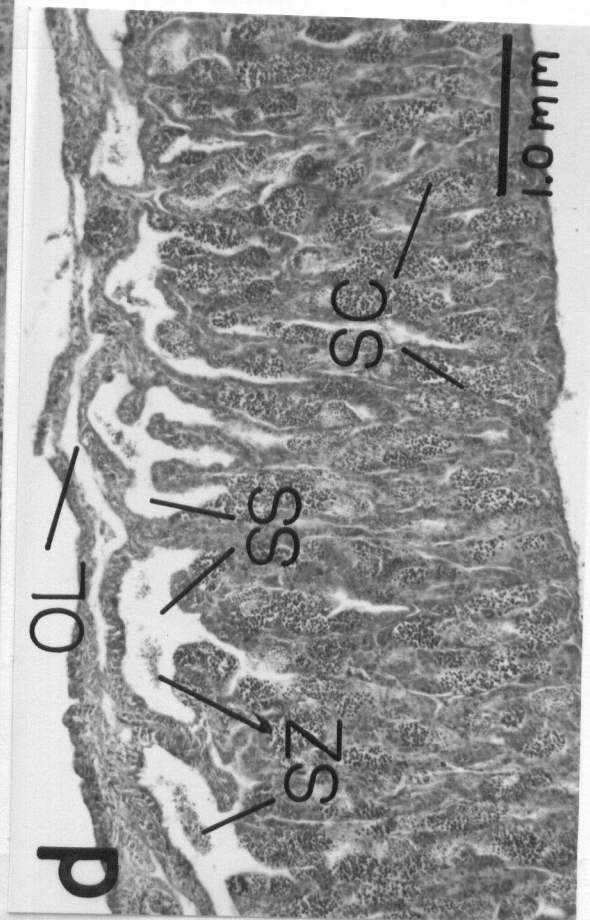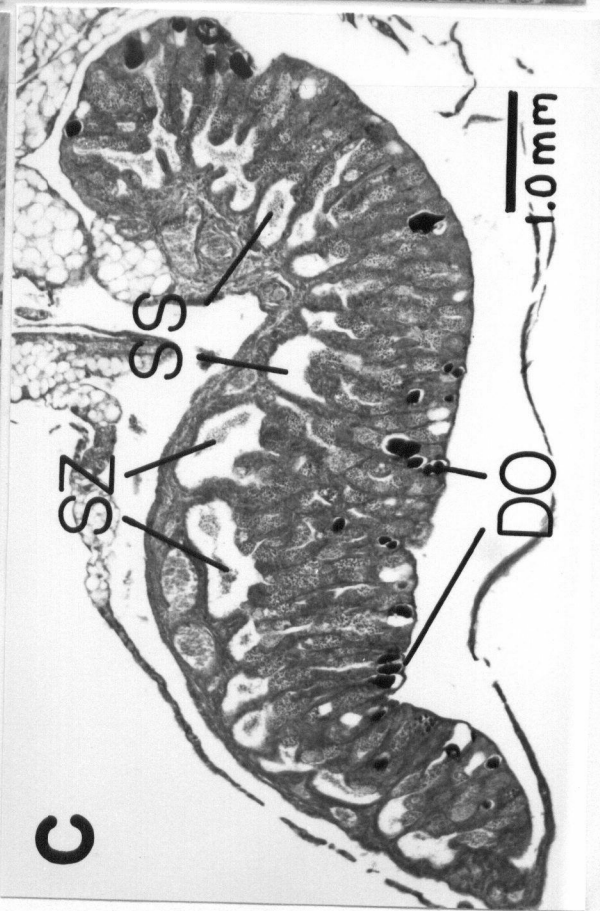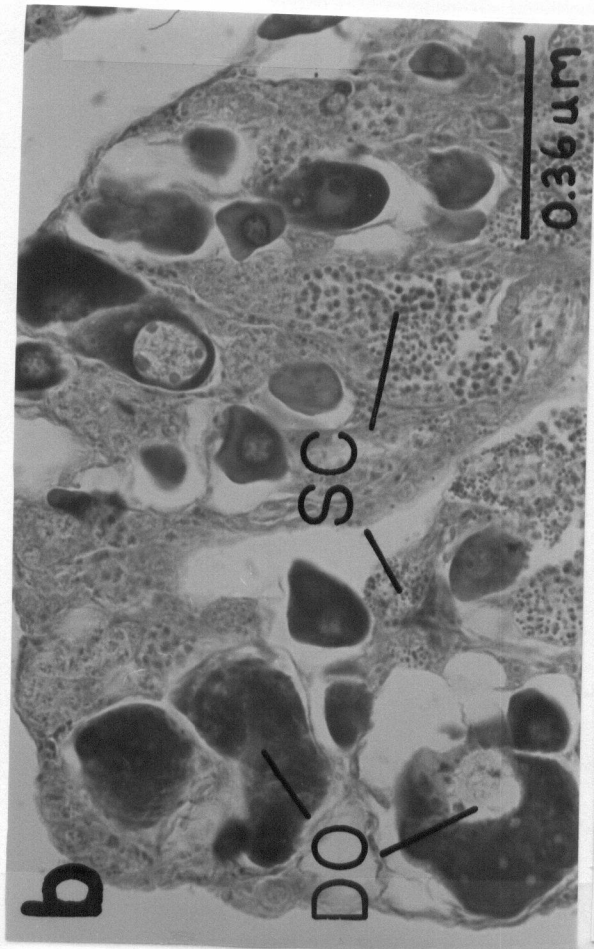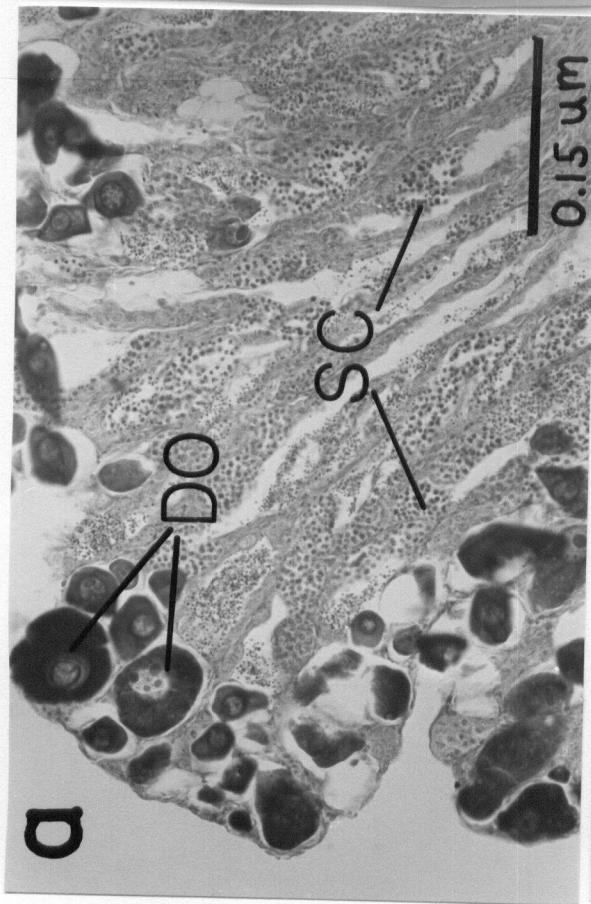
spermatozoa within sperm sinuses (see below). Atretic, previtellegenic ova were most pronounced in transitional gonads. However, transitional specimens also contained degenerating ova that appear to have attained later stages of vitellogenesis, suggesting that these fish had functioned previously as females.

The structure of all testes examined histologically (N=79) also suggests protogyny. All testes contained several sinuses adjacent to the medial wall of the gonad and between internal membranes (Figure 11c & d). These sinuses ran the length of the gonad and always contained free spermatozoa. Sperm sinuses of this type are often characteristic of sex-changing species because they form as separations in thickened areas of the former ovarian wall and membranes (Sadovy and Shapiro 1987). Many testes also contained degenerating ova, particularly on the lateral edge of the gonad opposite to sperm sinuses (Figure 11c). Fifty-four testes (68%) contained atretic previtellogenic ova and later-stage yolky ova were evident in 33 specimens (42%). A few testes also contained a narrow membrane-lined cavity that may be a remnant of the ovarian lumen (Figure 11d). This cavity was not apparent in most testes however, perhaps because it was occluded by densely packed spermatogenic tissues.

Behavioral sex change was observed in one fish following the removal of all males from that colony. By contrast, in all single male removals, females did not change sex and resumed spawning with a male that moved to encompass their territories (Chapter 6). Following removal of all males from a colony in 1985, all females remained on the site at least until my departure (15 days). No behavioral evidence of sex change was

observed during this period. In April 1986, one
fish was identified as a survivor from 1985 using distinctive
double tag scars together with records of her spots. The other
eight tagged females were not present on the experimental site
or in other colonies within at least a 100 m radius. The 1985
survivor was observed to court and spawn with two smaller
individuals that had recruited during my absence. Dissection
revealed that both smaller fish were females and the 1985
survivor was now a male. Histological examination showed that
the gonads of this fish were small but functional testes
containing a few atretic ova. The only other tilefish present
on this site were two small juvenile recruits.

DISCUSSION

Territoriality and Harem Polygyny

Female and male tilefish aggressively excluded all
conspecifics except their mate(s) from areas surrounding their
home burrows. Therefore, tilefish are territorial (sensu
Brown, 1975; Wilson, 1975; reviewed by Searcy, 1986).
Individuals each foraged, spawned and burrowed within these
"all-purpose" territories. The defense of territories by each
sex results in a well defined spatial structure within colonies.
Territories of females were adjacent to female neighbors on one
or more sides. The larger territories of spawning males were
arranged as a mosaic, with each territory being superimposed
over those of one or more females (Figure 7). Males were larger
and maintained social dominance over the females within their

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territories by means of aggression. Spawning data confirmed almost exclusive female mating fidelity with dominant males. Therefore, colonies each consisted of adjacent social and mating units that are appropriately referred to as harems (sensu Robertson and Hoffman, 1977).

Protogynous Hermaphroditism in Sand Tilefish

Histological and behavioral evidence indicate that M. plumieri is capable of functional sex change from female to male. Sperm sinuses that are derived as separations between ovarian membranes, atretic ova in testes, and observations on a known individual spawning first as a female and later as a male together are strong evidence of protogyny (Sadovy and Shapiro, 1987). To my knowledge, these results are the first evidence of functional hermaphroditism in the Malacanthidae. The presence of at least one morphological indication of gonad reorganization in all testes suggests that all male tilefish are derived through sex change (monandry). Monandry is common among species with harem mating systems. Presumably small males without territories are unable to breed because larger sex-changed territorial males are able to monopolize all available females (Warner, 1984a). Male reproductive tactics other than excluding competitors from territories occupied by female mates were not observed.

Although my results show that M. plumieri is capable of functional protogynous sex reversal, the factors that control the onset of sex change and the evolutionary significance of when individuals transform are not yet clear. Protogyny may

evolve when large males are able to mate with a disproportionately high number of the females in local populations. Under these conditions, individuals may maximize their lifetime reproductive success by functioning as females when small, and then changing sex when they are large enough to compete as males (the size-advantage hypothesis, Ghiselin, 1969; Warner et al., 1975).

Among the best support for the size advantage hypothesis are harem-forming species in which sex change occurs according to linear social hierarchies that are based on the relative size of fish within each mating unit (e.g., Robertson, 1972; Moyer and Nakazono, 1978; Hoffman et al., 1985). In such species, large females reportedly change sex only when the dominant male is removed, and sex reversal usually occurs over a relatively short time period. There are apparently no unmated "bachelor males" in these species, and sex-changing fish suffer few lost mating opportunities during the transformation (Hoffman et al., 1985).

Tilefish differ from these harem-forming species. Female tilefish did not change sex in response to removal of one male. One female ultimately transformed following removal of all males from her colony. However, only limited conclusions can be drawn regarding the proximate cues that triggered sex change in this instance. Fish were not observed for eight months during which time at least one female changed sex but eight others disappeared for reasons unknown. No behavioral changes by any of these females were evident during the two week observation

period immediately following removals. These results suggest that gonad reorganization in tilefish may take longer than two weeks, if it was triggered in this female by removal of males.

There is also no evidence that female tilefish are arranged in social hierarchies, within harems or colonies, that determine the sequence of female sex change should it sometimes occur in response to male removals. The outcome of social interactions among females was not determined by relative size as is reported for some other harem species (Hoffman, 1985). Finally, the presence in all colonies of either small transitional fish or large sex-changed but unmated males indicates that some individuals change sex without there being immediate opportunities to acquire females. Fifteen unmated tilefish males occupied territories without resident females for 2 to 4.5 months. These results suggest that some female tilefish change sex but do not spawn as males for long periods until a vacancy occurs. Similar observations regarding the onset of sex reversal have been reported for other species with harems (Clavijo, 1982; Moyer and Zaiser, 1984; Aldenhoven, 1986; Shapiro, 1987a).

Aldenhoven (1986) proposed a model for harem mating systems that compares the reproductive value of changing sex and becoming a bachelor male before there is an opportunity to acquire mates, with that of remaining female until there is an immediate male vacancy created by the death of a male. At certain population densities, "early sex-changed bachelor male" and "remain female" phenotypes may exist in a frequency-

dependent equilibrium that is evolutionarily stable (Aldenhoven, 1986). If the chance of obtaining a harem is higher for individuals that change sex before a male dies than those individuals that continue to spawn as females until a vacancy occurs, than there may be selection for some individuals to change sex when they are relatively small. Potential reproductive rewards for such bachelor males almost certainly would diminish as they become more abundant in local populations. Therefore, selection may also favor other individuals that remain female as long as male mates are present.

Several observations on M. plumieri are consistent with the hypothesis that some individuals change sex when they are relatively small and do not mate until a male vacancy occurs. Unmated males and/or transitional individuals that were smaller than nearby females were common in tilefish colonies. Forty-four percent (11 of 25) of experimental male removals resulted in an unmated male moving into vacant harems (Chapter 6). Also, the disappearance of a substantial percentage of tagged fish, presumably due to predation (Chapter 4), suggests that natural vacancies may occur frequently enough that the future potential for unmated males to acquire harems may be sufficiently high to favor early sex change. Together, these results suggest that a frequency-dependent balance between bachelor males that changed sex early, and fish that remain female unless male vacancies are not filled, may be at least plausible in sand tilefish.

CHAPTER SUMMARY

1. Both females and males occupy all-purpose home ranges surrounding their home burrows. Home range overlap among adjacent fish of the same sex is low and individuals defend exclusive use of much of their home range against all conspecifics except mates (i.e., territoriality).

2. Areas defended by males overlap the territories of up to 6 females, and male territory area is positively correlated with the number of female residents.

3. Males maintain dominance over females within their territories by aggression, including intervention into some female disputes.

4. Females spawn pelagically-dispersed eggs as frequently as every day. Each female spawns almost exclusively with the male whose defended area encompasses her territory (harem polygyny). Some males have up to six female residents within their territories

5. M. plumieri is capable of functional protogynous sex reversal, however, sex change is controlled by factors other than size-related social hierarchies within harems or colonies.

CHAPTER   6

THE FUNCTIONAL SIGNIFICANCE OF HAREM POLYGYNY

INTRODUCTION

Two hypotheses have been proposed to explain the evolution
of harem polygynous mating systems like that of M. plumieri.
The resource defense hypothesis proposes that an uneven
distribution of critical resources for females allows some males
to monopolize more than one mate (Emlen and Oring, 1977). The
female defense hypothesis proposes that males are able to
control groups of mates directly because females aggregate for
reasons that are unrelated to the acquisition of resources
necessary for reproduction, for example to reduce the threat of
predation (Emlen and Oring, 1977).

There are usually obvious advantages to males of obtaining
more than one mate. The evolution of harem polygyny, however,
must also depend on the consequences to females of sharing a
male and living in groups that can be monopolized by a male. In
species that nurture offspring, the costs to females of mating
in a harem and living close to conspecifics may include both
reduced paternal care and increased competition for resources
(Wittenberger, 1979). Selection should favor females that join
harems, provided that these costs are more than offset by
compensating advantages. Advantages may involve access either
to a better quality male and/or resources (Verner and Wilson,
1966; Orians, 1969; Altmann et al., 1977; Wittenberger, 1979),
or a reduction in predation from group living (Altmann et al.,

1977; Wittenberger, 1979).

Harem mating systems have also been documented in marine fishes other than M. plumieri that spawn planktonic gametes (reviewed by Kuwamura 1984; Thresher 1984). Obviously there is no cost to females arising from a reduction in paternal care in such species. However, female defense of exclusive territories or aggression toward consexuals that occupy fixed but overlapping home ranges (Robertson and Hoffman, 1977; Moyer and Nakazono, 1978; Stroud, 1981; Clark, 1983; Hoffman, 1985; Nemtzov, 1985; Victor, 1987; Baird, 1988) suggests that females may compete for resources in these systems.

Site-specificity by females appears to promote male monopolization of multiple mates. Understanding factors that shape female spatial behavior, therefore, is central to the question of whether males monopolize daily spawnings with multiple mates through control of resources, females, or both. The evolution of harems in pelagically-spawning tropical marine fishes has been attributed to both male defense of resources (Robertson and Hoffman, 1977), and to direct defense of females (Hourigan, 1986; Victor, 1987). In other species, this issue appears to be unresolved (Moyer and Nakazono, 1978; Moyer, 1979; Kuwamura, 1984; Kobayashi, 1986). Few if any studies, however, have examined empirically the factors that influence the location and distribution of females in harem-type mating systems.

I documented the territorial behavior of females and males and the mating system of M. plumieri in Chapter 5. The objective of the present chapter is to investigate the influence

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of conspecifics and resources on the locations of females and males to examine the evolutionary significance of harem polygyny in tilefish. The extent to which female and male tilefish are attracted to potential mates, and that the locations of individuals are restricted by intrasexual competition was examined in a series of removal experiments. Whether or not females occupy and defend certain locations may also be influenced by the distribution and abundance of food and other limited resources (reviewed by Davies and Houston, 1984; Vehrencamp, and Bradbury, 1984). The spatial distribution of food resources and female foraging was examined by observation of feeding behavior and quantitative assessment of potential invertebrate prey in surface sediments. The importance to females of specific burrows was investigated by recording responses to removal of these structures.

METHODS

Techniques For Fish Removal Experiments

Experiments involving removal of fish (singly or in groups) were conducted to examine the influence of conspecifics on the locations and behavior of remaining fish. More than one test was often conducted within large colonies. When multiple tests were performed, replicates were begun no sooner than two weeks after previous tests, well after fish locations had stabilized (see below). Responses to removals were measured by daily observations on all fish near experimental sites for a minimum of two weeks (range = 2-8 weeks) before and after each test. A

two week minimum period between multiple tests and for observation of responses was adequate because changes in locations of adjacent fish occurred within two days (see Results). Because tilefish occur on flat open substrates and are each restricted to specific burrows and territories, the locations of individuals before and after removals could be recorded readily. Most fish occupying territories next to removal sites were tagged. Untagged fish were identified by noting unique spot patterns. Fish were removed either by spear or by trapping them in burrows.

The locations of individuals were monitored for at least two weeks prior to each removal to control for the possibility of spontaneous changes in location (pre-removal controls). For tests involving removal of one fish, a second control consisted of monitoring another similarly sized fish of the same sex during the period when the test fish was removed (non-removal controls). Non-removal controls resided in the same colony, but on a territory not adjacent to that of the removed fish. Observed and predicted frequencies under null hypotheses for each type of experiment (see below) were compared using Binomial tests. Responses to removals were compared to controls with the Chi-squared statistic.

