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MATING SYSTEMS IN TROPICAL MARINE FISHES: THEORY AND CASE
STUDIES OF SIMULTANEOUS HERMAPHRODITISM AND PATERNAL CARE

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MATING SYSTEMS IN TROPICAL MARINE FISHES:
THEORY AND CASE STUDIES OF SIMULTANEOUS
HERMAPHRODITISM AND PATERNAL CARE

by

Christopher William Petersen

A Dissertation Submitted to the Faculty of the
DEPARTMENT OF ECOLOGY AND EVOLUTIONARY BIOLOGY

In Partial Fulfillment of the Requirements
For the Degree of

DOCTOR OF PHILOSOPHY

In the Graduate College

THE UNIVERSITY OF ARIZONA

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THE UNIVERSITY OF ARIZONA
GRADUATE COLLEGE

As members of the Final Examination Committee, we certify that we have read
the dissertation prepared by Christopher William Petersen

entitled Mating systems in tropical marine fishes: theory and case
studies of simultaneous hermaphroditism and paternal care

and recommend that it be accepted as fulfilling the dissertation requirement
for the Degree of Doctor of Philosophy.

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Christy W. Peltz

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ABSTRACT

This study investigates two aspects of tropical reef fish mating systems: the prevalence of paternal care in those species that exhibit some form of parental care, and the evolutionary stability of simultaneous hermaphroditism. Studies of three species of tropical reef fishes from the Gulf of California were used to investigate these two different types of mating systems.

Two species of demersal egg guarders with paternal care, Malacoctenus hubbsi and Abudefduf troschelii, were studied to determine the importance of a male's mating status (the number of eggs in his territory) in regard to female choice of mates. In both species, females did not base their choice of mates on the number of eggs in the male's territory, males increased their level of parental care with increasing egg number, and egg survivorship where estimated was independent of brood size. These results corroborate, and offer the first experimental field verification of a crucial assumption of a minimal-care hypothesis proposed a decade ago by Williams (1975).

Male reproductive success was studied in greater detail in one species, M. hubbsi. Territory parameters, rather than male size, were the major determinants of male

reproductive success. This independence relative to male size was attributed to the unpredictability of good future territories.

In Serranus fasciatus all individuals begin reproduction as simultaneous hermaphrodites, but lose female function at large sizes to become males. Males obtain disproportionate reproductive success by maintaining harems of hermaphrodites and defending them from adjacent males. These harems are similar to those found in some sequentially hermaphroditic species. Hermaphrodites obtain most of their reproductive success through female function by spawning with a male, but also engage in an alternative male strategy - streaking on pair spawns - to obtain some male reproductive success. This small amount of male reproductive success by hermaphrodites appears to stabilize simultaneous hermaphroditism with most resources allocated to female function. Facultative alternative male mating strategies in hermaphroditic individuals joins spawning reciprocation as the only known behavioral strategies that provide evolutionary stability for simultaneous hermaphroditic individuals in populations of tropical reef fishes.

CHAPTER 1

INTRODUCTORY SYNTHESIS

Two unique aspects of fish mating systems relative to those of all other vertebrates are the preponderance of male parental care when parental care exists, and the existence and apparent stability of simultaneous hermaphroditism. The purposes of these studies were to re-examine the theoretical explanations for each of these two phenomena, and to test some of the assumptions and hypotheses involved using natural populations of tropical reef fishes in the Gulf of California.

The three species studied are very different in morphology and phylogeny. Malacoctenus hubbsi and Abudefduf troschelii were chosen for study because they represent the two extremes in paternal care exhibited by species that guard demersal eggs. The third species, Serranus fasciatus, was chosen because it exhibits a unique form of hermaphroditism that combines aspects of sequential and simultaneous hermaphroditism. All three species are abundant in the central Gulf of California and occur in shallow, relatively clear water so intensive behavioral studies were possible. They all exhibit external fertilization that made quantification of male reproductive

success more reliable.