SPECIFIC TESTS

Factors Influencing the Distribution of Females

A. Intrasexual Competition

Defense of exclusive territories suggests that intrasexual

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competition may restrict use of space by females. To examine this hypothesis, individual females (N=38) were removed from territories that were adjacent to female neighbors on several sides. Assuming that males do not restrict female mobility (see Results), and if females do not compete for space, then each fish should occupy a preferred location and removal of one female should not result in spatial shifts by her neighbors. Alternatively, if competition restricts the location or size of female territories, removal of one female should result in spatial changes by adjacent fish.

B. Males

Movement by females may also be restricted by dominant males. Removal of one female often resulted in movement by female neighbors (see Results). Therefore, female removals could also be used to test whether males are not able to control movement by their mates. If females move to territories defended by other males when a female neighbor is removed, then the hypothesis of male control can be rejected.

Females may also choose locations on the basis of proximity to male mates. If this is true, then females should attempt to move closer to adjacent males when the mates of these females are removed. Neighboring females may resist encroachment by females attempting to move closer to other mates. However, females could move closer to adjacent males by digging new burrows or by occupying unused burrows closer to the edges of their existing territories. The possibility that females choose locations near males was examined by comparing the burrow

locations of females (N=54) before and after removal of their
mates (N=29). The identity of males with which females resumed
spawning was determined in 25 tests.

C. Burrows

Exclusive use of specific home burrows, even though unused
burrows are abundant, suggests a strong preference for certain
locations over other potential sites. The influence of home
burrows on female location was examined by removing the
structures occupied by "test" females (N=12) whose territories
contained at least one unused burrow. Burrow removals involved
dismantling these structures and moving all materials away from
the test subject's territory. Because occupation of burrows on
adjacent territories would probably be resisted by neighbors,
test females must either 1) excavate other burrows within their
territories, 2) reconstruct their original burrows, or, 3) do
without burrows. Refurbishing unused burrows should require
less time and energy than reconstructing removed burrows.
Therefore, females were expected to refurbish unused refuges
unless original burrow sites are preferred.

D. Food Resources

Even if females prefer particular burrow sites, territories
of tilefish females are much larger ($\bar{X}$ area = 140 m^2, Table 2)
than necessary to ensure access to burrows alone. The size of
female territories suggests that females may also defend other
resources, such as food. Rates of egg production and growth are
often influenced by food intake in female fishes (Scott, 1962;
Bagenal, 1969; Wootton, 1973; 1977; Hislop, et al. 1978).

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Furthermore, production of eggs each day almost certainly carries high energetic costs (Hoffman, 1983). Thus, if the distribution of prey is such that defense of a food supply is feasible, female tilefish may defend territories to ensure access to food resources near burrows.

To estimate the distribution of the benthic invertebrates found in tilefish stomachs (Chapter 5), samples of surface sediment were collected at pre-determined grid points spaced evenly (10 m apart) throughout five colonies. Each sample was collected by scooping 2.5 liters of sediment from a quadrat (0.25 m^2) to a depth of 5-7 cm. Organisms were sifted with a 2 mm mesh screen and preserved in 10% seawater-formalin. Invertebrates were later blotted dry and weighed to the nearest 0.01 g. Organisms were weighed whole, except for mollusks, from which the shell was removed. The spatial distribution of invertebrates within colonies was analyzed by calculating the variance to mean ratio of biomass per sample.

Spatial distribution of foraging was also analyzed for 54 females. The locations of all bites were recorded on territory maps. A grid of quadrats was then superimposed haphazardly over female territory maps and the variance to mean ratio of the number of bites that occurred in each quadrat was calculated. A quadrat area was chosen for each fish so that the total number of bites tallied, divided by the total number of quadrats in each territory was approximately 1.0. Scaling of quadrat area to the frequency of bites avoids bias towards or against a clumped distribution (see similarly, Kramer and Graham, 1976;

Baird, 1983), so long as quadrats are large enough to include numerous bites should they be concentrated. Quadrats ranged in size from 1-2 m^2 which were sufficiently large to include numerous bites.

Influence of Intrasexual Competition and Mates on the Distribution of Males

A correlation between male territory area and harem size, spatial overlap of male territories with those of mates, and a high degree of female spawning fidelity with the nearest male (Chapter 5) all suggested that male tilefish compete for territories to monopolize mates. The extent to which males defend territories to monopolize females was examined by removing individual males (N=29). If males compete for areas occupied by females, then removal of one harem-owner should elicit attempts by one or more adjacent males to control the vacant territory, and to monopolize spawnings with the mates of the removed male. Also, different responses to male removals were expected from unmated males and those with harems. Unmated males should abandon their locations and occupy the removed male's territory because they stand to lose only their current burrows and feeding areas. By relocating, these males may gain mating opportunities as well as new burrows and feeding areas. In contrast, mated males were expected to expand rather than relocate their current territories because the latter would involve losing mates.

The mating status (i.e., unmated, or mated, and most cases the number of mates) of adjacent males was determined by

spawning observations before and after 25 male removal tests. In six male removals, rates of intra- and intersexual aggression by adjacent males that shifted locations were recorded for two days before and after removals.

To examine the extent that tilefish males defend females independently of the resources within female territories, all females were removed from 13 harems (harem removals). If males defend females independently from resources, they might abandon their current territories and move toward other females when their mates are removed. Even though intrasexual competition probably restricts male mobility, the occurrence of extra-territorial forays by males (Chapter 5) suggested that some movement within colonies may be possible by males. Alternatively, if males defend one or more resources important to females, they would not be expected to abandon territories when their mates are removed.

RESULTS

Factors Influencing the Distribution of Females

A. Influence of Intrasexual Competition

Thirty-two of 38 (p<0.01, Binomial test) female removals resulted in rapid spatial changes by one adjacent female (Figure 12). Control females never changed their territories. Two types of changes followed removals. In 25 female removal tests, an adjacent female abandoned her burrow and occupied the removed female's burrow and territory within 2 days. In seven tests, an adjacent female expanded her existing territory to include the

Figure 12. Frequency of tests that one female changed territories and male mates without female removals (non-removal control), before a female was removed (pre-removal control, or following female removals.

area used by the removed occupant, but did not change her burrow. In six tests, no females relocated or expanded their territories into the vacant space.

B. The Influence of Males on the Distribution of Females

A female relocated into the territory of another male in 15 of 38 (p<0.01) female removal tests, whereas female controls did not move (Figure 12). By contrast, none of the 54 females changed the location of their burrows after removal of their current mates. Within two days an adjacent male occupied the removed male's territory and began spawning with resident females (see below).

C. Influence of Burrows

No females moved in response to removal of their burrows. Within 3-6 h of burrow removals, each female had excavated a temporary refuge that was little more than a hole dug out underneath a coral rock less than 5 m away from the original site. Rather than improving the temporary burrow or excavating unused mounds, females re-excavated a cavern within 0.5 m of the entrance of the removed burrow. Test females then gathered coral rock-rubble from throughout their territories and constructed a new roof and entrance over the next two to four days. The reconstructed burrow was then occupied, and the temporary refuge abandoned. These results indicate a strong preference for the home burrowing site over other potential sites.

D. Distribution and Abundance of Food

The invertebrates in sediment samples were the same as
those found in tilefish guts. Samples contained an average of
1.91 g of invertebrate biomass (N=103, SE=0.14), and a minimum
of 0.5 g was found in 91.3% of samples. Within colony variance
to mean ratios ranged from 0.11 to 1.31 (Table 5). None of
these were statistically greater than 1.0, indicating that
potential prey were not highly concentrated within a few areas
of these colonies. Foraging bites were spatially clumped
(p<0.05) within the territories of only 2 of 54 females, which
is not different from that expected by chance.

Distribution of Males

A. Influence of Intrasexual Competition and Females

Removal of one male resulted in rapid spatial changes by one
or more adjacent males in all 29 tests (Figure 13). In
contrast, only one control male relocated his territory
spontaneously. Within 1-3 h of male removals, one or more
adjacent males began to intrude frequently onto the territory of
the removed fish. Within two days, one of these males had
shifted his original territory to occupy part or all of the
removed male's former territory. During this period, the
frequency of aggressive interactions between the males that
moved and other adjacent males that did not move was much more
frequent than before the manipulation (Figure 14). In 21 tests,
the male that changed his territory abandoned his current burrow
and territory and moved into that formerly occupied by the
removed male. A male expanded his existing territory to include

Table 5.   Mean prey biomass/sediment sample collected from
five sand tilefish colonies.

		Colony Site			
		Reef Slope			
	Channel	C	D	E	G
Number of samples	47	10	10	21	15
$\bar{X}$	1.82	3.06	2.08	1.50	1.96
s^2	2.39	3.82	0.22	1.00	0.79
$s^2/\bar{X}$	1.31	1.25	0.11	0.67	0.40
t	1.49	0.53	1.89	1.04	1.59
p	NS	NS	NS	NS	NS

p is the probability that t-calculated is statistically
greater than 1.0.
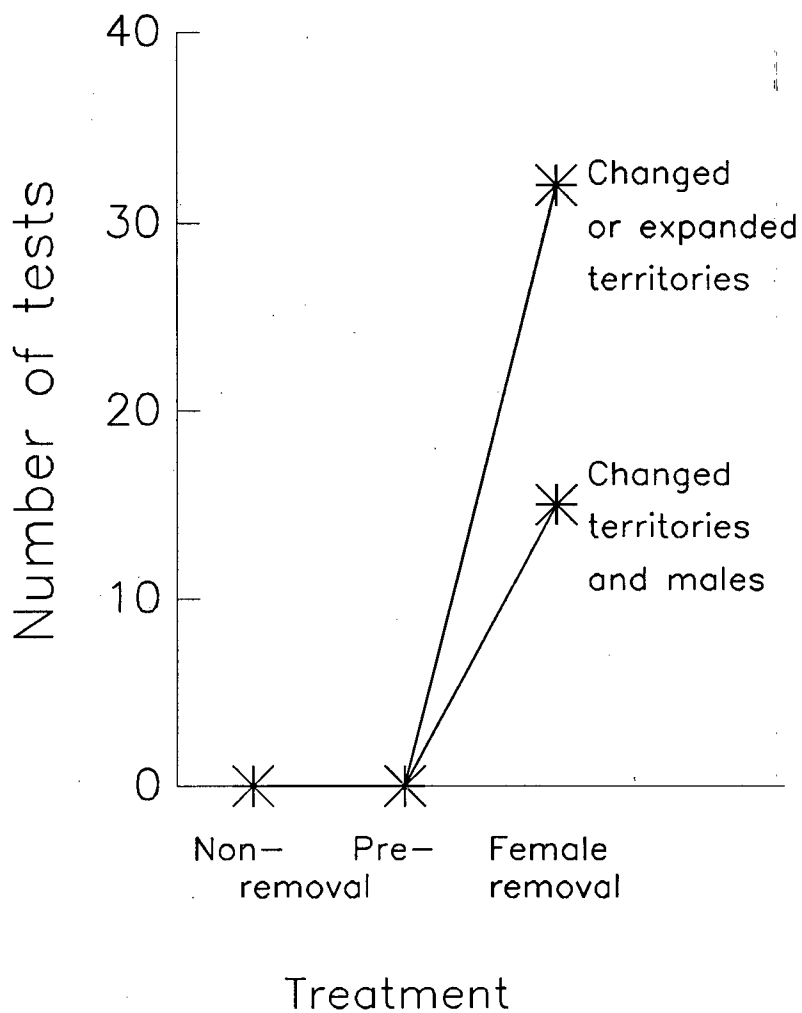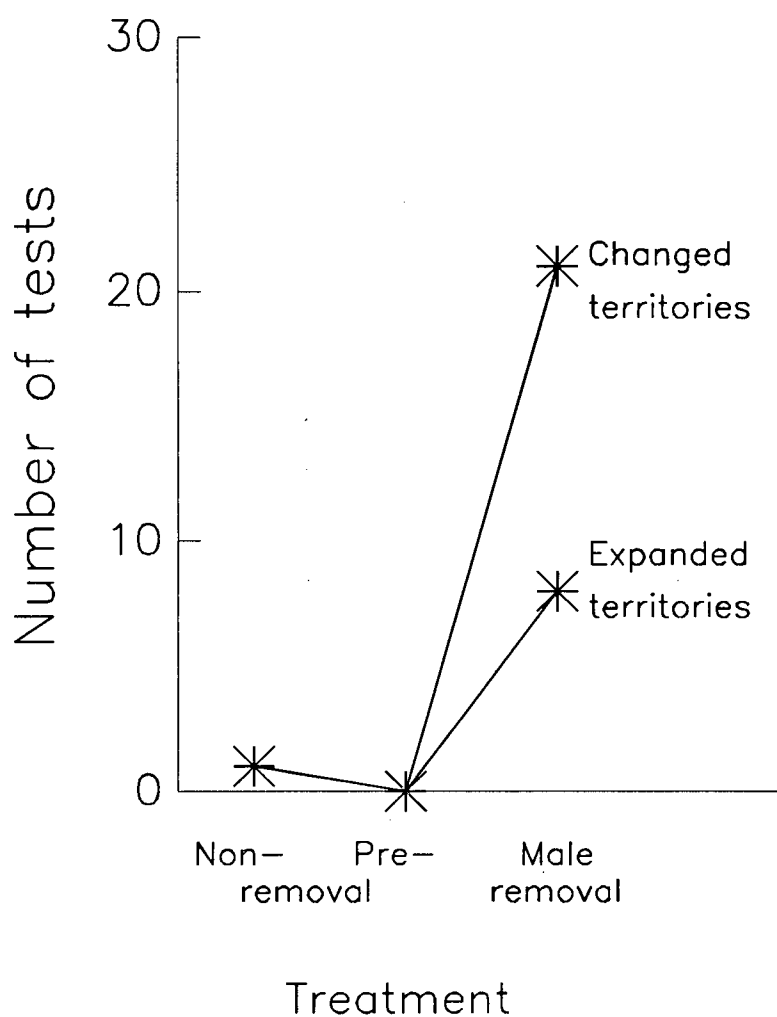
Figure 13. Frequency of tests that males changed territories without male removals (non-removal controls), before a male was removed (pre-removal control), or following male removals.
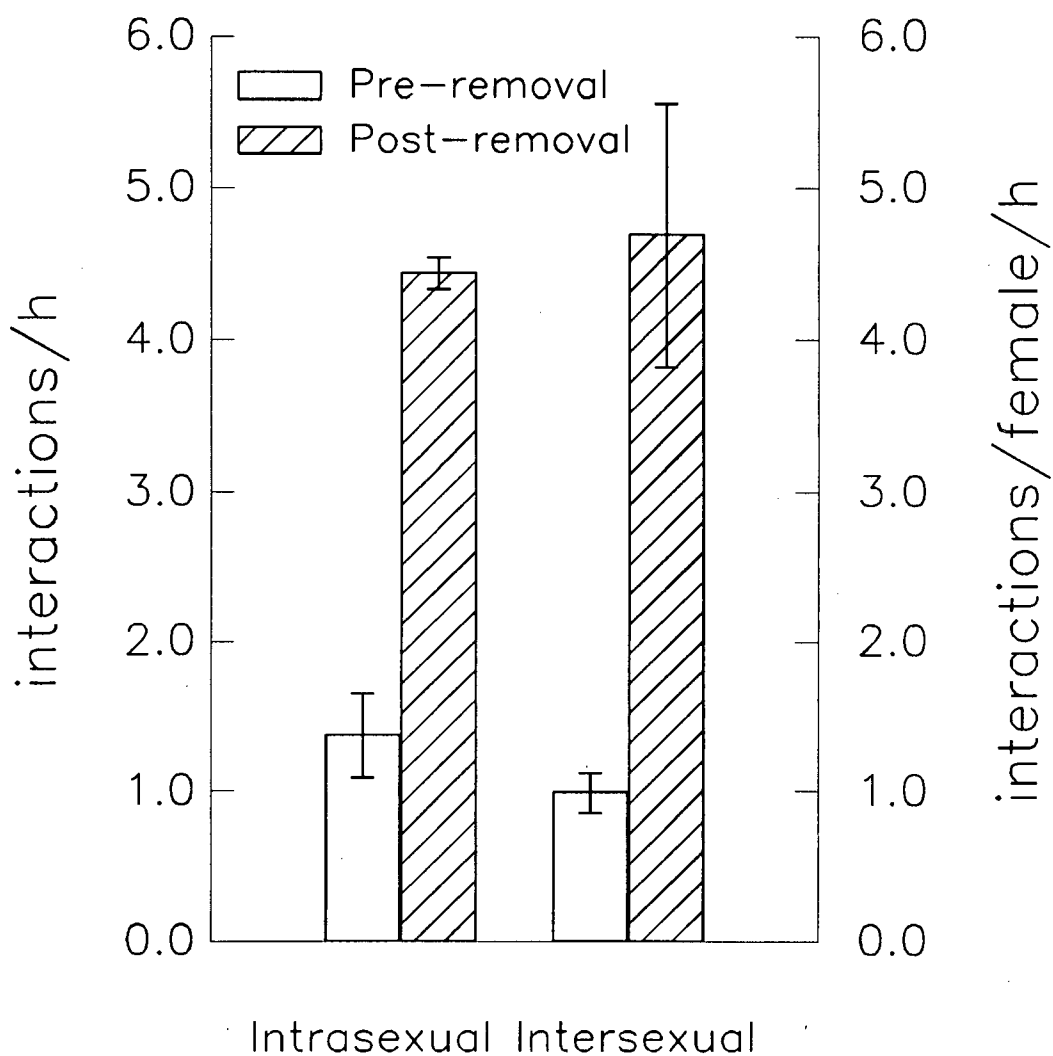
Figure 14. Rates ($\bar{X} \pm$ SEM) of intra- and intersexual aggression in males that changed locations before and after removal of one male. Intrasexual rates are bouts/h, intersexual rates are bouts/female/h.

most of the space formerly occupied by the removed male, without abandonment of his original burrow and territory in seven tests. In one instance of expansion, the territory of the removed male was divided by two adjacent males, neither of which occupied the removed male's burrow.

The responses of unmated males differed ($p < 0.01$) from those of mated males (Figure 15). In all 11 tests where an unmated male changed his territory, the unmated male abandoned his burrow and territory and relocated to that of the removed male. By contrast, when a mated male changed his territory, in nine of 14 tests these males expanded their territories but also retained their original territory and burrow. Of the five mated males that relocated, in three instances the move increased the harem size of the male that moved. In one case, the number of mates remained the same. The original harem size of the other male was not known.

Males that moved into new territories chased and attacked the former mates of removed males. These interactions occurred much more frequently ($t = 6.55$, $p < 0.01$) than those between removed males and these same females, prior to removals (Figure 14). Reproductive activity was usually disrupted during the first spawning period after removals by aggression among males, and of males with females. However, spawning resumed within two days in all of these tests. Invariably, females began spawning with the male that had expanded or moved his territory to encompass their territories.
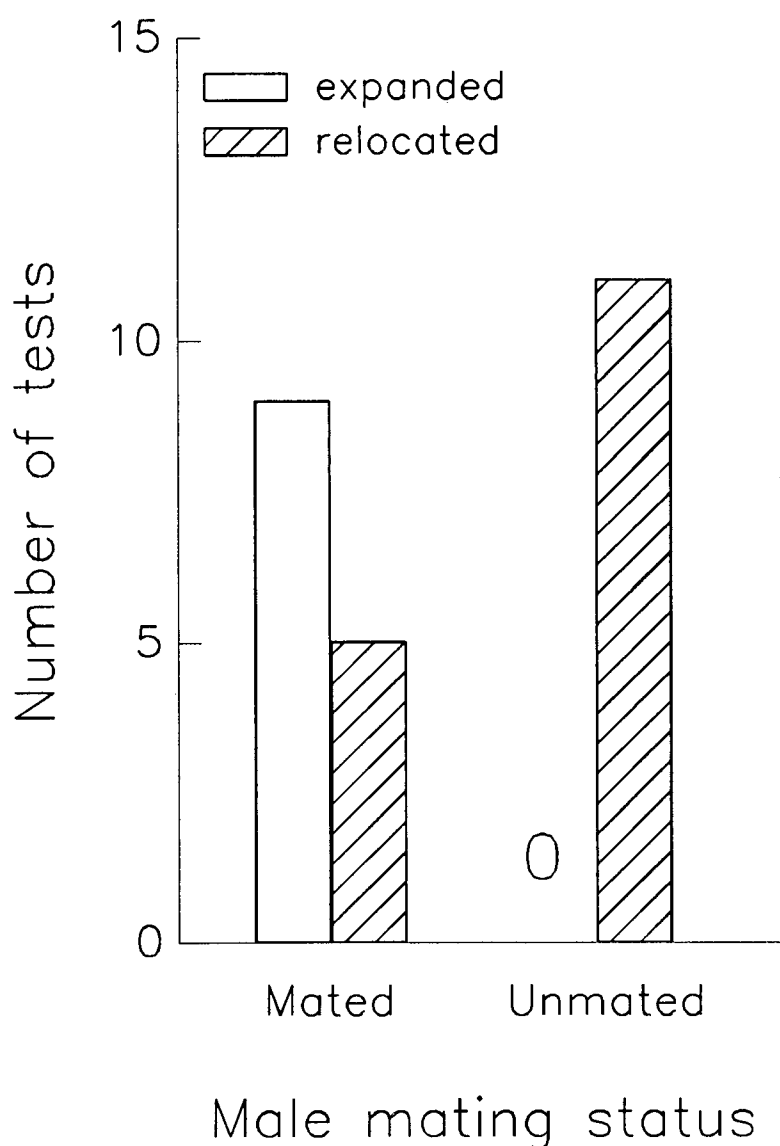
Figure 15. Effects of male mating status on responses to
male removals. Hatched bars are tests where adjacent males
abandoned their current burrows and relocated their territories
to monopolize new mates. Open bars are tests where males
expanded their existing territories.

B. Effects of Removing Harems

In six harem removals, at least one smaller individual (presumably a female or juvenile) moved into a burrow and space formerly occupied by removed females within two days. In seven tests no fish had recruited onto the vacant territories 2-8 weeks after removal of the females. Males did not change their locations in any of the 13 tests.

DISCUSSION

Benefits and Costs of Harem Formation to Males

One beneficial consequence of group-living to some tilefish males is that they are able to monopolize multiple mates. Results of male removals confirm that male competition for territories is related to mate acquisition. The presence of unmated males outside of areas occupied by females indicates that competition excludes some males from access to females. As expected, unmated males increased their mating success by abandoning burrows and moving to territories containing females when these became available. Mated males, in contrast, more often expanded territories to include new females. It is noteworthy that in the few tests in which mated males abandoned territories, these fish had only one mate and they usually increased the sizes of their harems by moving. A role of male aggression in establishing mating relationships with new females is indicated by the marked increase of male interactions with the females residing in recently annexed areas. Perhaps during extra-territorial forays (Chapter 5) males assess the number and

location of potential mates and competitor males in adjacent
harems. The potential for increasing mating success, in
relation to the time and energy required to drive off male
competitors, may influence whether or not males expand or
relocate when vacancies result from natural predation events.

Harem ownership almost certainly carries costs. Continued
defense of territories when all females had been removed and no
replacements had recruited suggests that males acquire mates by
defending female territories as well as females. The costs of
harem ownership, therefore, are probably similar to those of
territory defense. Energetic and temporal costs, and predation
risk associated with patrolling territories may increase with
the size of defended areas (Hixon, 1980; 1987; Schoener, 1983).
Because each female occupies a non-overlapping space, male
territory area increases with the size of tilefish harems
(Chapter 5). Increasing costs to males of defending space to
accommodate additional females, therefore, may be one factor
that limits harem size in M. plumieri.

Distribution of Females

The failure of females to relocate when their mates were
removed suggests that females do not choose a location solely on
the basis of proximity to males. Also, even though females are
subordinate to males (Chapter 5), males do not prevent movement
by females when vacancies occur. If it were feasible for males
to restrict the location of mates through aggression, males
should not tolerate departures from their harems.

Single female removal tests indicate that female tilefish

compete for space, and that competition limits female movement within colonies. That competition forces some fish to occupy less-preferred areas is suggested by the rapidity with which females relocated. Territory expansion shows that competition restricts the size of areas defended by some females. Whether females relocated, expanded, or did not change their territories was not related to their absolute or relative body size, or to the size of their territories prior to removals. Perhaps qualitative aspects of the resources or males on vacant territories influence whether or not adjacent females change territories following removals. Further experimentation is required to evaluate the relative importance of such factors.

The rapid reconstruction of removed burrows strongly suggests that refuges at familiar sites are valuable resources to females. Clifton and Hunter (1972) also found that, not only did tilefish rebuild partially disassembled burrows, but that fish incorporated many of the same coral fragments during reconstruction. Individuals of both sexes invest considerable time and energy maintaining home burrows (Chapter 3) which serve as the primary refuges from predatory attacks (Chapter 4). Therefore, the cost of not having immediate access to home refuges when attacked is probably high. Exclusive use and maintenance of one site should ensure that it be unoccupied and in suitable condition when needed. Under such conditions, defense and maintenance of one burrow is probably advantageous, even when unoccupied burrows are not limiting.

Defense of exclusive feeding territories is feasible when; 1) food is moderately dispersed rather than highly concentrated,

and 2) food is renewed rapidly enough that foraging does not quickly deplete the supply (Horn, 1968; Jarman, 1974; Holldobler and Lumsden, 1980; Davies and Houston, 1984). Selection may favor defense of exclusive feeding territories particularly when individuals are restricted to home sites (Waser and Wiley, 1979; Carpenter 1987; Hart 1987) such as burrows. Feeding experiments demonstrate that food intake limits investment in both reproduction and growth in tilefish females. Female territoriality would ensure access to a food supply without risking foraging trips distant from home refuges. Familiarity with a particular area may also enhance efficient prey detection while still permitting a high level of vigilance for potential predators. Sampling indicated a random or even distribution of prey organisms. Also, tilefish prey are probably renewed within local areas by recruitment of planktonic invertebrate larvae. Dependence on home burrows, food limitation of reproduction and growth, and a randomly distributed but renewable food resource together are conditions under which selection likely favors defense of feeding territories by tilefish females.

Costs and Benefits of Harem-Formation to Females

Because tilefish are colonial, monopolization of harems might be feasible for males even if there is no net advantage of this mating system to females. Costs of intrasexual competition among female tilefish, however, are not so high as to prevent occupation of adjacent territories such that some males are able to defend harems. Several factors may moderate the intensity of aggression among tilefish females. Prolonged intrusions into

adjacent territories might be selected against because the risk
of predation increases away from home burrows, and aggression
probably carries other costs such as time and energy
expenditures and risk of injury. The nature of female
territorial disputes (Chapter 5) supports this interpretation.
Although neighboring females interact frequently, disputes
usually take place along adjoining territory borders and
prolonged excursions by females into adjacent territories are
avoided. Also, tilefish males often attack female mates when
they fight one another, terminating these disputes (Chapter 5).
Such male intervention into female disputes may prevent female
aggression from escalating to such high levels that competition
costs exceed potential anti-predator advantages derived by
females from settling near to conspecifics.

It has been suggested for protogynous fishes that females
may also remain in harems to improve their future reproductive
potential. By remaining within harems and growing large,
females may enhance their social rank within mating groups,
thereby promoting their chances of changing sex should the
dominant male die (Robertson and Hoffman, 1977). Observations
on tilefish are not consistent with this hypothesis. First,
there is no indication that female tilefish exhibit social
hierarchies like those of some harem species (e.g., Robertson
and Hoffman, 1977; Hoffman, 1985). More importantly, female
tilefish did not change sex when harem-owners were removed.

Harem formation may be a successful reproductive tactic for
females, however, when maintaining close proximity to home

burrows is required for predator avoidance. Mortality of planktonic embryos, like those of tilefish, is high and unpredictable (Barlow, 1981; Victor, 1983; Doherty, et al. 1985). Therefore, selection probably favors tilefish females that spawn regularly and frequently such that mortality risks are spread over numerous batches of offspring (Strathman 1974; Levinton 1982). Because females each defend a refuge and territory that contains both food resources and a mating site (Chapter 5), they should only further require access to a male to spawn dependably. Swimming throughout colonies to select from available males would probably increase both predation risk and aggression from female neighbors, diminishing potential advantages gained by choosing "superior" males. Moreover, because males locate their territories where females reside, reliable spawning opportunities near to burrows are assured for females. The ability of males to exclude competitors should be a reliable indicator to females of male quality. Also, sharing a male should not be costly to females, provided that male fecundity is sufficient to perform "fertile" spawnings with all harem members. Under these conditions, selection probably favors females that spawn with whichever male occupies a territory that surrounds their home burrow and feeding space, regardless of whether or not that male also spawns with other females.

1. Females each defend a home burrow and surrounding feeding space.

2. Intrasexual competition restricts the location and amount of space occupied by some females. Males did not restrict the location of females, and males did not abandon their territories when their mates were removed.

3. Females spawn with whichever male occupies their feeding area, rather than locating territories to be near to males.

4. Net costs of intrasexual competition to females are not so great as to prevent their joining colonies, and settlement near conspecifics may promote dependable spawning opportunities for females near to their burrows.

5. Male tilefish compete for territories to acquire mates, and colony formation promotes monopolization of more than one mate by some males.

CHAPTER 7

HABITAT DIFFERENCES IN POPULATION DENSITY

AND REPRODUCTIVE EFFORT

INTRODUCTION

The adaptive significance of the distribution and behavior
of individuals of the same species in different habitats is
poorly studied, especially in tropical marine fishes. Two
models have been proposed to examine the influence of resources
and costs of territory defense on the selection of habitats by
individuals in species with seasonal breeding habits (Fretwell
and Lucas, 1969; Fretwell, 1972). The ideal free model predicts
that habitats with high quality resources attract more
individuals than poorer habitats. Selection will favor
individuals that settle in areas with the best resources, so
long as the costs of defense do not completely offset the
advantages gained. When the costs of defense exceed the
benefits of access to high quality resources, selection will
favor settlement of poorer habitats. Because habitats with
poorer resources also attract fewer competitors, the
reproductive success of individuals that settle these areas is
expected to equal that of individuals in high-quality habitats
(Fretwell and Lucas, 1969; Fretwell, 1972).

The ideal dominance model proposes that the territorial
behavior of dominant individuals limits the number of
competitors that are able to breed in high-quality habitats.
Reproductive success is expected to be correlated positively

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with population density under the ideal dominance model, because the costs of competition do not increase as rapidly as the benefits of breeding in the best habitats (Fretwell and Lucas, 1969; Fretwell, 1972).

Either of these models might explain the marked difference in tilefish density in reef slope and channel habitats at Glover's Reef. However, both the ideal free and ideal dominance models assume that individuals move between different habitats to select breeding territories. This assumption may not be valid for many marine fishes, such as M. plumieri, in which adults that breed throughout the year appear to remain near where they settled from the plankton as larvae (see similarly Warner and Hoffman 1980a; 1980b; Warner, 1984; Shapiro, 1987b). If adults are sedentary, then the distribution and abundance of fish may be an emergent consequence of larval settlement processes (Victor, 1984; Shapiro, 1987a) rather than an adapted consequence of habitat selection.

The reproductive success of individuals in different local habitats may also be influenced by factors other than the quality of resources and competition costs, particularly if adults are sedentary. For example, lifetime reproductive success depends on the probability of survival so that future reproductive potential can be realized (Cody, 1966; Williams 1966; Stearns, 1976; Resnick and Bryga, 1987). The intensity and type of predation risk, therefore, may have an important influence on how individuals in different habitats achieve reproductive success. Particularly when adults do not choose habitats, selection may favor flexibility in behavioral and

life-history tactics to maximize reproductive success under the types of predation threat that exist in local areas (Resnick and Bryga, 1987).

For example in tilefish, high investment in present reproduction may be advantageous when predatory attacks are unpredictable and the threat of adult mortality is high, as is suggested for channel fish (Chapter 4). Under these conditions, high levels of present reproduction may be selected because the probability of realizing future breeding opportunities are diminished and uncertain. Individuals may opt for lower levels of present reproduction in reef slopes, where attacks from stalking-type predators might be more predictable (Chapter 4). Lower rates of spawning may be advantageous under these conditions, particularly if breeding acts or the acquisition of the resources necessary to reproduce increase vulnerability to attacks by stalking predators.

The objective of this chapter is to compare the reproductive behavior and life-history traits of reef slope and channel tilefish to examine the extent to which: 1) the ideal free or ideal dominance habitat selection models may explain the distribution of M. plumieri, 2) the distribution of adults arises from factors that influence larval settlement, and 3) investment in present reproduction and growth is flexible and is correlated with apparent habitat differences in survival.

First, I assess the quality of reef slope and channel habitats by comparing: 1) daily batch fecundity and frequency of spawning, 2) body size and growth rates, and 3) the availability

of resources that probably limit reproduction in each sex. Reproduction in females is most usually limited by the energy that can be invested in production of offspring (e.g. Bateman, 1948; Williams, 1966; Trivers, 1972; Borgia, 1979; Hoffman, 1983). When embryos and larvae are planktonic, maternal investment is restricted to the nutrients allocated to egg production. Therefore, food may play an important role in the reproductive output of tilefish females.

The importance of food intake in female egg production and growth is examined by supplementing the diet of females and comparing egg production, spawning rate, and growth in fed and non-fed females. I also assess the availability of food in reef slope and channel habitats by comparing the biomass of potential prey in sediment samples (Chapter 6).

Male mating success is usually limited by access to females when paternal care is absent (Bateman, 1948; Williams, 1966; Trivers, 1972; Hoffman, 1983). In species with harems, male reproductive success is largely dependent on harem size. The distance separating neighboring females may be one factor that influences the number of mates that males are able to monopolize, because female territories do not overlap. However, because males also must exclude competitors to monopolize spawnings, the intensity of pressure from intruders may also influence harem size. Pressure from intruding males is probably correlated with the number of competitors relative to the number of potential female mates within each colony. To assess the potential for males to monopolize mates in reef slope and channel habitats, I compare both the spacing of females and the

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overall sex ratio within each colony.

To examine the predictions of the ideal free and ideal dominance models, I combine estimates of the average daily mating success of females and males with relative measurements of survival (Chapter 4) to derive estimates of net reproductive rate (after Warner, 1984b) in each habitat.

Lastly, if investment patterns in present egg production and growth are influenced by habitat-specific probabilities of survival to future breeding periods, then channel and reef slope fish may have different responses when the availability of a critical resource is increased. To test this possibility, I compare the effects of diet supplementation on frequency of spawning, rates of growth, and indices of fecundity in reef slope and channel females.

METHODS

Frequency of Courtship and Spawning

Reproductive behavior in tilefish is restricted to 1630-1830 each day. Furthermore, females exhibit almost exclusive fidelity to one mate (Chapter 5). Therefore, the frequency of spawning by all fish in a harem could be monitored by following individual males. Reproductive activities were recorded on at least five days for channel (N=54 females, N=17 males) and reef slope (N=44 females, N=22 males) fish, from approximately 1630 h until fish entered their burrows for the night.

Body Size and Growth Rates

Size-frequency distributions of males (N=27 reef slope, N=34 channel) and females (N=63 reef slope, N=89 channel) were compiled to compare the size of fish in the two habitats. Only males that were observed to spawn, and females that were observed to spawn or had ovulated ova were included in comparisons. It was possible to measure 95% of the fish in reef slope colonies and 80% of the fish within the channel study area. Therefore, my samples include most of the populations of reproductively active adults in these areas.

Growth rates of females (N=13 reef slope, N=13 channel), males (N=7 reef slope, N=6 channel), and juveniles (N=3) were calculated as the change in SL measured between the date of tagging and date of recapture, divided by the total number of days determining that period (40-60 days). Standard length was measured to the nearest mm as the distance from the tip of the lower jaw to the edge of the most posterior scale in the crease at the caudal peduncle caused by bending the fish's tail.

The purpose of growth measurements is only to compare relative rates in the two habitats. Sample size was small and the time period between tagging and recapture was short. Also, tagging causes tissue damage, the repair of which may diminish growth. Therefore, the measured rates may underestimate the natural growth rates of M. plumieri.

Male Harem Size

To examine the relationship between female spacing and male harem size, I measured the distance between each

female's burrow and the burrow of her nearest female neighbor (inter-female distance). Harem size was then examined in relation to the mean inter-female distance in harems with more than one female. In harems with only one female, the inter-female distance was measured between female burrows and the next nearest female in a neighboring harem. I also examined the distance between male and female burrows (male-female distance) in reef slope and channel harems. The distance between each male's burrow and the burrows of the six closest females was measured in seven reef slope colonies (N=17 males) and for 23 males within the channel study area during 1984, 1985, and 1986. Females were ranked according to proximity to males. The mean male-female distance for each ranking (i.e., nearest females, second nearest ... sixth nearest) was then compared for reef slope and channel habitats.

To examine the relationship between mean harem size and the sex ratio within local populations, I determined the number of females mating with the males in the channel study area during 1983-1986 and in seven reef slope colonies.

I also estimated gonosomatic indices of males (GSI) to determine if there was a relationship with harem size, or if GSI of similarly sized reef slope (N=15) and channel males (N=11) differs. Male gonosomatic index was calculated as follows:

$$GSI = (testis\ mass/total\ body\ mass) \times 100.$$

Testes were dissected from males captured before spawning, preserved in bouin's fixative, blotted dry and weighed to the nearest 0.001 g on a mettler balance. Body weights of these fish are not available due to the malfunction of my balance.

Therefore, total male body mass was estimated by a least squares regression of body mass on length in males that were weighed and measured previously, described by the equation: total body mass = -420.1 + 2.21 standard length (r=0.94, p<0.001, N=30).

Estimates of Food Abundance and Female Foraging

Observations of feeding and examination of stomach contents revealed that tilefish feed primarily on benthic crustaceans, mollusks and annelids (Chapter 5). I compared the percentage of stomachs in reef slope (N=12) and channel (N=13) females containing remains of each prey type to examine whether females in the two habitats ingested similar prey. The abundance of potential prey in reef slope and channel habitats was estimated by measuring the total biomass of each type of invertebrate and the size of a random sub-sample of these organisms in surface sediment samples (Chapter 6). To examine foraging effort in channel and reef slope females, I recorded the number of foraging bites per unit time and the distance over which females swam during spatial traces. Distance travelled was measured by tracing maps of swimming paths with a digitizing tablet. The total distance travelled during replicate traces was divided by the total minutes of observation to yield a rate of movement.