Several hypotheses have been presented to explain the preponderance of male care in fishes: order of gamete release (Dawkins and Carlisle 1976, Carlisle 1981), differential rate of gamete production between sexes (Baylis 1981), differential increases in fecundity for females (Emlen 1973, Gross and Sargent in press), differential certainty of parentage between the sexes (Barlow 1976, Keenleyside 1978, Ridley 1978, Blumer 1979, Perrone and Zaret 1979), or the ability of males to provide parental care without a loss in their ability to attract additional mates (Williams 1975, Wittenberger 1979, 1981). Except for the last, all these hypotheses have been criticized for being theoretically untenable (Maynard Smith 1978, Graften 1980, Werren, Gross, and Shine 1980, Wittenberger 1981, Gross and Sargent in press) or for being unsupported by general empirical trends at the generic or familial level (Gross and Shine 1981).

In species with more highly developed paternal care, males are believed to be constrained in their ability to evolve polygyny (Trivers 1972, Emlen and Oring 1977). Since males are thought to suffer reduced additional matings while being parental, they will usually be under intense selection to abandon young unless they can greatly increase offspring fitness by providing care. Females are thought to discriminate against parental males that are

caring for more offspring because their young would receive a smaller fraction of the male's parental investment. However, females should not discriminate against parental males if their offspring do not suffer reduced fitness under the care of a polygynous male. This may be the case in fishes, either because parental care has a low energetic cost or because care is shareable between all young in a brood. Females could then base their mate choice on the quality of the oviposition site or some phenotypic aspect of the male, and should not discriminate against males providing care for more eggs. A female might even prefer males with more eggs in their territories, either because it is an indication of the male's quality or because males with large clutches may be more aggressive defenders than those with fewer eggs (Pressley 1981a, Carlisle 1985).

The critical assumptions in this hypothesis, that female choice and offspring survivorship are not negatively affected by current brood size of a parental male, have never been tested in nature. To test these assumptions, two tropical reef fish species that show paternal care Malacoctenus hubbsi and Abudefduf troschelii, were studied during 1981 and 1982 (Chapter 2). In both species, female choice was found to be independent of brood size or its correlates over the range of brood sizes found in nature. At extremely large brood sizes females might discriminate

against mated males because nest sites become full or male time for spawning becomes limiting, but this does not appear to occur over the normal range of brood sizes in these populations.

In Chapter 3 the determinants of male mating success are analyzed in more depth for M. hubbsi, a species with a low level of care that approximates the hypothesized primitive form of paternal care in fishes. Territory characteristics were found to be the major determinants of male reproductive success, although there was extreme variance both within and between years. This variance appeared to be a major factor causing the lack of a significant correlation between male size and estimated male reproductive success, and may explain the slightly smaller size of adult males relative to adult females. These results suggest that the dynamics of sexual selection and life history evolution cannot be understood without a thorough understanding of both the determinants of reproductive success within a sex and the variance and predictability of these parameters for a given individual.

Chapter 4 presents a field study of a unique hermaphroditic reef fish, Serranus fasciatus, the only shallow water simultaneous hermaphrodite known from rocky reefs in the eastern Pacific. The initial goal of the study was to determine the effect of size on the gender allocation pattern, and to examine the role of the social

and mating system in determining these patterns. The gender allocation of S. fasciatus changes predictably with size. Most individuals observed were hermaphroditic and appeared to devote most of their reproductive allocation to female function, although the largest individuals had lost their female function and had become males (Hastings and Petersen in press). This is the first report of this gender allocation pattern from a natural population of vertebrates (and possibly animals). The social and mating system of S. fasciatus is reviewed and the evolutionary stability of this unique gender allocation pattern is evaluated by comparing it to other possible gender patterns. The gender pattern of S. fasciatus appears uninviable by other allocation strategies, although a sequential hermaphrodite strategy may have similar fitness. The rarity of this pattern in fishes appears to be due both to the unusual ecology of S. fasciatus and to its evolutionary history of simultaneous hermaphroditism.

Serranus fasciatus has a harem social system in which a large dominant male restricts access of other males to a group of 1-8 hermaphrodites. The behavioral ecology of this species was also examined and compared to harem-forming sequentially hermaphroditic and gonochoristic fish species. These results are remarkably similar to other harem social systems with female territoriality and no

dominance hierarchies among females. A decrease in activity by S. fasciatus hermaphrodites during the reproductive period is consistent with the hypothesis that they are attempting to use alternative male mating strategies to enhance their total current reproductive success.