Female Investment in Present Reproduction

I examined female investment in present reproduction by calculating gonosomatic index (GSI) as follows:

GSI = (ovary mass/total body mass) X 100.

GSI is only a valid measure with which to compare reproductive investment in females from different habitats if the allometric relationship between ovary mass and body mass is controlled by comparing fish of similar size (DeVlaming et al., 1982; Erickson et al., 1985). To control for effects of body mass, females were chosen for comparison so that the mean size of reef slope ($\bar{X}$=23.4 cm SL, SE=0.7) and channel females ($\bar{X}$=22.0 cm, SE=0.5) was not statistically different.

Between group comparisons of GSI also require that females are in like stages of gonad development (DeVlaming et al. 1982). To satisfy this requirement, GSI was estimated only in females whose ovaries contained eggs that had been released into the ovarian lumen (ovulation) and had absorbed water during the final stage of development (hydration). Because reproduction in tilefish is restricted to the 2 h period prior to sunset (Chapter 5), ripe females could be captured before spawning by caging them at the beginning of the reproductive period. Captured females were maintained alive in 15 l containers for at least 1 h to ensure that eggs were fully hydrated. Fish were then pithed, and the ovaries extracted. Ovaries plus all running hydrated eggs were preserved while fresh in 10% seawater formalin and later blotted dry and weighed (2 replicates/specimen) to the nearest 0.01 g. Estimates of female body mass for GSI calculations were derived from a regression of body mass on standard length described by the equation: total female body mass = -199.2 + 1.36 standard length (r=0.97, N=82, p<0.001).

Estimates of Female Daily Batch Fecundity

The ability to collect females shortly before spawning made it possible to estimate the number of hydrated eggs present in ovaries at the beginning of the daily reproductive period (average batch fecundity). Hydrated ova were washed out of preserved ovaries that were dissected under magnification. Ovulated eggs in the ovarian lumen were easily distinguished as they were unattached to ovarian tissue, translucent, and much larger than opaque non-hydrated eggs. The total number of ovulated eggs collected from each specimen were then blotted dry and weighed. Fifty preserved eggs that had undergone hydration were chosen at random from each specimen and the greatest diameter was measured under magnification. Eggs from individuals varied little in size. Therefore, I counted the number of eggs in subsamples from each specimen. Subsamples were then weighed to determine the relationship between egg mass and egg number. Total egg mass from each specimen could then be converted to an estimate of daily batch fecundity.

Female tilefish sometimes spawned more than once during a single reproductive period, particularly in the channel (see below). To compare the number of hydrated ova present in ovaries before second spawnings with the number present before first spawnings, I collected ovaries from a small sample (N=6 channel, 1 reef slope female) of females before they spawned a second time. Females that had been observed to spawn once were watched continuously until they performed an arc display and paired together a second time with their mate. Before these

females spawned again, they were speared through the head so as not to damage the ovaries. The number of eggs released during third daily spawnings was not estimated because these acts were rare (see results) and unpredictable.

<u>Estimates</u> <u>of</u> <u>Net</u> <u>Yearly</u> <u>Mating</u> <u>Success</u>

To perform an unequivocal test of the predictions of the ideal free and ideal dominance habitat selection models, it is necessary to compare the lifetime reproductive success of fish in reef slope and channel habitats. Measurement of reproductive success in tilefish requires information on the number of planktonic offspring that survive to reproduce. I did not measured survival of planktonic tilefish larvae. Rather, I measure spawning frequency and number of mates in males, and spawning frequency and egg production in females to estimate daily mating success. For purposes of comparing the relative mating success of reef slope and channel fish, I assume equal survivorship of the larvae spawned in the two habitats.

Estimates of lifetime reproductive success also require information on reproductive lifespan. Attempts at aging tilefish by counts of otolith rings proved inconclusive. Also, sample sizes of growth measurements are too small to reliably back-calculate age from body size measurements. Therefore, I limit comparison of reproductive success in reef slope and channel fish to estimates of net mating success (see below) of females and males over an arbitrarily chosen one-year period.

Net mating success is the expected mating success over a given time period discounted by the probability of mortality

during that period (Warner, 1984b). My estimates of net
mating success are based on empirically determined mean values
for several parameters, and are therefore subject to problems of
compounded errors. Several assumptions (stated below) regarding
parameters for which data are unavailable are also required.
Comparison of estimated yearly net mating success of reef slope
and channel fish, therefore, is an equivocal test of the
two habitat selection models.

My estimates of average male mating success in reef slope
and channel habitats require two assumptions. First, I assume
that the average percentage of eggs that is fertilized is the
same for males spawning in the two habitats. Similar GSI's in
reef slope and channel males supports this assumption, because
testes of similar size probably produce similar quantities of
spermatozoa. Second, I assume that the average number of eggs
released/spawn by reef slope and channel females is similar. In
support of this assumption, neither estimates of the number of
ovulated eggs in ovaries before spawning, nor female GSI's were
statistically different in similarly sized non fed reef slope
and channel females (see below). If these assumptions are
correct, then the average daily frequency of mating with
females that have not already spawned estimates the average
daily mating success of males. Average mating success for males
in reef slope and channel habitats was calculated as:

average daily $=$ average # of $\times$ $\bar{X}$ % of days that
male mating success $\quad$ female mates $\quad$ females spawned

The average number of eggs spawned per day estimates the
daily mating success of females, assuming equal fertilization

rates and equal offspring survivorship in the two habitats. I
also assumed that females hydrate a single batch of eggs and
then release them during one or more spawnings rather than
hydrating a separate batch before second and third spawnings.
The small number of hydrated eggs present in specimens captured
immediately before second spawnings (see below) suggests that
this assumption is justified. If females ovulate a single
batch, then the number of ovulated eggs in ovaries prior to
spawning should estimate daily batch fecundity. The average
number of eggs spawned per day by females in each habitat was
estimated as:

$$\text{Average \# of eggs/day} = \bar{X} \text{ \% of days that females spawned} \times \bar{X} \text{ number of ovulated eggs in ovaries}$$

Frequencies of disappearance (Chapter 4) were used to
derive estimates of the per capita daily death rate (after
Warner, 1984b) in each habitat as:

$$\text{daily per capita death rate} = \text{\% of tagged fish disappearing/day} \times \text{total number of fish tagged}$$

Assuming that the variables in the above equations remain
constant over one year, then net yearly mating success over a
year is calculated as:

$$\text{Net yearly mating success} = \text{expected mating success during 1 year} \times \text{probability of surviving 1 year.}$$

Food Supplementation Experiments

Supplemental feeding was accomplished by luring specific
fish to chopped pieces (2-4 mm^3) of conch (_Strombus_), and
intertidal top shells (_Cittarium_) placed at the entrances of
their burrows. Mollusks are a natural food item of tilefish
(Chapter 5). Fish were quickly attracted and ate until their

abdomens were distended. Non-fed females that lived within the same or adjacent harems served as controls (N=23 channel and 23 reef slope). Control females as well as males were prevented from eating by enclosing them inside their burrows with a cage. When experimental fish were satiated, any uneaten food and cages were removed. Feedings were completed within 30 min, therefore, the activities of control fish were disrupted for only a short time. Females (N=16 channel, 16 reef slope) were fed each day between 1000 and 1200 h for 20-23 days up until and including the day of collection. Control females were collected simultaneously with experimental fish.

Control and experimental females were selected so that the initial size of reef slope (non-fed $\bar{X}$ SL=23.4 cm, SE=0.7; fed $\bar{X}$ SL=23.1 cm, SE=0.7) and channel (non-fed SL $\bar{X}$=22.0 cm, SE=0.5; fed $\bar{X}$ SL=22.7 cm, SE=0.7) subjects were not statistically different within and between habitats or treatments. Therefore, comparisons of GSI's and batch fecundities of females from different habitats and treatments are not confounded by differences in body size (see above). Collection of fish and measurement of GSI and growth were done as described above. Two-way analysis of variance was performed to determine if fed females grew faster, had higher GSI's, or produced more eggs than controls, and if responses differed in reef slope and channel females. Means were were compared using Tukey's A test.

Observations on spawning were also conducted to examine the effects of food supplementation on spawning frequency. Spawning

observations were conducted on females (reef slope N=7, channel
N=10) on days 5, 6, and 7 of female food supplementation.
Beginning on the eighth day of female feeding, males (N=7 reef
slope, N=12 channel) in these harems were also fed. Spawning
observations were conducted again when females had been fed for
10-12 days and males had been fed for 5-7 days.

RESULTS

Habitat Comparisons of Body Size and Growth Rates

The average size of females in the channel was smaller
(t=14.49, p<0.01) than in reef slope habitats, and the
smallest reproductively active females were also observed in the
channel (Figure 16a). Males were also smaller (t=13.85, p<0.01)
in the channel (Figure 16b). Mean growth rates of non-fed fish
of both sexes were low. Six of thirteen reef slope females, and
five of thirteen channel females did not exhibit detectable
changes in SL between tagging and recapture. Three of seven and
two of six males did not grow in reef slope and channel habitats
respectively. Mean growth rates of non-fed reef slope and
channel fish of both sexes were not statistically different, but
were about 1.6 times higher in channel females and 1.9 times
higher in channel males (Figure 17).

Male Spawning Frequency

Channel males spawned more than twice as frequently
(t=5.43, p<0.01) as reef slope males (Figure 18), primarily
because harems were larger (t=3.50, p<0.01) in the channel
(Table 6). However, channel males also spawned more than twice
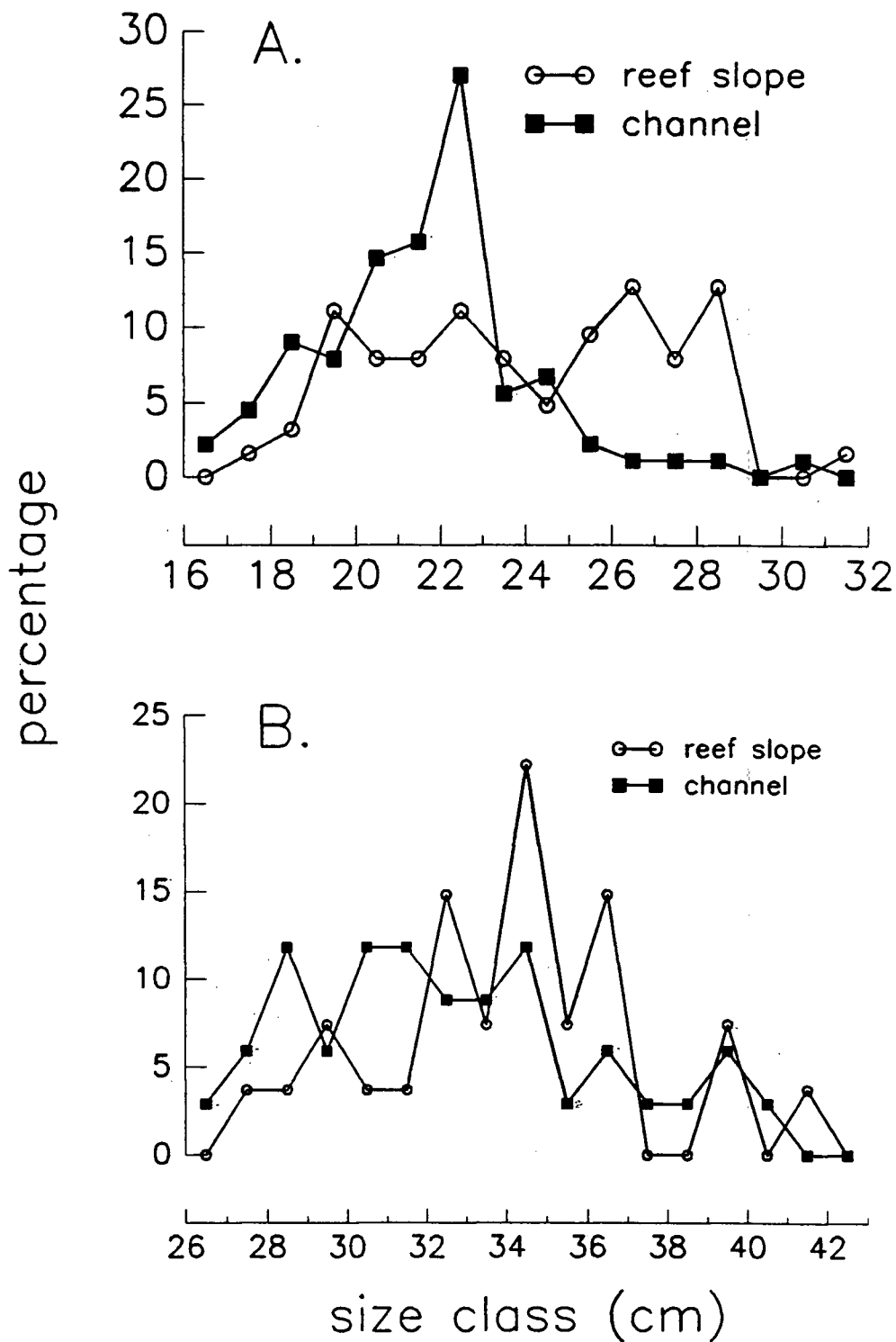
Figure 16. A. Size distribution of reef slope (N=63) and channel females (N=89). B. Size distribution of reef slope (N=27) and channel males (N=34). Data are the percentage of the total sample in 1.0 cm size classes.

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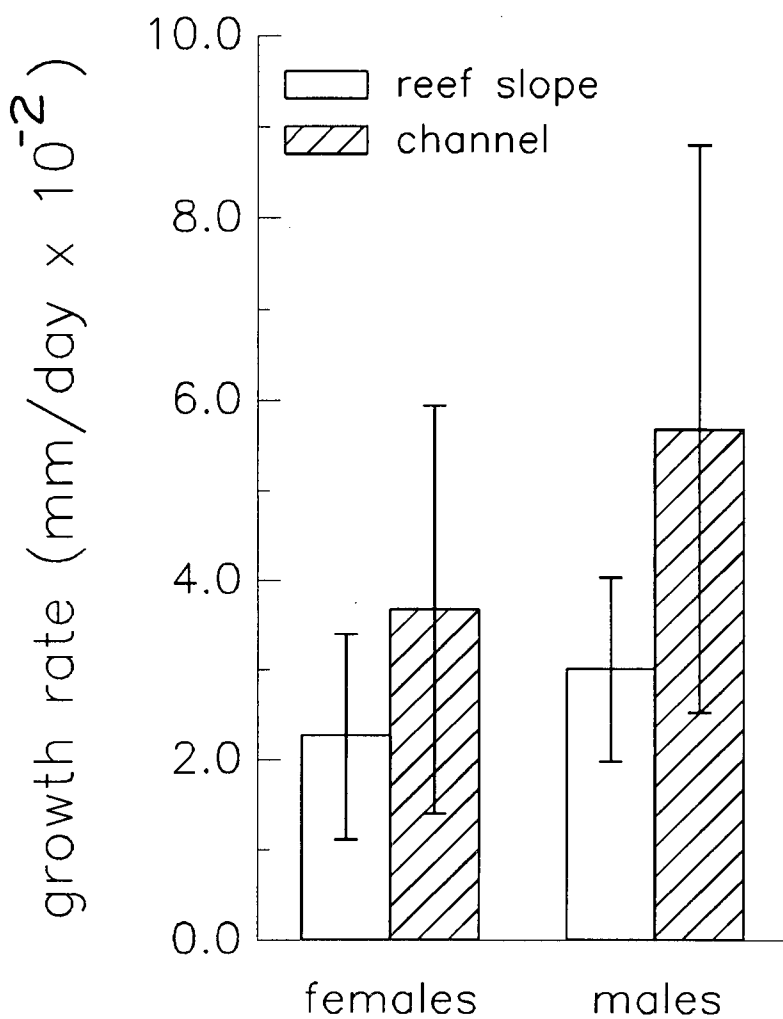
Figure 17. Growth rates ($\bar{X} \pm$ SEM) of non-fed reef slope and channel females and males.
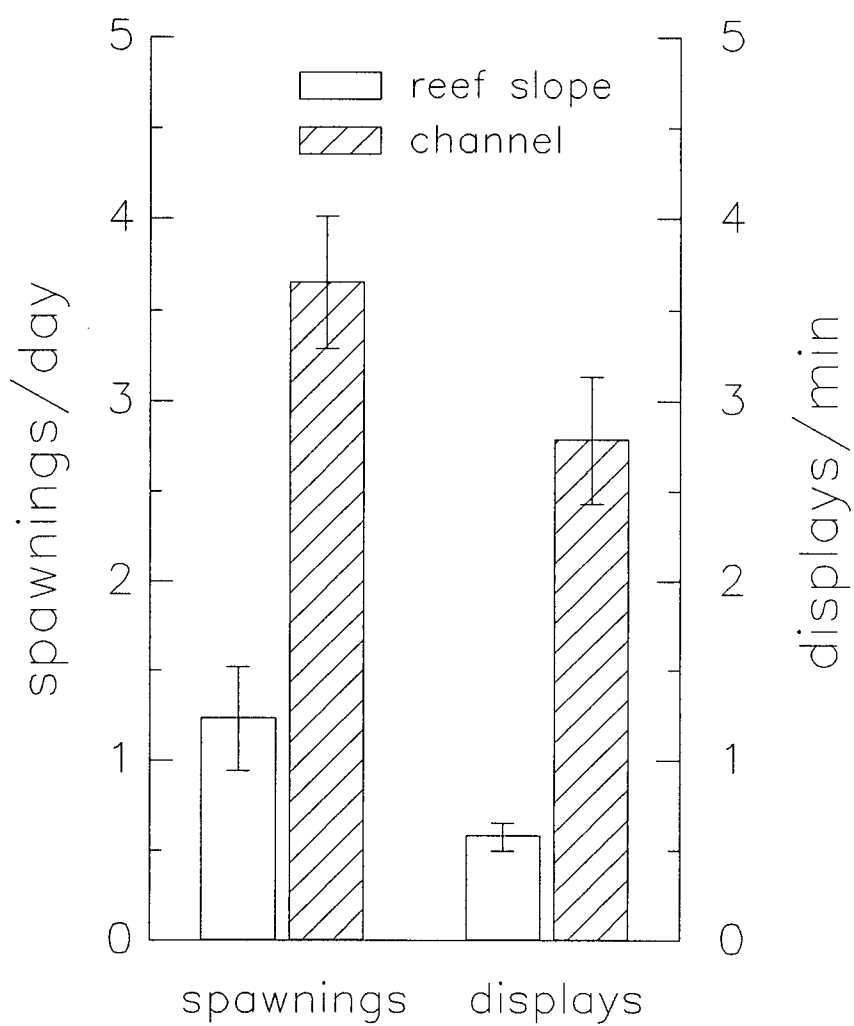
Figure 18. Spawning and display rates ($\bar{X} \pm$ SEM) in reef slope (N=22) and channel (N=17) males.

Table 6. Daily mating success [1] ($\bar{X} \pm$ SEM) in reef slope and channel males.

	Mean Harem size	Percentage of days that females spawned	Average male daily mating success[1]
Reef slope (N=22)	1.8 (0.2)	59.8 (4.6)	1.08 (0.09)
Channel (N=17)	2.8 (0.2)	86.5 (2.3)	2.42 (0.01)

[1] daily male mating success is the product of the number of female mates and the average percentage of days that males spawned with females that had not already spawned that day.

as frequently (t=10.07, p<0.01) with each female, and performed advertisement displays at more than five times the rate (t=6.31, p<0.01) of reef slope males (Figure 18). GSI's of reef slope ($\bar{X}$=0.0022, SE=0.0003, N=15) and channel ($\bar{X}$=0.0028, SE=0.0004, N=11) males were similar and there was no correlation between male GSI and harem size (r=0.19).