Finally, the dynamics of certain mating systems are examined in light of current theory for the evolution of both paternal care and simultaneous hermaphroditism. For the paternal care species studied, there was general agreement between the results of field observations and manipulations and the ideas currently held by most workers. The results of the work done on the hermaphroditic fish Serranus fasciatus is in contrast to that of other studies of hermaphroditic and harem reef fishes. The social and mating system of this species is explainable using current life history and gender allocation theory and may provide some crucial insights toward a general understanding of gender allocation patterns in fishes and the evolution of social and mating systems in animals.

CHAPTER 2

THE EVOLUTION OF PATERNAL CARE IN FISHES: EFFECTS OF BROOD SIZE ON FEMALE CHOICE

Introduction

One of the goals of behavioral ecology is to understand patterns of parental investment and mate choice both between and within phylogenies. In teleost fishes, paternal care is much more common than maternal care (Ridley 1978, Blumer 1979, 1982). This pattern of predominately male dominated parental care in fishes has recently received a great deal of attention (Williams 1975, Barlow 1976, Dawkins and Carlisle 1976, Loiselle 1978, Ridley 1978, Perrone and Zaret 1979, Blumer 1979, 1982, Keenleyside 1981, Wittenberger 1979, 1981, Gross and Shine 1981, Gross and Sargent in press). Explanations for the evolution of paternal care in fishes have focused either on the low energetic cost involved (Williams 1975) or the shareable nature of aerating and guarding demersal eggs (Wittenberger 1979, 1981), the most common and presumably most primitive form of parental care in fishes. These arguments assume that female mate choice should be independent of the number of eggs already being cared for

by a male. Little support has been found for hypotheses emphasizing differences in certainty of parentage between the sexes or the order of gamete release (Gross and Shine 1981, Gross and Sargent in press).

If offspring survivorship is independent of brood size for the kinds of parental care fishes typically provide demersal eggs, then females need not discriminate against mated males. Females may actually prefer mated males, either because males defending more eggs may be willing to take more risks during egg defense (Pressley 1981a, Carlisle 1985) or because the offspring of these males will be more successful at attracting mates (Weatherhead and Robertson 1979). Whether or not females prefer males guarding more eggs or do not use egg number in their choice of a mate, the benefit for male desertion would be reduced compared to a species where females discriminate against mated males. This pattern of female choice, with females giving equal or greater preference to males providing care to a larger number of eggs, should often lead to male defense of oviposition sites, and paternal care of eggs would be more likely to evolve.

This scenario is based on two critical assumptions:

- 1) female choice of mates is independent of the current brood size of the male, or at least that males with higher numbers of eggs are not discriminated against by females,

and

2) survivorship of eggs is not adversely effected by increases in brood size.

These two arguments stem from the general observation that the ability of the parent to maintain a brood does not decrease for high brood sizes. Williams (1975:134) neatly summarized the situation when he said that for a male fish guarding eggs, "It must be nearly as demanding to defend a hundred as a million.". In fish species where the above assumptions are invalid, the evolution of maternal care, biparental care, or sexrole reversal in paternal species may be more common.

To test experimentally the validity of the first assumption, it is necessary to manipulate either the number of eggs at the oviposition site or in a species with cryptic eggs the number of spawning females, and then to compare the future reproductive success of these males with that of unmanipulated males. If the first assumption is correct, males with more eggs would gain at least as many additional eggs in their territories as equivalent males with fewer eggs.

Female teleost fishes typically deposit thousands of small demersal eggs in the territories of males. This makes it very difficult to quantify survivorship of broods. A proper test of the second assumption would be to estimate

egg survivorship for broods of various sizes, the assumption would be supported if, for males with initially equal brood sizes, raising the brood size of one male does not change the survivorship of the eggs in his brood relative to the other male.

These assumptions are critical components of the current theory for the evolution of paternal care in fishes. Except for one study of sticklebacks by Ridley and Rechten (1981) that is difficult to interpret, the first assumption has never been tested. No experimental evidence exists to evaluate the second assumption. The purpose of this paper is to provide experimental tests of the first assumption, to provide preliminary data concerning the second assumption, and to examine the relationship between parental behavior and brood size.