Correlations With Male Harem Size

There was a weak correlation (r=-0.36, p<0.05) between harem size and inter-female distance (Figure 19). However, inter-female distance in the channel ($\bar{X}$=11.3 m, SE=1.1, N=44) and reef slope colonies ($\bar{X}$=10.1 m, SE=0.6, N=46) was not statistically different (t=0.24) even though harems were larger in the channel. Distance from male burrows to the second, third, fourth, and fifth closest females were not statistically different in reef slope and channel habitats (Figure 20). Distance to closest females was greater (t=2.99, p<0.01) for channel males, whereas distance to the sixth nearest females was greater (t=3.61, p<0.01) in reef slope males. The slopes of the regression lines relating male-female inter-burrow distance to female proximity rank (Figure 20) were not different (t=0.39) in the two habitats.

The ratio of females to males in the channel study area ($\bar{X}$=2.4, SE=0.1, N=4) was twice that (t=6.19, p<0.01) observed in reef slope colonies ($\bar{X}$ number of females/male=1.2, SE=0.2, N=7). There was a strong positive correlation (r=0.96, p<0.001) between the mean harem size in each colony and the overall ratio of females to males on each site (Figure 21). Also, fifteen
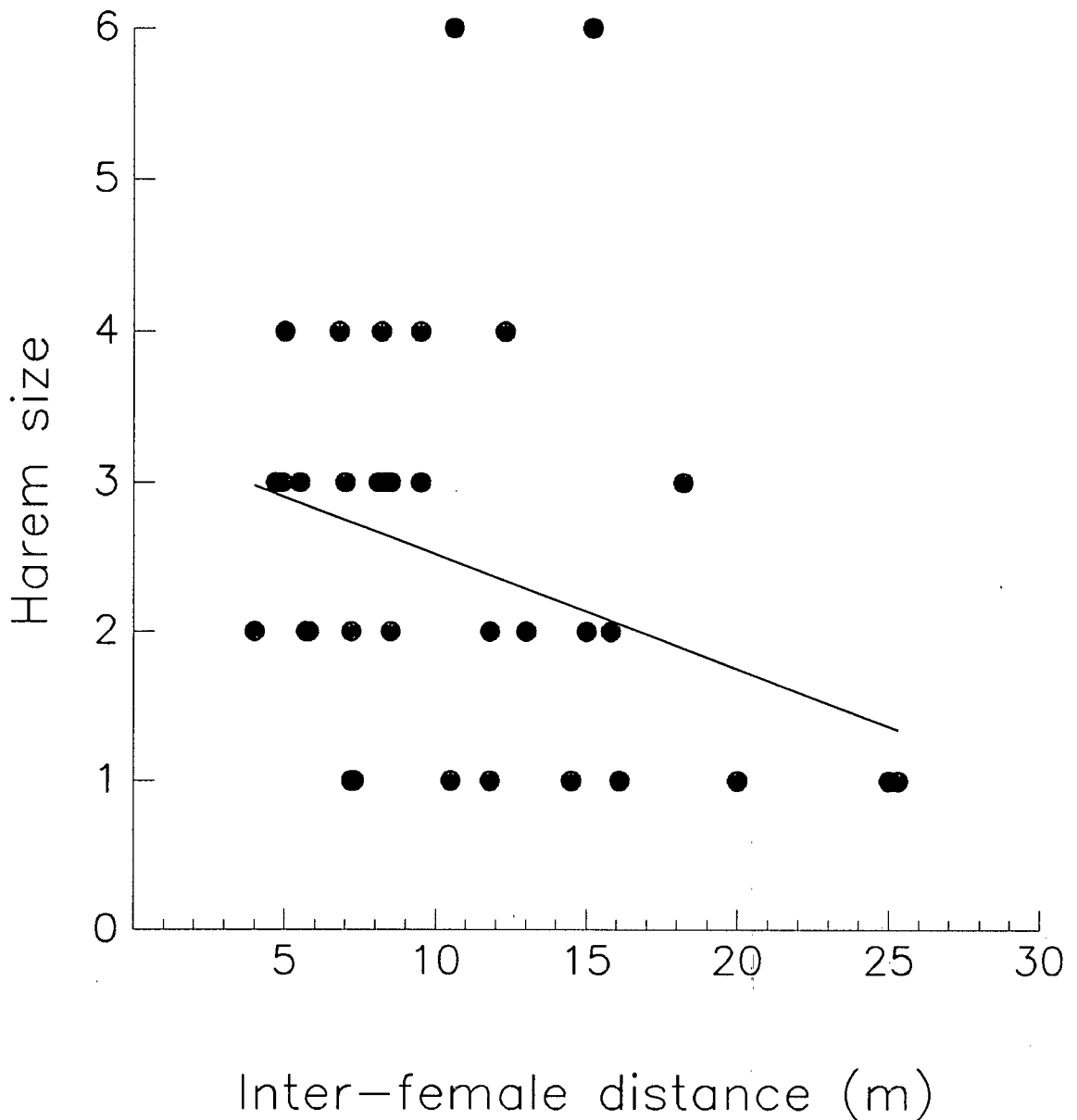
Figure 19. Harem size (number of females) graphed as a
function of the distance between each female and her nearest
female neighbor. Data are mean inter-female distances for each
harem (channel, N=19; reef slope, N=23). Line is least squares
regression for all harems pooled (N=42) described by the
equation: harem size = 3.35 x -0.08 inter-female distance.
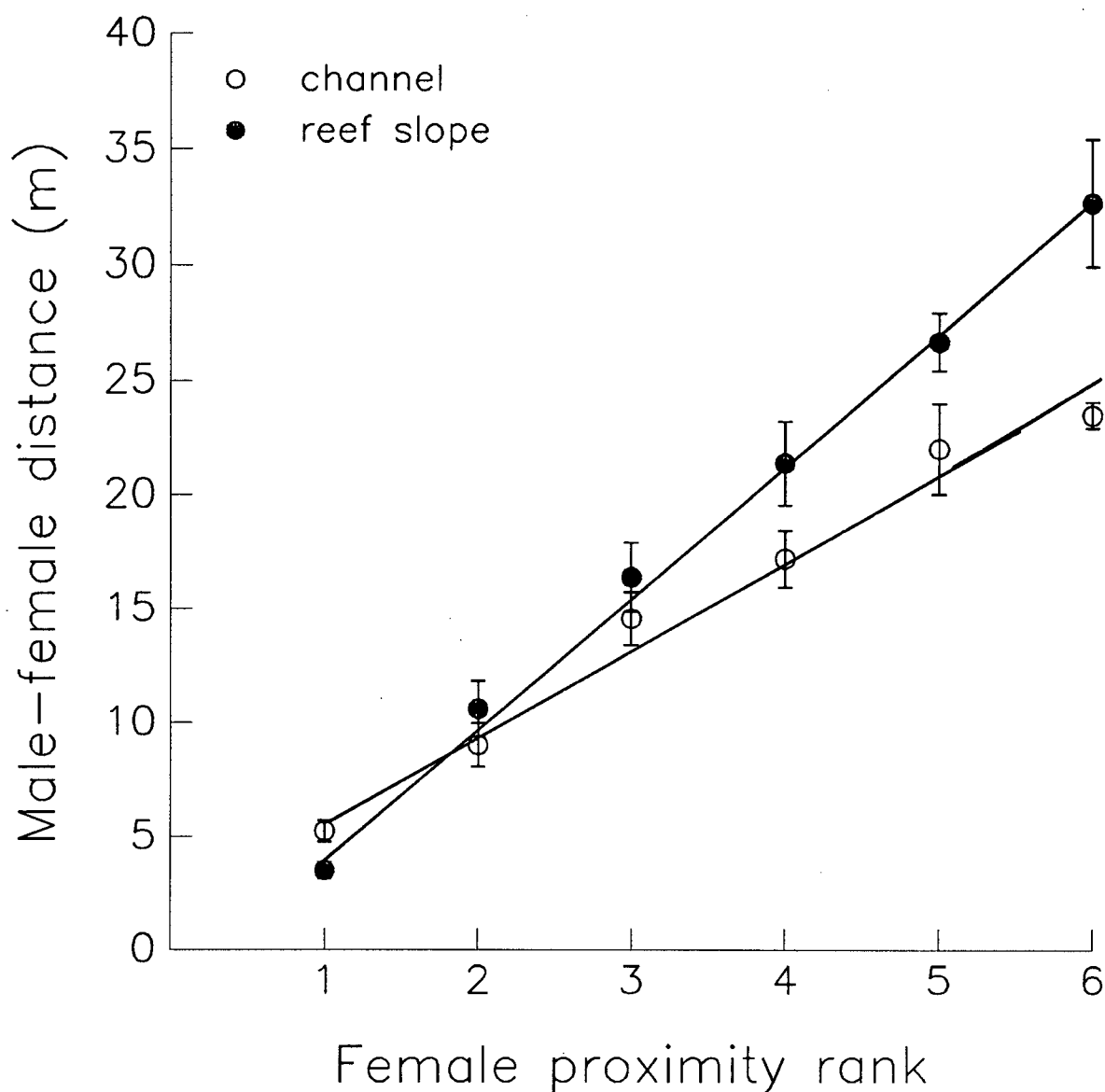
Figure 20. Distance between males (N=23 channel, N=17 reef slope) and the six closest females graphed as a function of female proximity rank (nearest to farthest). Data are mean male-female distances for each proximity rank and 95% confidence intervals. Lines are least squares regressions for each habitat described by the equations: solid line = reef slope, male-female distance = 1.97 + 3.80 female proximity rank; dashed line = channel, male-female distance = -1.38 + 5.69 female proximity rank.
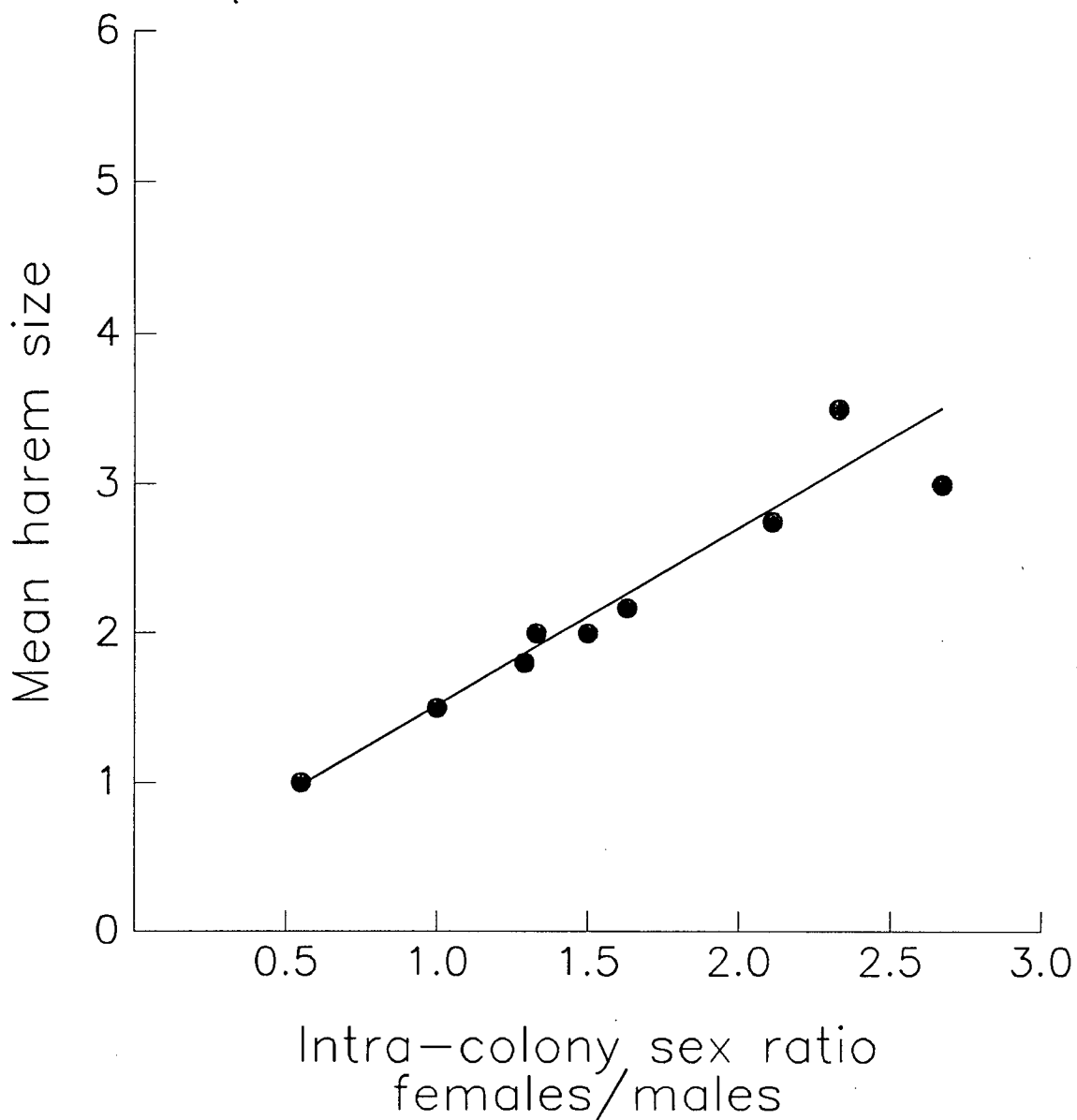
Figure 21. Mean harem size in reef slope colonies (N=7) and the channel (N=4 years) graphed as function of the ratio of females to males. Line is least squares regression described by the equation: mean harem size = 0.33 + 1.19 female to male ratio.

unmated males were observed in reef slope colonies, where average harem size was small, whereas only three unmated males were observed in the channel. I monitored the locations of 15 unmated males (3 channel, 12 reef slope) to determine whether or not they moved to other habitats. All of these males remained on territories without resident females for at least two months. Following male removals, eleven unmated males relocated to adjacent territories with resident females within these same colonies (Chapter 6), while the others occupied the same locations until they were collected or until the end of observations 2-4.5 months). One male that remained unmated from April 1985 to the end of observations in August, 1985, occupied an adjacent territory and had two mates in April 1986.

Female Spawning Frequency

Mean daily spawning frequency of channel females ($\bar{X}$=1.12, SE=0.06) was higher (t=4.73, p<0.01) than that of reef slope females ($\bar{X}$=0.67, SE=0.06). Reef slope females failed to spawn on a higher percentage of days (t=7.39, p<0.01) than channel females (Figure 22). Females in the two habitats spawned once a day on a similar percentage of days, but channel females spawned twice a day more frequently (p<0.01, t=4.98). Also, channel females spawned three times on 4.8 percent of days, while reef slope females were not observed to spawn three times in a day.

Female Foraging Behavior and Abundance of Potential Prey

The foraging behavior of channel and reef slope females differed markedly. Channel females swam nearly 2 m farther per
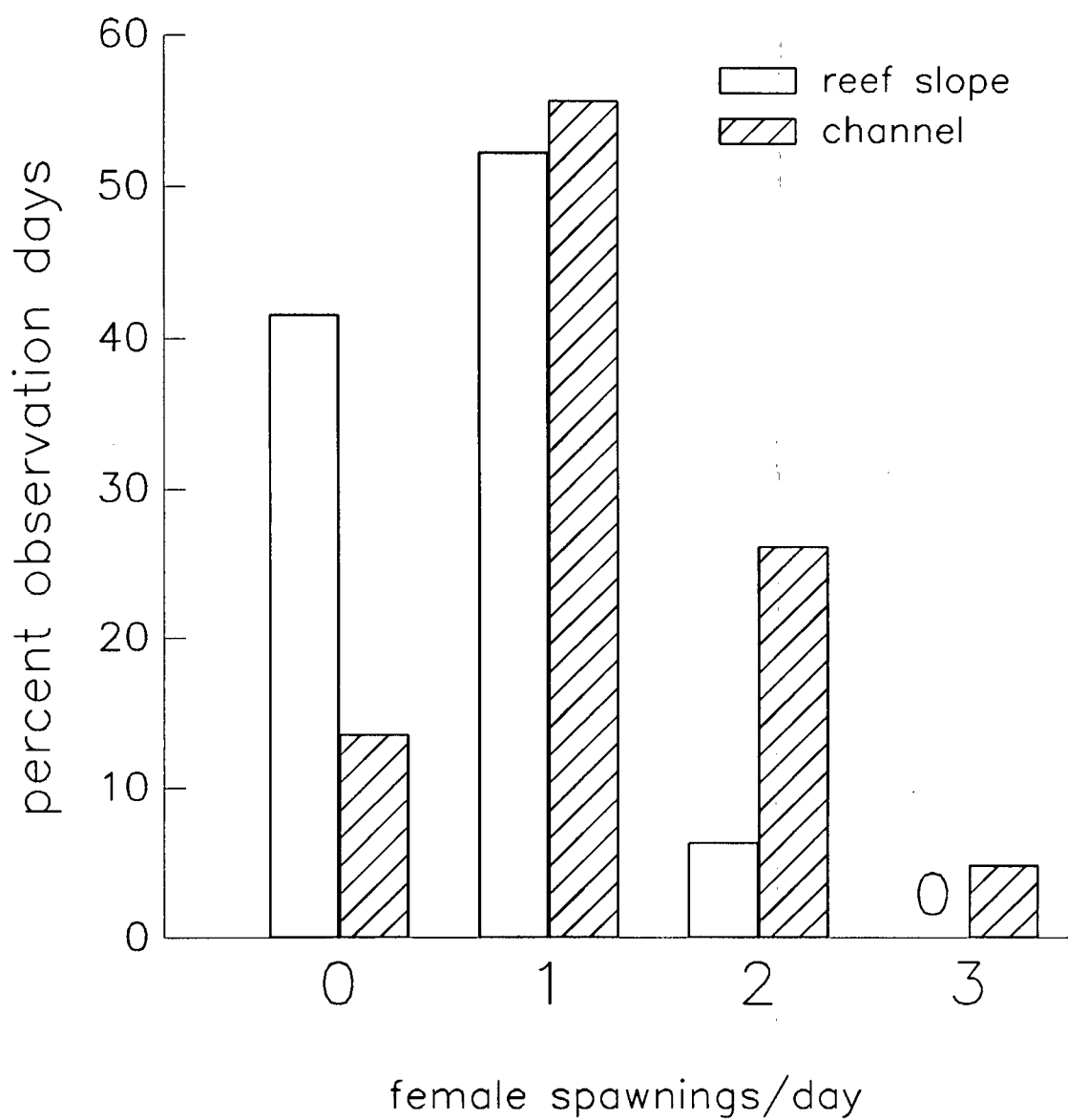
Figure 22. Daily spawning frequency in channel and
reef slope females.

min (t=4.91, p<0.01) and average bite rate of channel females was 1.7 times higher (t=4.00, p<0.01) than that of reef slope females (Figure 23). The proportion of female stomachs containing remains of mollusks, polychaetes and crustaceans were not different (X^2=1.77, df=2) in reef slope and channel specimens (Figure 24). The total biomass of invertebrates of the type and size found in female stomachs were not different in samples of surface sediments collected in reef slope and channel habitats (Figure 25). The mass of mollusks/sample was higher (t=3.62, p<0.01) in channel habitats, while that of annelids was similar in reef slope and channel samples. The mass of crustaceans/sample was somewhat higher in reef slope habitats, but the difference was not statistically significant (Figure 26). Crustaceans were larger (t=4.03, p<0.01) in the channel, but the size of mollusks and polychaetes were not different in the two habitats (Figure 26).