Natural History of Study Species

If the above scenario for the evolution of paternal care in fishes is correct, then it must apply to a wide variety of fishes with paternal care of demersal eggs. To test this hypothesis, two species of teleosts (Abudefduf troschelii and Malacoctenus hubbsi) that show the extremes in paternal care of demersal eggs were chosen. The reproductive biology and natural history of the two species are summarized in Table 1.

Table 1. Summary of reproductive biology in Malacoctenus hubbsi and Abudefduf troschelii in the central Gulf of California.

	<u>M. hubbsi</u>	<u>A. troschelii</u>
Family:	Labrisomidae	Pomacentridae
Adult description:	cryptic, rests on substrate	brightly colored swims above substrate
Adult size:	60-75mm	140-170mm
Spawning season:	April=August	June=October
Territory:	all-purpose (both sexes)	reproductive (males only)
Brood cycle:	no	yes
Egg color:	cryptic pale brown	bright purple
No. of females a male spawns with:	up to 6/day	up to 5/brood cycle

Abudefduf troschelii

The Panamic sergeant major is a common omnivorous fish found throughout the eastern tropical Pacific. Their behavioral ecology appears almost identical to two congeners: A. saxatilis and A. abdominalis (Cummings 1968, Helfrich 1958, Thomson, Findley and Kerstitch 1979). Females lay conspicuous demersal eggs on hard substrates and are never territorial. Adult males are only territorial while defending eggs. After hatching the larvae become planktonic and paternal care ceases. Males exhibit discrete brood cycles, courting females for two days and then defending the eggs for approximately four more days when the eggs hatch and parental care ceases. A. troschelii is polygamous, as many as five females may deposit eggs in the territory of the male during a brood cycle.

Paternal care in A. troschelii involves preparation of the nest site, maintenance of the eggs, and defense of the site from potential egg predators. Preparation of nests includes exposing bare rock surfaces by excavating sand with the anal and caudal fins and removing saxicolous organisms. Males attempt to chase away all potential egg predators, which in general are much smaller and offer no predation threat to adults. Care of the eggs includes "mouthing" the eggs and fanning the eggs with either the pectoral or a combination of the anal and

caudal fins. In the central Gulf of California, spawning was not related to a lunar cycle. However, A. troschelii exhibits lunar spawning rhythms in other locations with more extreme tidal ranges (S. Foster, in litt.). Males and females reproduce several times during a season.

Malacoctenus hubbsi

The redbase blenny is a small blennioid fish characterized by having low levels of parental care and showing only slight changes in foraging behavior and habitat utilization during the reproductive season. Both males and females maintain feeding territories throughout the year. Parental care is provided solely by the male and is restricted to minor modification of an oviposition site and chasing away potential egg predators. During the reproductive season males attempt to attract females every day and individual females typically reproduce on alternate days. Females lay cryptic eggs that attach to benthic algae in adhesive strands. Up to five females may be in the male's territory at one time during the early morning spawning period.

Methods

Abudefduf troschelii

Panamic sergeant majors were studied from June through August in 1981 and 1982 in the vicinity of San Carlos, Sonora, Mexico in the central Gulf of California. The study site was a shallow area adjacent to a sandy beach (Lalo Beach) with a mixture of rock and sand bottom ranging in depth from 1-5 meters. Groups of up to 200 males guarded eggs in this area at any one time. The arrival of males at nest sites was synchronized, with up to 200 males beginning excavation activities within a day in an area where no parental males had been observed for 1-37 days. The number of eggs in the territory of a male A. troschelii was determined by estimating the area covered by the monolayer of eggs on the male's territory using a one dm² wire square. The area of egg coverage can be as high as 16dm² for an estimated brood size of over 300,000 eggs.

To determine if female choice was affected by the number of eggs in a male's territory, males with approximately equal numbers of newly deposited eggs and similar territories were paired during the first day of the brood cycle. For each pair of males, eggs were added or subtracted from one nest while the second male served as an unmanipulated control. The additional eggs deposited in each territory after the manipulation were recorded on the

third day of the brood cycle, when males were no longer receiving eggs and no eggs from the current brood had hatched. This experiment was replicated 23 times (12 additions, 11 removals) between 1981 and 1982.

Egg survivorship was estimated for 18 nests of varying brood sizes, including two sets of males that had brood sizes manipulated. To estimate eggs survivorship, three 4cm² sub-samples were taken from tiles that had been placed in nests before the start of the brood cycle and that contained a monolayer of eggs by the end of the second day. A second set of three sub-samples was taken two days later. Egg survivorship was considered the corresponding change in density over those two days. This small egg sample was chosen because removing such a small percentage of the brood was assumed to have little effect on the parent's behavior, and three samples of this size still represented between two and three thousand eggs. The time between the two collections was limited to two days of the 5-6 day brood cycle since a longer interval would confound the data due to additional egg laying (if the eggs were collected sooner) or potential hatching of eggs (if the eggs were collected later).

The number of egg-fanning bouts were recorded over 10-minute periods to determine the correlation of egg number to egg maintenance levels. Changes in fanning rate with brood size could be due to intrinsic differences

between individual males, or responses to increased egg numbers, or both. To test for these effects, males were divided into three categories, with egg number either kept constant, reduced, or increased. Parental activities of males were monitored periodically through the rest of the brood cycle.

Malacoctenus hubbsi

The redbase blenny was studied in a protected cove (Bahia Las Pintas) adjacent to the A. troschelii site. Data were collected during June in 1981 and during July in 1982.

The cryptic eggs of M. hubbsi make it difficult to test for changes in female choice based on the number of eggs in a male's territory. Females could use the presence of other females as an estimate of the male's relative reproductive success and thereby the number of eggs in his territory. The effect of a female depositing eggs in a given territory was examined by pairing males of approximately equal past reproductive success and removing a single female from one male. This removal was done on a day when the first female for both males arrived at approximately the same time. The subsequent reproductive success of each male was monitored for the rest of the day.

In separate experiments in 1982, males with approximately equal reproductive success were paired and

one male was chosen for a complete female removal treatment. Females entering the territory of this male were removed within 10 minutes of their arrival. This manipulation was continued every reproductive period until one of the two males deserted its territory.

Maintenance of the egg site is indicated by the male taking bites at the nest. Bite rates were monitored on the paired males used in the total female removal experiment. Because males had been paired according to past reproductive success and were randomly assigned to a treatment, any differences in bite rate between treatments would be due to increases in egg number. This was done to control for possible confounds due to female preference for males exhibiting higher rates of paternal care.

Results

Abudefduf troschelii

Augmentation or removal of eggs had no significant affect on the subsequent reproductive success of territorial males (Table 2). This supports the hypothesis that females do not base their mate choice on the number of eggs in a male's territory.

Estimated egg survivorship was similarly independent of brood size when males did not abandon nests ($p > .1$, $r_s = +.37$, $n = 18$). This was true in both unmanipulated

Table 2. The effect of changes in clutch size on a male's ability to attract females in A. troschelii. \neq Manipulation of egg number has no significant effect on male reproductive success. Relative egg numbers are given in terms of dm^2 of rock covered with a monolayer of eggs. Significance levels are from Wilcoxon paired-ranks tests. Mean standard errors are given in parentheses.

treatment	initial egg number (dm^2)	net change in egg number	new egg number (after manipulation)	additional eggs received (post-manipulation)
eggs added	5.25 (.70)	2.67 (.77)	7.92	2.46 (.77)
control	5.21 (.62)	0	5.21	2.96 (.73)
n=12				p>.1
eggs removed	7.23 (.60)	\neq 2.14 (.32)	5.09	2.36 (.78)
control	7.05 (.52)	0	7.05	2.09 (.70)
n=11				p>.1

nests and in the two sets of nests where total brood size was manipulated. Estimated egg survivorship over the two-day portion of the brood cycle did not differ significantly from 100% (\bar{x} =99.1%, standard error mean=2.3, n=18). This result supports the hypothesis that egg survivorship is not affected by brood size.

These results must be treated cautiously as this test may not incorporate other factors that affect egg survivorship. The estimate of egg survivorship was based on two days in the middle of the brood cycle. If the critical period of egg mortality occurs early or late in the brood cycle, subsequent effects on survivorship would have been missed by this technique.

There was a slight trend for males with smaller clutches to obtain more eggs (Table 2) and for the survivorship of those eggs to be higher ($r_s = -.37$). The power of the statistical techniques used may have been insufficient due to the relatively small sample size. However, these trends, if they do exist, are small and do not prevent males from being polygynous.