Daily Female Batch Fecundity

The number of ovulated eggs in ovaries of females collected prior to spawning varied markedly among females in both habitats (Table 7). The number of hydrated eggs within both non-fed and fed treatments were not statistically different in both reef slope and channel females. Daily batch fecundity was not correlated with body mass in either control (r=0.07) or fed (r=0.34) females, but ovary mass was correlated with body mass in both control (r=0.43, p<0.01) and fed (r=0.53, p<0.01) females. Five and eight non-fed reef slope and channel females respectively had fewer than 200 hydrated eggs, while the others

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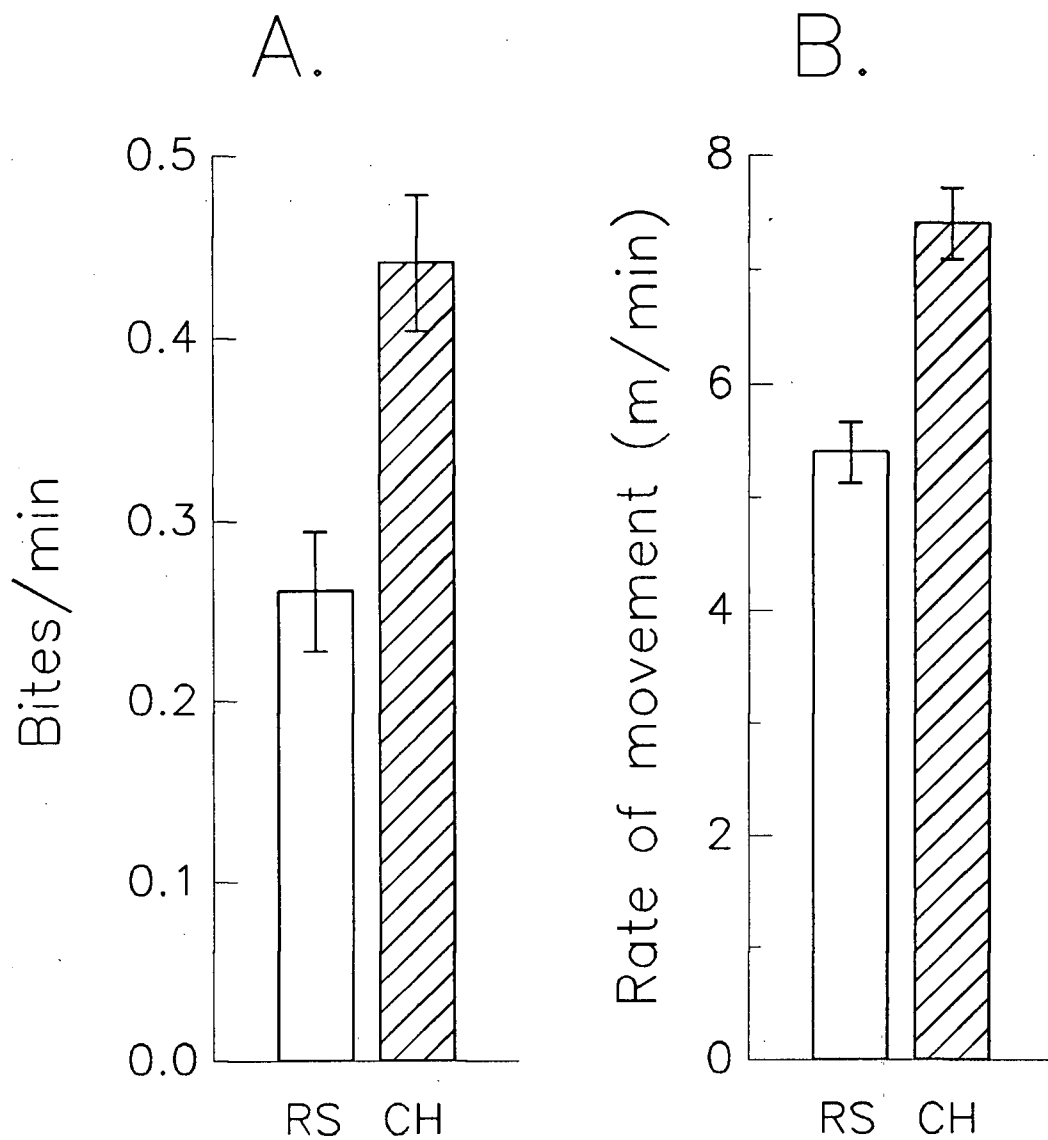
Figure 23. Comparison of foraging behavior ($\overline{X} \pm$ SEM) in reef slope (N=29) and channel (N=25) females. Panel A shows bite rate, panel B shows mean rate of movement.
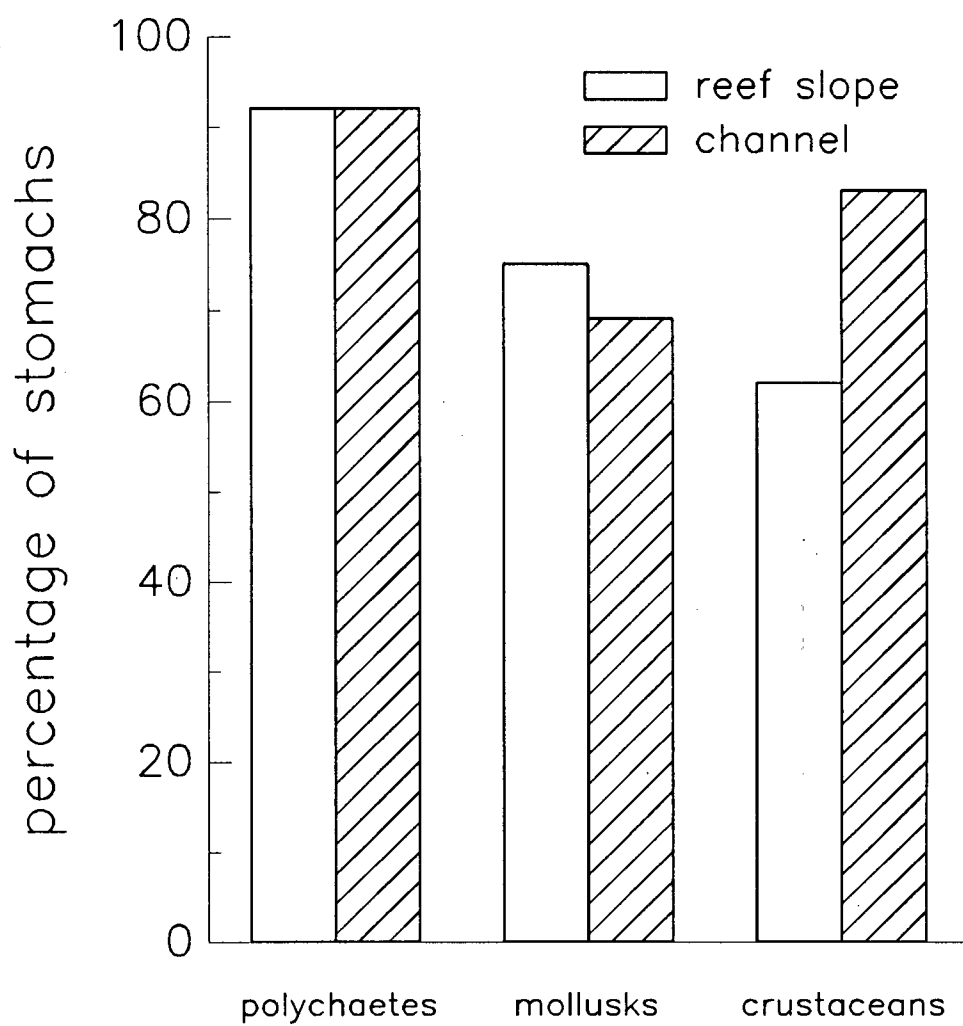
Figure 24. Percentage of reef slope (N=12) and channel (N=13) female stomachs containing remains of polychaetes, mollusks, and crustaceans.
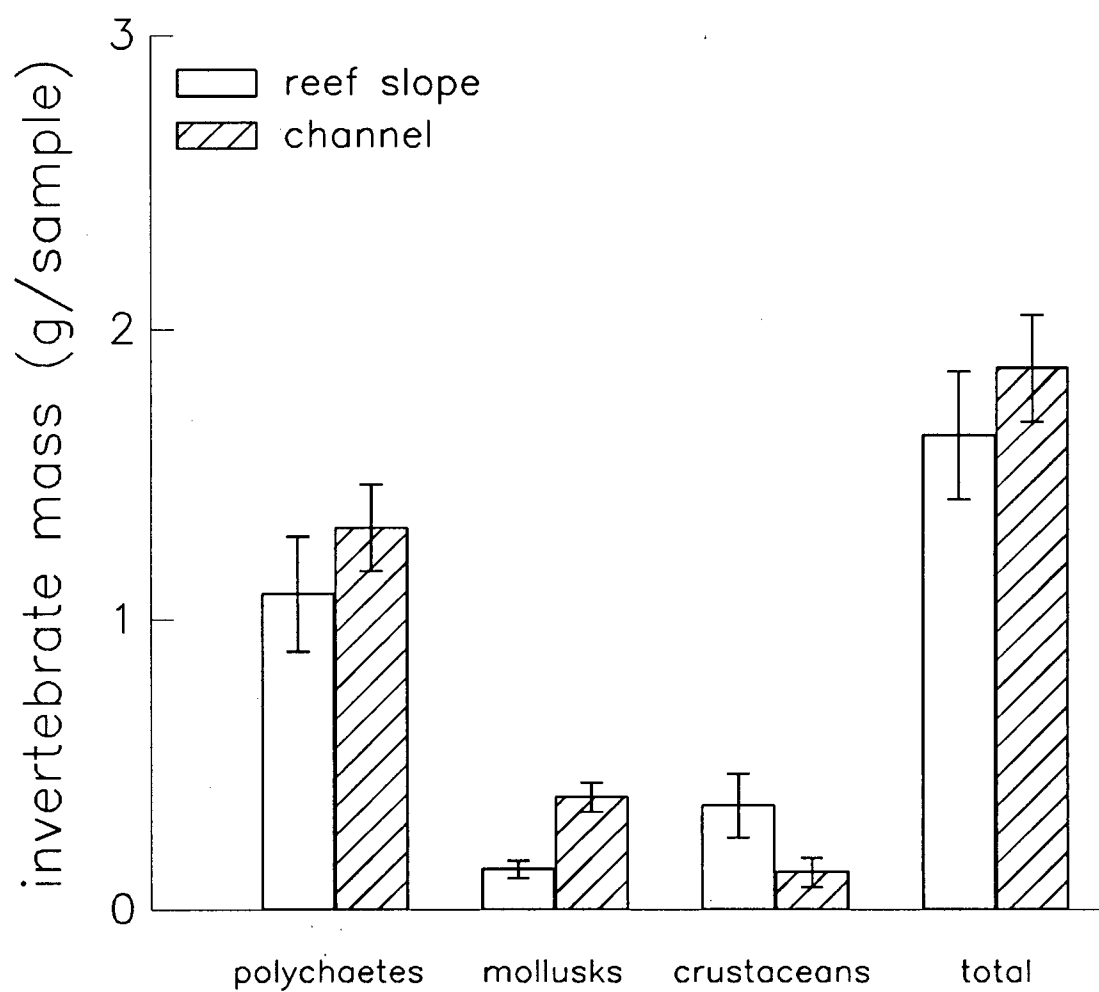
Figure 25.   Mass ($\overline{X} \pm$ SEM) of invertebrates per sample from channel and reef slope habitats.
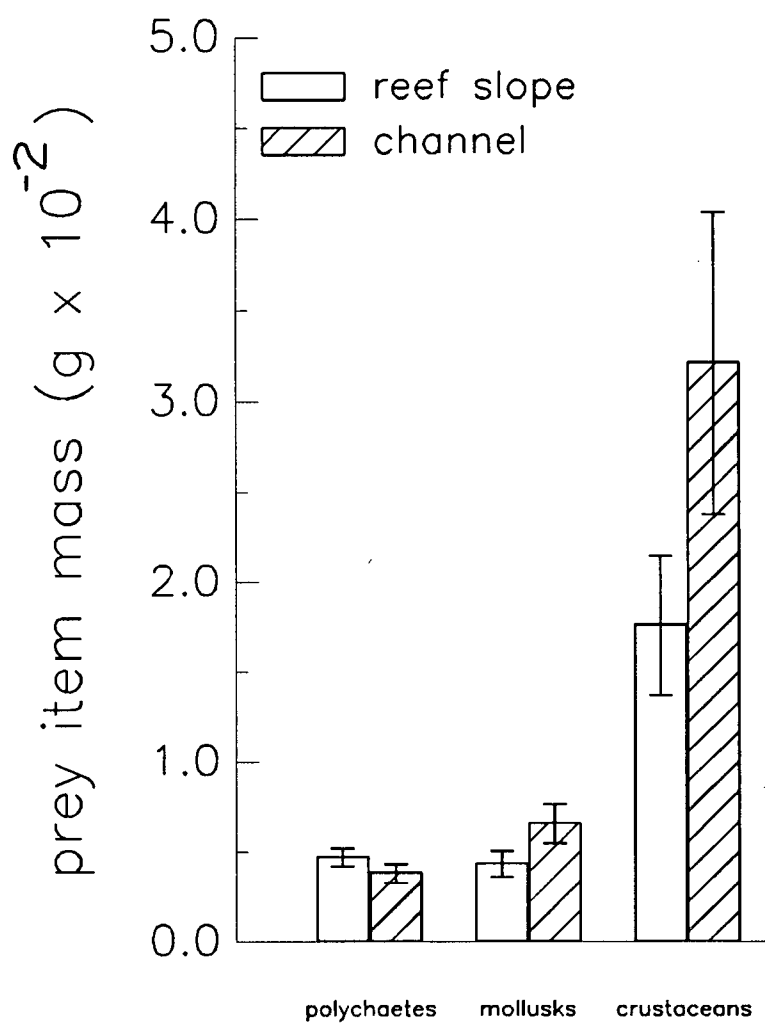
Figure 26. Individual mass ($\overline{X} \pm$ SEM) of polychates (N=100), mollusks (N=30), and crustaceans (N=30) in samples from reef slope and channel habitats.

Table 7. Number of eggs ($\overline{X} \pm$ SEM) spawned per day in reef slope and channel females of similar size.

	SL (cm)	Ovulated eggs in ovaries	Percentage[1] of days when females spawned	Eggs spawned/day
Reef slope (N=23)	23.4 (0.7)	4,001 (1,471)	0.58	2,321 (853)
Channel (N=23)	22.0 (0.5)	2,694 (643)	0.75	2,021 (482)

[1] calculated as the number of days when females spawned, divided by the total number of female observation days.

had between 250 and 24,000 eggs. In fed females, all but one
reef slope specimen and all channel specimens had more than 500
hydrated eggs.

Second daily spawning ascents were noticeably shorter than
those of first spawnings, suggesting that they may involve
release of fewer eggs. Consistent with this observation, the
number of hydrated eggs collected from females prior to second
spawnings (X=75 eggs, SE=43, N=7) was only 2.2% of the average
number collected prior to first spawnings (Table 7). Third
spawning ascents were even shorter and lower than second daily
spawnings, suggesting that third spawnings probably also involve
the release of few eggs.

Net Mating Success of Females and Males

Estimates of average mating success of channel males were
more than twice that of reef slope males, because channel males
had larger harems and channel females spawned on a higher
percentage of days (Table 6). Even when discounted by the
higher per capita mortality rate in the channel, the expected
net mating success for channel males over one year is two
times that of reef slope males (Table 8).

In females, the standard errors around the mean daily batch
fecundities of similarly-sized channel and reef slope females
are extremely large and overlap considerably (Table 7). As a
consequence, the estimates of the average number of eggs
spawned/day are not statistically different in the two
habitats, even though channel females spawned on a higher
percentage of days. When discounted by mortality, the expected

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Table 8. Estimated net mating success in reef slope and channel males.

Habitat	Daily mating success ($\bar{X}$ spawns±SE)	Expected 1-yr. mating success (# spawns)	Per capita daily death rate[1]	Expected per capita probability of mortality during 1 yr.	Net 1 yr. mating success[2]
Reef slope	1.08 (0.9)	394	4.6×10^{-6}	0.002	393
Channel	2.42 (0.1)	883	4.3×10^{-5}	0.016	869

[1] calculated as the percentage of tagged fish disappearing/day/total number of fish tagged in each habitat.

[2] net 1 year mating success = (# of spawns expected during 1 year) x (1.0 - probability of mortality during 1 year)

number of eggs spawned during one year by reef slope females is only slightly higher (1.16 times) than that of channel females (Table 9). The magnitude of this difference is well within the range of the standard errors of estimates of average daily batch fecundity.

Effects of Food Supplementation

Neither feeding females alone or feeding females and males increased spawning rates. In both habitats, the three-day spawning frequency of fed females was similar to their rates before feeding, and to that of non-fed control females. Similarly, there was no increase in the total frequency of male spawnings/day, daily spawnings/female, or the frequency of advertisement displays when both males and females were fed.

Growth rates of food-supplemented females were markedly higher ($F=10.19$, $p<0.01$) than those of controls in both habitats (Figure 27). The interaction between habitat and growth rate was not statistically significant ($F=2.41$, $p>0.05$). However, the mean growth rate of fed reef slope females was more than four times that of controls ($p<0.05$, Tukey's A test) compared with only a 1.9 fold difference in the channel (Figure 27).

Gonosomatic indices of fed females were higher ($F=11.67$, $p<0.01$) than non-fed females in both habitats (Figure 28). The interaction between habitat and effects of feeding on GSI was not statistically significant ($F=0.42$). The gonosomatic index of fed females in the channel, however, was higher ($p<0.05$, Tukey's A test) than that of control females. By contrast, GSI of food-supplemented reef slope females was not statistically higher

Table 9. Estimated net mating success (number of eggs) in similarly sized reef slope and channel females.

Habitat	# of eggs released/ day[1] ($\bar{X}\pm SE$)	Expected # of eggs released /1-year	per capita daily death rate	Expected per capita probability of mortality during 1 yr.	Net 1 yr. mating success[2]
Reef slope	2,321(853)	847,165	4.6×10^{-6}	.002	845,471
Channel	2,021(482)	737,665	4.3×10^{-5}	.016	725,862

[1] based on estimates of the number of hydrated eggs in ovaries of females collected prior to spawning.