At very small brood sizes, males appear more likely to desert nests. The three observed cases of brood desertion all occurred at very small brood sizes (1, 4.5, and 5 dm² of eggs, vs. overall median brood size 10 dm²). However, brood desertion occurs infrequently at this site and females do not appear to select against males without

eggs. Over 95% of the males that was observed courting eventually were observed with eggs in their territories.

For unmanipulated nests, fanning rate was slightly but significantly correlated with number of eggs ($p < .05$, mean 4.9 bouts/10 min., $r = .21$, $n = 93$). In nests where brood size had been manipulated, the final number of eggs still had a significant effect on fanning rate, whereas the pre-manipulation brood size and brood age did not (Table 3). Because fanning rate can be changed by altering brood size, fanning rate cannot be considered simply an intrinsic male attribute. This experiment shows that nest fanning does increase with brood size.

Malacoctenus hubbsi

There was no difference in either the number of females attracted to, or the estimated number of eggs deposited in, the territories of paired males in the single-female removal experiment (Table 4). In addition, treatment males in the total-female removal experiment showed no difference in the number of females attracted to their nests than paired control males (Table 4).

The rate of egg maintenance behavior increased for individuals as a function of estimated brood size. Over a five-day period, males that received more eggs took significantly more bites in the area of the nest during the non-spawning period ($r = .67$, $n = 11$, $p < .05$). When males with

Table 3. Stepwise multiple regression on the effects of brood parameters on fanning rate in Abudefduf troschelii. -- Data collected from 9 males observed from three to four 10-minute periods throughout the brood cycle.

Variable	Cumulative R^2	Variance accounted for	F	Significance of r^2
final egg number	.405	.405	22.01	$p < .001$
change in brood size	.451	.046	2.49	$.05 < p < .1$
egg age	.466	.015	.84	$p > .25$

Table 4. Female removal experiments and subsequent reproductive success in Malacocotenus hubbsi. - In the single-female removal experiment there was no difference in either the number of additional females attracted or in the amount of time they stayed in the territory. In the total-female removal experiment, males with females removed as they arrived on the territory attracted as many females as control males. Both results were not significant using a Wilcoxon paired-ranks test. Ranges are in parentheses.

1981 Single-Female Removal (n=10)		
Treatment	Additional no. of females (range)	Mean no. of censuses/female
Removal	1.2 (0-2)	7.0
Control	1.2 (0-2)	6.6
Level of sig.	p>.1	p>.1
1982 Total Female Removal (n=6)		
Treatment	Total no. of females attracted (range)	
Removal	1.8 (0-5)	
Control	2.5 (0-4)	
Level of sig.	p>.1	

similar estimated male reproductive success were paired and females were restricted from spawning with a randomly selected member of the pair, this pattern still held. In all five replicates, the males with reduced reproductive success had lower nest bite rates even though some eggs remained on the territory. Maintenance behavior of eggs increases as a function of the number of eggs on the territory, and cannot be completely attributed to individual differences in male parental ability.

Discussion

In both Malacoctenus hubbsi and Abudefduf troschelii females did not base their choice of mates on the number of eggs in the male's territory or on correlates of egg number available to them. This supports the hypothesis that, in species with paternal care of demersal eggs, females do not discriminate against males that care for larger clutches.

In species of birds and mammals with parental care, as a male increases the number of young he cares for, the number of additional females he is able to attract and mate with should decrease (Orians 1969). This prediction is based on the assumption that in birds and mammals the number of young a male cares for will be negatively correlated with the benefit each offspring receives from the male. All else being equal, females should therefore

prefer males that care for fewer offspring.

In A. troschelii, the negative correlation between benefit received per young and brood size was not found to exist using the two-day egg survivorship estimate. Thus, there is no apparent reason for females to discriminate against males with larger broods. Female choice can then be based solely on other parameters that increase the fitness of their offspring: oviposition site quality, the male's genetic quality, or the male's ability as a parent.