[2] net 1-year mating success = (expected # of eggs released/year) x (1.0 - probability of mortality during 1 year), assumes 100% fertilization and offspring survival (see text).
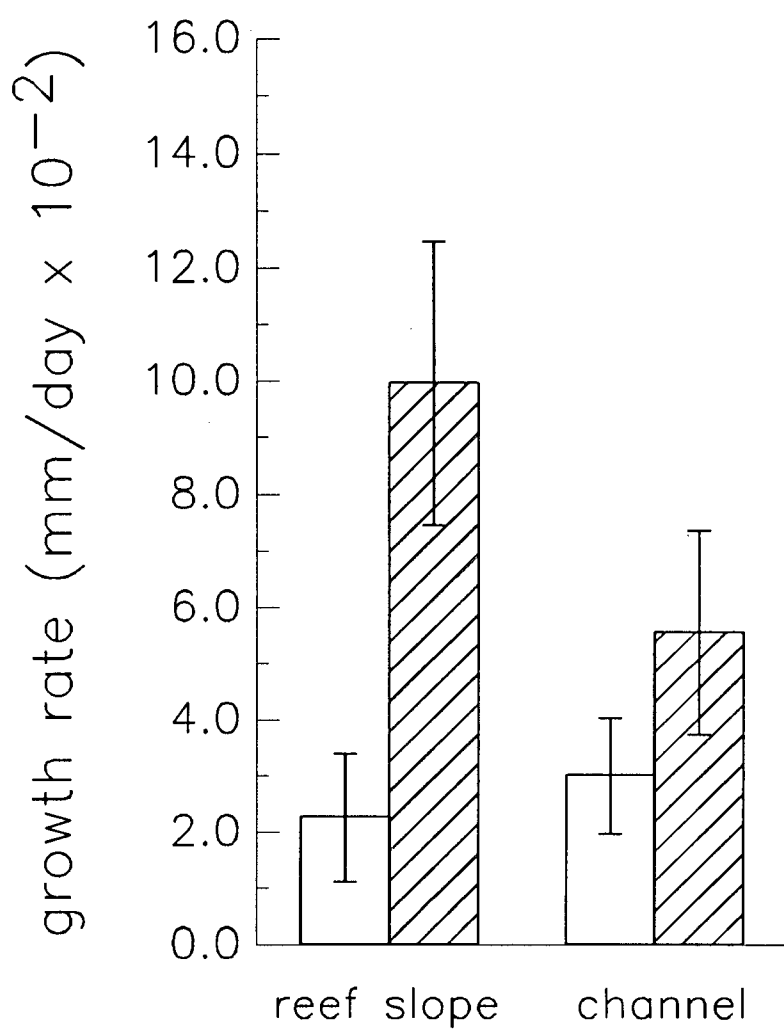
Figure 27. Growth rates ($\bar{X} \pm$ SEM) of non-fed and fed reef slope and channel females.
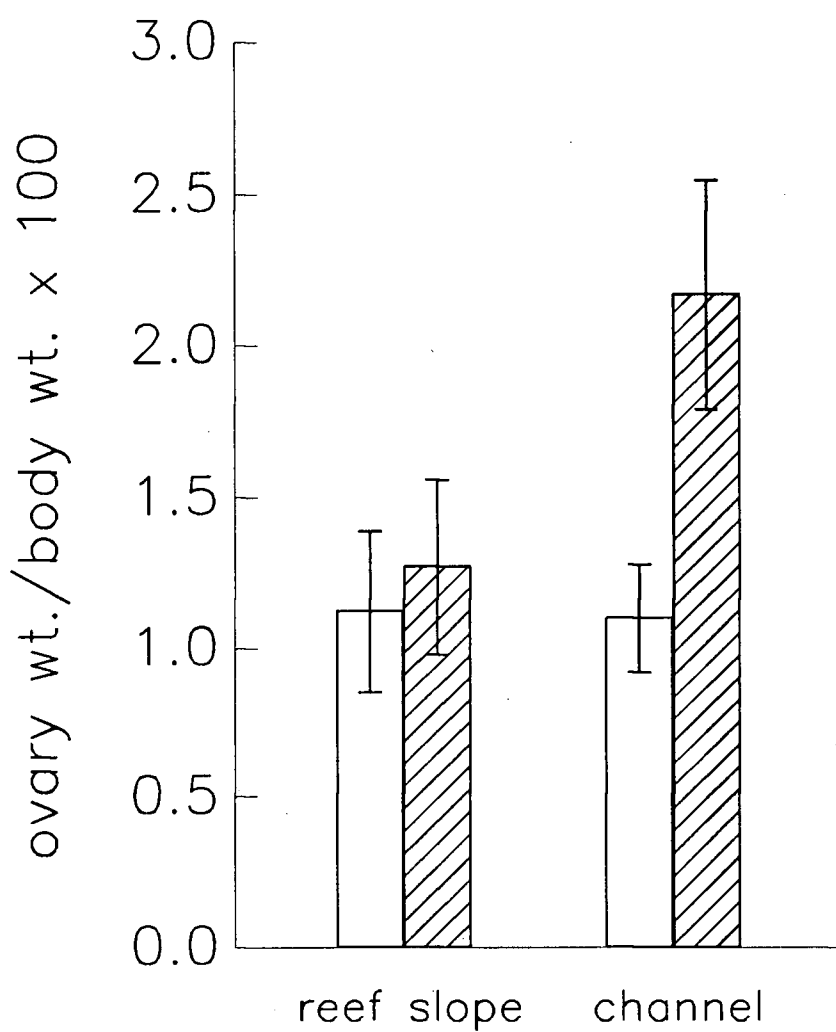
Figure 28. Gonosomatic indices ($\overline{X} \pm$ SEM) of non-fed and fed reef slope and channel females.

than that of controls (Figure 28). Ovaries of all fed females contained more than 500 hydrated ova, and the number of eggs was higher (F=12.45, p<0.01) than that of non-fed females in both habitats (Figure 29). The mean number of hydrated eggs in fed females were 1.7 and 1.9 times higher than those of non-fed females in reef slope and channel habitats respectively, however, these differences are not statistically significant.

DISCUSSION

Male Harem Size

Channel males had larger harems and spawned more frequently with each female than reef slope males (Table 6). Harem size was related to female spacing as well as to the within-colony ratio of females to males. Inter-female distance, however, accounted for only a small proportion of the variance in harem size (r^2=0.13), and neither inter-female distance nor male-female distance were shorter in the channel where harems were larger. By contrast, the ratio of females to males accounted for a large proportion (r^2=0.90) of the variation in harem size, and female to male ratios were larger in the channel. These results are more consistent with the hypothesis that male harem size is limited by the ratio of competitors to potential mates than by the distance separating females.

Unlike some other polygynous vertebrates, high mating success in tilefish males does not appear to be related to large body size. Unmated males were sometimes larger than mated males within their colonies, and the largest males often did not have
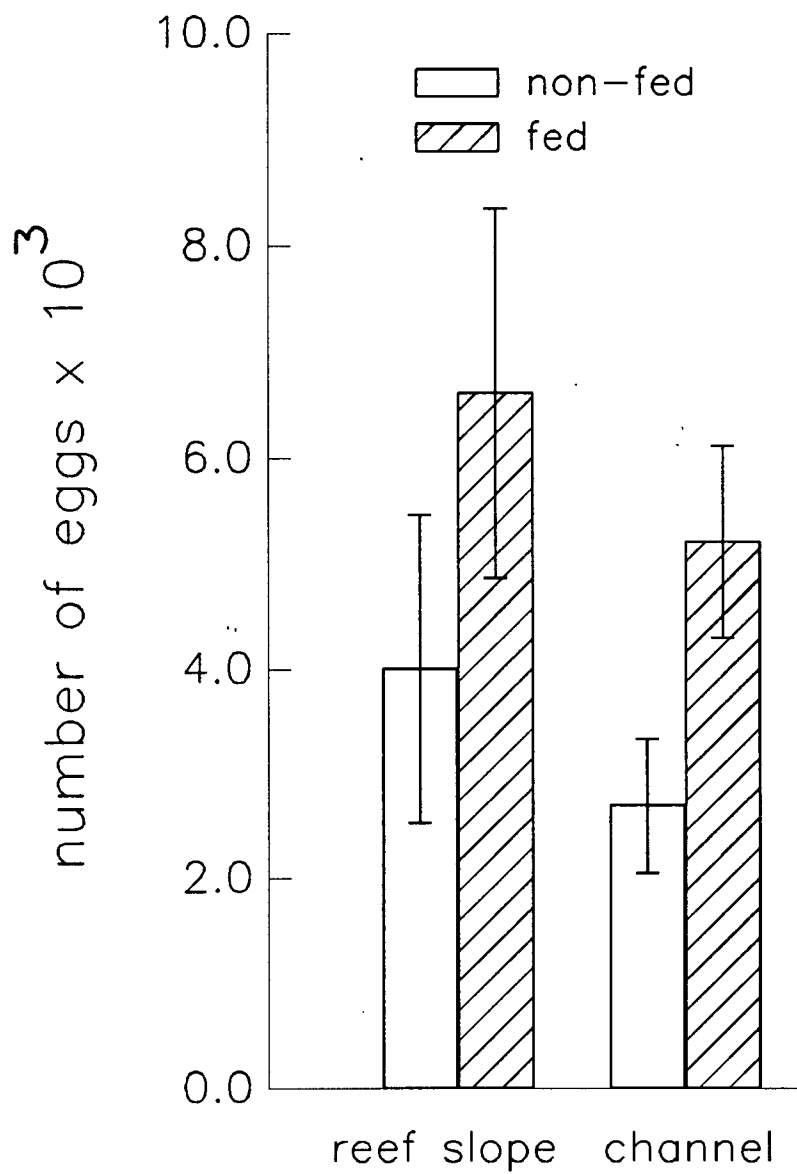
Figure 29. Estimates ($\bar{X} \pm$ SEM) of the number of hydrated eggs in ovaries of non-fed and fed reef slope and channel females collected prior to spawning.

the largest harems. The results of male removals suggest that harem size may be influenced more by predation and recruitment events than by effects of size on social status. In all male removals, replacement males were the occupants of neighboring territories even though larger males were often present elsewhere within these colonies. Perhaps prior residency on a neighboring territory influences which males can move into vacant areas. Predation on females may also influence the number of mates that males monopolize. Therefore, the size of a particular male's harem at any point in time may reflect the history of predation events and recruitment in that local area.

Spawning Frequency and Fecundity of Females

Female tilefish sometimes spawned more than once per day, especially in the channel. Multiple daily spawning appears to be unusual among marine fishes that broadcast planktonic gametes, but has been suggested for M. plumieri (Colin and Clavijo, in press), and documented in at least two labrids (Olla et al., 1981; Hoffman, 1983). The presence of very few eggs in the ovaries of tilefish females that had paired with their mates a second time suggests that females release most of their daily egg batch during first spawnings.

Information on the temporal cycle of oocyte maturation in relation to spawning frequency and periodicity is apparently scarce in tropical marine fishes that can spawn more than once each day. Although it is possible that separate batches of eggs are ovulated prior to each multiple daily spawning, it seems more likely that ovulation occurs once per day. Very few

eggs were found in ovaries prior to second spawnings. Also,
second spawnings occurred as soon as 6 min after first
spawnings. These data suggest that second and third spawnings
probably release residual eggs from a single batch that is
ovulated before first spawnings.

The observation that females do not spawn every day raises
the question of whether eggs are sometimes ovulated and retained
until future reproductive periods rather than being released
during that same day. Twenty-eight percent of non-fed females
collected before spawning had fewer than 200 hydrated eggs. If
ovulated eggs that have undergone hydration may be stored until
future reproductive periods, then it is possible that these
females were not ready to spawn when they were collected. I did
not determine empirically if hydrated ova are stored, and
whether they remain viable until future reproductive periods.
If ripe ova can be stored, then females may accumulate eggs over
more than one day prior to spawning. The option to store ripe
eggs could be advantageous in the event that environmental
conditions for spawning become adverse on a particular day. For
example, females sometimes did not spawn following barracuda
attacks directed at them or their mates, or when males were
involved in heightened aggression following male removals
(Chapter 6).

Under the hypothesis that eggs may be stored, the number
of eggs released on a given day could vary with the number of
days since eggs were last spawned. Such factors may have
contributed to both the large variability in estimates of daily
batch fecundity, and the absence of a correlation between the

number of hydrated ova and body mass, even though ovary mass is correlated with body mass. Also, although the difference was not statistically significant, the ovaries of non-fed reef slope females tended to contain more ovulated eggs than ovaries of channel females of similar size (Figure 29). This trend might also be explained by egg storage. There is a higher probability of capturing a reef slope female that had stored eggs for more than one day, because females spawned less frequently in this habitat (Figure 22). Because several factors may influence the number of eggs that are ovulated on a given day, I conclude that gonosomatic index is the more reliable estimate of the energy invested by females in present reproduction.

Influence of Food Intake on Female Reproduction and Growth

Feeding did not increase the frequency of female spawning, but fed females in both habitats had higher GSI's, growth rate, and daily fecundities, than non-fed females. Increased GSI and daily fecundities of fed fish clearly suggests that present egg production of females is limited by food intake. Increased growth rates of fed females indicates that growth, and therefore, future capacity to produce eggs, is also limited by energy intake. Responses to feeding lend further support to my interpretation of removal tests that the function of female territoriality is defense of a food supply surrounding home burrows (Chapter 6). In species where males compete for mates, sexual selection theory predicts that female reproductive success is limited by resources that can be devoted to production of offspring rather than by access to males (Bateman,

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1948; Williams, 1966; Trivers, 1972; Borgia, 1979; Alexander and Borgia, 1979). My results are consistent with this prediction.

Influence of Habitat Selection and Larval Settlement on the Distribution of Adults

Estimates of net yearly mating success are similar in reef slope and channel females (Table 8). This result is consistent with predictions of the ideal free model, assuming that estimated parameters used in this calculation are constant over the reproductive lifespan of females. If this assumption is valid, then density may be high in the channel because females settle in this area preferentially until increasing costs of competition make it more profitable to move to reef slopes. Other observations on females are also consistent with predictions of the ideal free model. All six of the harem removals where no recruitment occurred were in reef slope colonies. In contrast, rapid recruitment followed all seven channel harem removals (Chapter 6), supporting the notion that females settle preferentially in the channel. On the other hand, the food resources that limit female reproduction were not more abundant in the channel as would be expected under the ideal free model.

In contrast, the high net mating success of channel males relative to reef slope males is consistent with predictions of the ideal dominance model. If the ideal dominance model applies to M. plumieri males, then superior competitors are able to acquire territories in the channel where potential mates are

most abundant, and inferior competitors are forced onto reef

slopes with fewer potential mates. Unmated males that were more

common in reef slopes, might be fish that could not obtain

territories in the channel and were displaced into reef slope

habitats.

Both of these habitat selection models are predicated on

the assumption that adults are able to move freely between

habitats to assess resources and competitor density prior to

choosing a territory (Fretwell and Lucas, 1969; Fretwell, 1972).

I found no evidence that settled tilefish move among reef slope

colonies or between the reef slope and the channel, although I

cannot be certain that adults do not actively choose from among

available habitats. Such movements seem unlikely because

tilefish remain near home burrows to avoid predators (Chapters 3

and 4). Movement between colonies would require swimming across

large unfamiliar sand flats where there are no burrows to serve

as refuges from predator attacks. Relocation of territories was

not observed unless one or more neighbors were removed. Even

then replacements moved from adjacent territories rather than

from other colonies (Chapter 6). Although unoccupied space was

available, new adults did not recruit into study colonies as

might be expected if movements by adults were common. Also,

unmated males in colonies where only a few females were present

relative to the number of males, probably had the most to gain

from moving to other habitats. Nonetheless, these males did

not move from territories without females for the duration of

observations, periods of up to 4.5 months. The apparent absence

of movement between colonies, therefore, suggests that adult tilefish do not actively assess territories in more than one habitat as assumed by the ideal free and ideal dominance models.

Observations on the distribution of larvae in tilefish and other species, and current patterns at Glover's Reef are consistent with an alternate hypothesis that the distribution and abundance of sedentary adults is a consequence of planktonic larval settlement. Much of the oceanic water that flows onto Glover's Reef enters through passages like the channel between Long and Northeast Cays (Stoddart, 1962). Therefore, large numbers of tilefish larvae may encounter the channel before they reach reef slope sites inside the lagoon. Shapiro (1987) has presented evidence for Anthias squamipinnis that planktonic larvae settle on the first suitable substrates that are encountered, even though these locations do not appear to be the best available sites. Opting for early settlement may be the best strategy for larvae because factors that affect survival in the plankton are highly stochastic (Barlow, 1981; Victor, 1983; Doherty et al., 1985), and there is no guarantee that a better site will be encountered if settlement is postponed. Early settlement in the first habitat encountered, therefore, may explain the large dense concentration of tilefish in the channel.

In support of this hypothesis, juveniles were 15 times more common in the channel than in reef slope colonies (Chapter 4). Also, replacement by small females or juveniles occurred much more readily in the channel following fish removals. Lastly, examination of another east-west passage through the northern

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part of the atoll also revealed the presence of a large tilefish colony. All of these observations support the hypothesis that, even though high predation risk may make it more dangerous than reef slopes, many recruits settle in the channel as a consequence of prevailing water circulation.

Food availability and Female Spawning Frequency

Feeding did not increase spawning frequency. This suggests that a higher rate of food intake probably does not explain why channel females spawn more frequently than reef slope females. On the contrary, higher bite and swimming rates suggest that it may be necessary for channel females to expend more effort foraging, possibly because food resources are inferior in this habitat. Estimates of food availability, however, do not support the latter hypothesis either. Stomach contents revealed that females in the two habitats ingest similar prey. The only evidence that prey are more scarce in the channel is the lower biomass of mollusks. Overall, the estimates of prey abundance are similar in the two habitats, and crustaceans of the size range that tilefish eat, were even larger in the channel. Finally, estimates of daily batch fecundity, GSI, and growth rates of non-fed females in the two habitats were not statistically different, suggesting that reef slope and channel females probably have access to similar amounts of food. Together these results suggest that the abundance or quality of food resources alone does not explain the striking differences in rates of spawning and foraging by females in the two habitats.

The Relationship Between Female Reproductive Effort and the Behavior of Predators

Disappearance rates of tagged fish suggest that risk of predation is higher in the channel. Where predation risk is high, females might be expected to spawn less frequently and forage closer to their burrows to minimize vulnerability. Conversely, reef slope females might be expected to forage farther from their burrows and perhaps spawn more frequently because predation risk is lower. I observed the opposite pattern.

One possible explanation of this paradox is that the different behavior patterns of reef slope and channel females are related to differences in the hunting tactics used by barracuda in the two habitats. In reef slope habitats, spawning frequently and foraging distant from burrows might greatly increase vulnerability to attack, because barracuda lurk on these sites and stalk tilefish. By remaining closer to burrows and opting for a lower rate of spawning and foraging, reef slope females are apparently able to counter the effectiveness of lurking predators.

By contrast, channel females appear to suffer higher predation risk, yet they exhibit behavior that makes them vulnerable to attack. It is not clear why such behavior is maintained. One possibility is that channel females do not readily detect the predators that swim above them, and behave as if risk of attack were low. Channel females might also habituate to the daily migration by large piscivores through the

channel, and simply do not react as readily as reef slope
females.

Another possibility, however, is that channel females are
making the best of a bad situation by spawning frequently in a
high risk habitat. When the risk to individuals of attack is
high and unpredictable, bet-hedging theory predicts, that
individuals should maximize present reproductive efforts. The
behavior of channel females is consistent with this prediction.
Foraging at a high rate, distant from burrows suggests increased
efforts to obtain the food resources that limit egg production
even though foraging may also increase vulnerability to attack
and reduce vigilance. The most striking indication that channel
females maximize present reproductive effort is the frequent
occurrence of multiple daily spawnings. Second and third daily
spawnings were much more common in channel females even though
only a small number of eggs was released during these matings.
When predator attacks occur at any time with little warning, the
best reproductive tactic may be to take the fullest advantage of
present spawning opportunities. The frequent occurrence of
multiple spawns, even though they contribute relatively few
eggs, is consistent with the hypothesis that channel females
maximize immediate spawning opportunities.

By contrast, reef slope females had much lower rates of
spawning even though food availability and GSI were as high as
those of channel females. Attacks by lurking predators may be
more predictable, and thus avoidable, than in the channel. Under
this type of predation threat, reef slope fish might opt for a
lower rate of spawning because the probability of predation

before future reproductive bouts is lower.

The different response by reef slope and channel females to increased food intake is the strongest evidence to support the hypothesis that female reproductive tactics are influenced by the type of predation risk. Neither channel or reef slope females spawned more frequently when fed experimentally. However, there was an obvious trend in how females allocated additional energy to somatic growth and to ovaries. Reef slope females grew proportionately more and thereby increased to a greater degree their capacity for future egg production. High growth rates in response to increased food intake might be expected when the risk of predation before future reproductive periods is low. By contrast, channel females might be expected to invest more energy in egg production when resources are abundant, because the risk of predation before future reproductive bouts is higher. In accordance with this expectation, fed channel females had higher GSI's and a tendency to produce more eggs, suggesting that they allocate more energy to present reproduction than fed reef slope females.

1. Average size of both sexes was smaller in the channel, while growth rates in the two habitats were similar.

2. Channel males had larger harems and spawned more than twice as frequently as reef slope males. Harem size was correlated more strongly with the within-colony ratio of females to males than the distance separating females.

3. Channel females forage at higher rates over larger areas, and spawn more frequently than reef slope females.

4. Abundance and size of prey in substrate samples from reef slope colonies and the channel were similar.

5. Daily batch fecundity of non-fed females was highly variable and was not statistically different in reef slope and channel habitats.

6. Diet supplementation did not increase spawning frequency, but fed females in both habitats grew faster, produced more eggs, and had higher GSI's than non-fed controls.

7. Estimates of net yearly mating success were similar in reef slope and channel females, while net mating success of channel males was more than twice that of reef slope males. These estimates are consistent with predictions of the ideal free model in females and the ideal dominance model in males. However, active habitat selection in adult tilefish appears unlikely because they apparently do not move freely between

habitats.

8. The distribution of juveniles in relation to prevailing current patterns, is consistent with the alternate hypothesis that the distribution and abundance of adults is a consequence of larval settlement processes.

9. Different responses to diet supplementation by reef slope and channel females that are correlated with differences in predation, support the hypothesis that individuals may modify reproductive tactics in accordance with risk of predation before future reproductive periods.

CHAPTER 8

GENERAL DISCUSSION

The Role of Female Territoriality in Marine Fish Harems

In pelagically-spawning marine fishes, the degree to which polygynous males monopolize more than one of the same females may be related to the spatial distribution of females during spawning periods. When females depart their feeding ranges and migrate independently to a limited number of favorable spawning sites, it may not be feasible for males to maintain contact with and monopolize spawnings with the same set of mates (Robertson and Hoffman, 1977; Robertson, 1981). In addition, predictable congregations of females that are ready to spawn would almost certainly attract large numbers of male competitors, making it more difficult for individual males to monopolize daily spawnings with a harem. Consequently, the mating systems of species in which females congregate in certain spawning sites may resemble leks rather than harems. In lek-like species, certain males establish temporary territories each day in areas preferred by females for spawning (e.g., Moyer and Yogo, 1982; Warner, 1984b; 1987; Hoffman, 1985). Territorial males may mate with numerous females each day, but they do not maintain social contact and monopolize daily spawnings with the same females over prolonged periods.

By contrast, when females each spawn within an all-purpose territory, they do not migrate, and are not highly aggregated during spawning periods. In species in which females are territorial, male monopolization of harems may be feasible when

females are located sufficiently close together that males are able to exclude competitors from more than one female territory. Kuwamura (1984) has argued that harems do not form in species with territorial females. Kuwamura (1984) suggests that harems consisting of territorial females are rare, and that intersexual competition for food prevents formation of harems when females defend feeding territories. The cleaner wrasse, L. dimidatus, has been regarded as a good example of a species with harems composed of adjacent territorial females (Robertson, 1972; Robertson and Hoffman, 1977), but Kuwamura (1984) concluded that females in this species do not defend true feeding territories.

Data on tilefish show clearly that males may monopolize harems when females are territorial. Sand tilefish harems are composed of adjacent female territories encompassed by the territory of one male. Both sexes feed within territories that overlap the territories of their mates. Therefore, intersexual competition for food does not prevent the formation of harems in M. plumieri.

Social organizations similar to that of M. plumieri have been described in a number of pelagically-spawning marine fishes. Females defend territories that are used for feeding in a reef-dwelling angelfish (Hourigan, 1986), two sand flat-dwelling razorfishes (Clarke, 1983; Victor, 1987; Baird, 1988), and a weaverfish (Stroud, 1981). In each of these species, males monopolize spawnings with a number of females by defending all-purpose territories that overlap those of females. These studies indicate clearly that harems composed of adjacent

territorial females are not rare as suggested by Kuwamura (1984).

In tilefish, two aspects of spacing behavior distribute females in a way that may facilitate rather than prevent harem formation. Under the risk of predation, selection may favor females that settle near other tilefish (i.e., colony formation). Females are only moderately concentrated within colonies, however, because they defend non-overlapping territories. A moderate concentration of site-restricted females is precisely the condition under which some males might be expected to monopolize more than one mate (Emlen and Oring, 1977).

Harems in Pelagically-Spawning Marine Fishes: Female or Resource Defense?

Pelagically-spawning fishes that breed year-round present a particularly difficult challenge for the question of whether harems arise through resource or female defense. In most (if not all) of these species where spawning data on individuals has been collected to document harem-type mating systems, males apparently defend permanent territories that contain both females and their resources. Therefore, unlike many harem-forming homeotherms, whether males defend resources or attach themselves to female groups cannot be distinguished readily by differences in the degree to which males and females are restricted to, or disperse from breeding sites (Greenwood, 1980; Armitage, 1986).

The critical question in pelagic-spawning fishes is: Why
are females restricted to sites such that males are able to
monopolize daily spawnings with more than one mate? So long as
males are able to monopolize multiple mates, at least in part
because females are restricted to areas where they consume food
allocated to daily egg production, the resource defense
hypothesis cannot be rejected entirely. Invoking female defense
in lieu of resource defense should be reserved for species for
which it is demonstrated that: 1) males monopolize females that
are site-restricted exclusively for reasons unrelated to
acquisition of food or other resources necessary for
reproduction, or 2) males control mobile females that group
together for reasons unrelated to reproduction.

Results of this study strongly suggest that tilefish males
monopolize mates by defending territories containing food
resources that are important for egg production. Also, tilefish
males neither control the movement and location of their mates,
nor abandon territories when their mates are removed. These
results support a role of resource defense in the evolution of
tilefish harems. Females in most other pelagic-spawning fishes
that are known to form true harem mating units also occupy
feeding territories or fixed but undefended feeding ranges
(Robertson & Hoffman, 1977; Moyer & Nakazono, 1978; Stroud,
1981; Clark, 1983; Hoffman, 1983; Kuwamura, 1984; Hourigan,
1986; Victor, 1987; Petersen and Fischer, 1987). Therefore,
exclusive male spawning access to multiple females that mate
daily may be feasible only when females are restricted to sites

where they forage (Robertson, 1981).

On the other hand, tilefish males clearly position their territories where females reside. It is probably only feasible for males to defend more than one mate because females occupy adjacent territories. Such group living in tilefish may, at least in part, be selected because proximity to conspecifics reduces predation risk (Chapter 4). Similarly, razorfishes that form harems like those of M. plumieri, also appear to accrue anti-predator benefits from living in groups (Clark, 1983; Victor, 1987). Harem formation in species that live in groups to reduce predation risk is consistent with the female defense hypothesis.

I suggest that a dichotomy between resource and female defense, may not apply well to harem-forming fishes where females are site-restricted and production of planktonic eggs is iterated year-round. Among the clearest examples of resource defense are marsh-nesting birds in which males establish territories prior to the arrival of females in nesting habitats (Searcy & Yasukawa, 1983; Robinson, 1986). Such an obvious indication that males control areas to which females are attracted is lacking in fishes where females and males maintain breeding relationships throughout the year, and spawning is not limited to certain locations. Direct female defense is perhaps most clear in ungulates where males actively herd together female mates (Gosling, 1986), or in marmots where males dominate female kin groups (Armitage, 1986). Although so-called "pure female defense" has been suggested for harem-forming fishes

(Kuwamura, 1984; Hourigan, 1986; Victor, 1987), this conclusion

seems unwarranted when males are able to monopolize mates partly

because females are restricted to territories or home ranges

where they feed and spawn. I urge caution in concluding that

either mechanism alone explains the evolution of harems in these

fishes without rigorous demonstration. In my view,

characterization of harems as female defense polygyny alone

requires: 1) documentation of consistent mating fidelity among

females in highly mobile aggregations and individual males that

defend these groups, or 2) demonstration that males abandon

their territories when females are removed and move to seek

other mates. As far as I know, neither of these situations has

yet been demonstrated in pelagic-spawning fishes with harem-type

mating systems.

Burrowing and Coloniality in Marine Fishes: Possible Adaptations to Life in Open Seabed Habitats

Coloniality is thought to be rare in fishes compared with

birds, rodents, and pinnipeds. The nesting colonies of male

bluegill sunfishes are the best known example of fish

coloniality (Dominey, 1981; Gross and MacMillan, 1981), although

colonial nesting has also been described in cichlids

(Loiselle, 1977). Bluegill sunfish are characterized by highly

synchronized nesting, egg-laying, and nest-guarding, as is also

seen in some colonial birds (Wittenberger, 1981 and references).

Perhaps coloniality is more common but has not been recognized

widely among tropical marine fishes because few (if any) species

lay eggs in nesting colonies. Nevertheless, several of the same

species that construct burrows in open seabed habitats also form groups that fit Wittenberger's (1981) definition of coloniality. Two species of burrowing razorfishes, X. martinicenis (Victor, 1987), and X. pentadactylus (Clark, 1983) live in colonies on sand flats. Fricke and Kacher (1982) report that another tilefish, Hoplolatilus geo, occurs in discrete colonies within which individuals or pairs occupy fixed mounded burrows. Finally, the burrowing garden eels, Taeniconger hassi and Gorgasia sillneri, and the yellowheaded jawfish also concentrate in colonies, even though apparently suitable unoccupied substrate is abundant (Fricke, 1970; Colin, 1973).

The occurrence of burrowing and coloniality in marine fishes from at least four families suggests that this lifestyle is a response to selection pressures that are peculiar to life in open seabeds, such as vulnerability to predators. Similarities between the the behavior of some rodents that occupy open terrestrial habitats and colonial burrowing fishes lends support to this hypothesis. Prairie dogs, marmots, and ground squirrels, for example, dig complex burrows that provide the primary shelter from predation. Furthermore, these species live in dense colonies (e.g., Carl, 1971; Armitage and Downhower, 1974; Hoogland, 1979; 1980), sometimes characterized by harem social and mating organizations (Downhower and Armitage, 1971; Wittenberger, 1979). Colonial rodents usually share centrally-located communal burrows (Wittenberger, 1979), rather than each occupying separate refuges as in burrowing fishes.

Both burrowing rodents and fishes are hunted by large

predators (i.e., raptors for rodents, large piscivores for

burrowing fishes) that may attack suddenly, and from any

direction. Moreover, some of these rodents have evolved

elaborate social signals for predator avoidance (e.g., Waring,

1970; Sherman, 1977; Owings and Virginia, 1978; Hoogland, 1979).

Among the burrowing fishes, at least tilefish, garden eels, and

straight-tailed razorfish are known to exhibit contagious

reactions to alarm responses by neighbors (Fricke, 1970; Victor,

1987). The adoption of parallel behavior patterns by

phyletically diverse species suggests a common solution to

problems imposed by similar environmental conditions (Alcock,

1984). I suggest that adoption of a burrowing and colonial

lifestyle among rodents and phyletically distant marine fishes

is a convergent evolutionary solution to the extraordinary

predation risk associated with occupying open environments where

shelter is scarce.

The Distribution of Tropical Marine Fishes: Adult Habitat
Selection or Consequence of Larval Settlement?

The ideal free and ideal dominance habitat selection models

were proposed for dispersive species in which individuals

migrate into breeding habitats each season where they establish

reproductive territories (Fretwell and Lucas, 1969; Fretwell,

1972). Individuals in such species are almost certainly able to

move freely among available habitats to select sites,

particularly before they have established territories.

In contrast, tilefish apparently hold territories and

spawn year-round (Chapter 5). I found no evidence of adult migration between channel and reef slope habitats or among reef slope colonies (Chapter 7), although I cannot be certain that such movements never occur. There is growing evidence that some tropical marine fishes spend most of their lives in the habitats where they settled as larvae, and that immigration into local populations is limited to recruitment by planktonic larvae. Populations of T. bifasciatum on patch reefs, for example, are believed to be linked only by mixing of planktonic larvae (Warner and Hoffman, 1980a; 1980b; Victor, 1983; Warner, 1984b). Anthias squamipinnis is most abundant on deep reefs, even though the larger size of individuals on shallow reefs suggests that, if adults were mobile, it would be advantageous to migrate from deep to shallow areas (Shapiro, 1987). Angelfishes have been observed to occupy the same areas for as long as 3.5 years (Aldenhoven, 1986), and Moyer (1986) has observed individuals of five species in the same locations for from 5 to 14 years. These observations suggest that movement between different habitats is uncommon in tropical marine fishes. Such site-restriction in tilefish would prohibit individuals from assessing territories in more than one habitat patch and then settling in the best available site. As the ability to disperse freely among habitats is a fundamental assumption of the ideal free and ideal dominance models, these hypotheses are not likely to apply to tilefish or other sedentary marine species with planktonic larvae.

If adult tilefish do not change habitats once they have settled, then colonies would persist in the same locations only if at least some victims of predation are replaced by recruitment of juveniles. Extinction of colonies was not observed over four study seasons, although the presence of burrows on unoccupied sites indicates that colonies might sometimes become extinct. No new colonies were discovered where tilefish were absent during previous years, and juveniles were encountered exclusively near adults rather than in all juvenile groups. These observations suggest that preferential settlement near adults by larvae and/or juveniles also may occur in M. plumieri, and that this process perpetuates colonies through time. Larval attraction to adults has been demonstrated in some sessile invertebrates (Levinton, 1982).

Relative Lifetime Reproductive Success of Reef Slope and Channel Fish

Although the dense colony of tilefish in the channel may be largely a consequence of larval transport, settlement in such areas may also be advantageous if some individuals survive long enough to obtain large harems and garner high lifetime reproductive success despite high predation risk. Histological evidence suggests that most if not all male tilefish are sex-changed females (monandry, Chapter 5). If tilefish are monandric, then the lifetime reproductive success of fish that change sex and obtain harems includes their success as a female plus that as a male. Estimated net yearly mating success of similarly sized females was not statistically different in the

two habitats (Table 8). In marked contrast, the net yearly mating success of channel males was over twice that of reef slope males (Table 9). Therefore, if one assumes that offspring spawned in the two habitats survive equally well, and that the duration of the mating lifespan as females and males is similar in the two habitats, then channel fish will obtain higher lifetime reproductive success than reef slope fish. Also, opportunities for sex change and acquiring harems may increase with population density (Aldenhoven, 1986; Warner, 1988). The smaller size of channel males even though they grew at similar or higher rates suggests that sex change may occur earlier in this habitat. Selection may favor settlement in the channel, therefore, because the lifetime mating success of fish that survive long enough to change sex and then acquire large harems is higher than that of sex-changed reef slope fish that obtain fewer mates. Under this hypothesis, sex-changed reef slope fish may be making the best of a bad situation.

Alternatively, the lifetime mating success of reef slope fish may equal or surpass that of channel fish, if reef slope fish reproduce over a longer lifespan. I did not determine the age of tilefish. Therefore, I cannot accept or reject the possibility that the average lifespan of male reef slope fish is sufficiently long to balance the short-term reproductive advantage of channel fish. The lower rates of disappearance and the larger size of reef slope fish, however, are both consistent with this hypothesis.

Habitat Differences in Predation Risk and Female Spawning Rates

It is conceivable that females with high and low spawning rates are two genetically fixed behavior patterns, and that habitat differences result because each genotype settles preferentially into a habitat where its reproductive behavior is best suited. Such habitat selection would have to occur during larval settlement if adults are sedentary. For this hypothesis to be plausible, larvae would need to assess at the time of settling the type of predation threat experienced by adults. I cannot reject this as a possibility. However, assessment of the intensity and type of predation on adults prior to actual settlement on the site seems unlikely.

It seems much more likely that females in reef slope and channel habitats are not genetically distinct populations, because pelagic larvae originating from different habitats are mixed during the planktonic dispersal phase (Avise and Shapiro, 1987). If reef slope and channel fish are not genetically distinct types, then habitat differences in spawning rates may be two conditional reproductive tactics, where the adoption of one or the other depends upon the type of hunting behavior exhibited by predators in the two habitats. In reef slope habitats, spawning may increase vulnerability to a greater degree than in the channel, because predators lurk on these sites. By contrast, because channel females are subject to high unpredictable attacks from mobile predators, frequent spawning may not increase risk beyond that of what it would be if females spawned less frequently.

Two other recent field studies on fishes have suggested
that reproductive tactics are conditional upon local
environmental conditions. Resnick and Bryga (1987) report
shifts in the reproductive tactics of guppies in response to an
experimental manipulations of predation risk. Unlike tilefish,
Resnick and Bryga's (1987) study involves isolated
subpopulations, such that shifts in reproductive tactics may
involve genetic changes. However, differences in reproductive
tactics in response to conditions in local habitats have also
been shown in a marine fish where planktonic larval dispersal
ensures genetic homogeneity among adult subpopulations. The
amount of time and energy that male wrasses, <u>Thallasoma
bifasciatum</u>, allocate to present reproductive effort versus
growing to large size to enhance future competitive ability is
conditional upon present and future probabilities of acquiring
mates through intrasexual competition (Warner, 1984b).

Similarly, there may be selection for flexibility in the
reproductive tactics of female tilefish in response to different
types of predator activity. For such selection to occur would
require: 1) that habitat variation in the type of predator
activity has been prevalent during the evolutionary history of
<u>M. plumieri</u>, and 2) sufficient genetic flexibility that
individuals are capable of adjusting their behavior and
investments in egg production and growth according to
environmental cues of predation risk. Such cues might include
the type of attacks exhibited by predators, the frequency of
predator sightings or unsuccessful attacks. Pronounced habitat
variation in the type of predator activity that <u>M. plumieri</u> is

exposed to is likely, considering the potential for dispersal into a variety of habitats through the plankton. Differential responses to food supplementation demonstrate the potential for flexibility in reproductive tactics. I suggest, therefore, that habitat differences in female spawning rates may be a manifestation of a flexible reproductive strategy in which present reproductive effort depends upon the type of predator activity in local habitats.

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Troy Alan Baird

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Baird, T.A. and Liley, N.R. In press. The evolutionary significance of harem polygyny in the sand tilefish, *Malacanthus* *plumieri*: Resource or female defense? Anim. Behav.

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Baird, T.A. 1989. The adaptive significance of coloniality and harem polygyny in the sand tilefish, *Malacanthus* *plumieri*. Ph.D. thesis, Department of Zoology, University of British Columbia.

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