Fanning in A. troschelii and nest bites in M. hubbsi appear to be energetically inexpensive and to take up only a small fraction of the parent's total activity budget. These behaviors increase in frequency as brood size increases, and in A. troschelii are adequate to maintain high egg survivorship over a wide range of brood sizes. These results support the ideas of Williams (1975) and many later workers, that the evolution of paternal care in fishes in many species has been facilitated by the low levels of care required to achieve a large benefit for young.

In contrast to the idea that low levels of parental care in fishes has been a major selective agent in the evolution of paternal care, another hypothesis for the origin of paternal care in fishes has emphasized the shareable nature of the parental care (Wittenberger 1979,

1981). When care can be shareable, male reproductive success can still be limited by the number of females with which a male can mate, even with high levels of parental care. The existence of shareable care, especially in species with high levels of care, has probably been important in the continuation of male care without the sex-role reversal seen in species with high levels of nonshareable paternal care (Aronson 1949, Barlow and Green 1969, Breder and Rosen 1966, Jenni and Collier 1972, Jenni 1974, Smith 1979, Wittenberger 1979, Thresher 1984). Shareable parental care has been important in shaping sexual selection in species with high levels of care, but does not appear to have been necessary for the initial evolution of paternal care in fishes.

Some authors have suggested that females might prefer males with more eggs. In the only other experimental study on the effect of male mating status on female choice in fishes, Ridley and Rechten (1981) found a slight but significant preference of females for mated males in Gasterosteus aculeatus, the three-spined stickleback. This female preference of mated males over unmated males may have been due to (1) the reduced effects of cannibalism at high brood sizes (Rohwer 1978), (2) the increased site tenacity and egg defense by males with more eggs (Pressley 1981a), (3) possible benefits to the offspring from having the genes of preferred males (the

sexy son hypothesis, Weatherhead and Robertson 1979), or (4) females preferring males in the later phases of courtship in their brood cycle if the risk of egg predation is highest during the courtship period of the brood cycle (Ridley and Rechten 1981). In species where males are preferred when they are caring for eggs, we should also expect to see paternal care. In the three fish species with demersal eggs and paternal care studied to date, increased egg number does not appear to reduce the chance of a male obtaining additional mates.

The experiments reported here were conducted in the field on natural populations with natural variation in oviposition site quality. If territory quality was identical among all males, females might select for or against mated males for the reasons outlined above. If quality differences between territories or males are the primary determinant of survivorship of young in nature, females should base their choice of a male on these qualities and be relatively indifferent to brood size.

This paper has examined two species with simple paternal care of demersal eggs. In both, the results are consistent with the currently favored assumptions that female mate choice and egg survivorship are independent of the number of eggs being cared for by a male. This study offers the first experimental test of these critical

assumptions of this theory that use fishes with low levels of paternal care. Other fishes exhibit a wide variety of parental care patterns, including mouthbrooding and the defense of mobile young. In these and other cases, the benefit received per young may not be independent of the brood size. The less common cases of maternal care in fishes may be due at least in part to changes in the relationship between egg survivorship and brood size in these species.

CHAPTER 3

DETERMINANTS OF MALE REPRODUCTIVE SUCCESS IN MALACOTENUS HUBBSI (LABRISOMIDAE)

Introduction

Many of the hypotheses to explain the evolution and frequency of paternal care in fishes are based on the assumption that female choice is highly dependent on male genetic or territory quality and relatively unaffected by the number of eggs a male is currently caring for (Williams 1975, Perrone 1975, Blumer 1979, Perrone and Zaret 1979, Wittenberger 1979, 1981, Gross and Sargent in press). In bony fishes, male defense of preferred oviposition sites and incidental guarding of eggs (embryos) has been proposed as the ancestral form of parental care (Winn 1958, Barlow 1963, 1964, Williams 1975, Demartini 1976). Only a few studies have examined the determinants of male mating success and female choice in natural populations of fishes with low levels of paternal care (Breder and Rosen 1966, Downhower and Brown 1979, 1980, Cole 1982, Yanagisawa 1982). An understanding of species that approach the presumed ancestral pattern is critical for the elucidation of the evolution of parental care patterns in fishes.

There are four general criteria that females can use to choose mates in species with paternal care: the attributes of the male's phenotype, the quality of the territory or resource defended by the male, the parental status of the male (how many offspring and their ages), and the ability of the male as a parent. These four criteria should not be considered independent variables; for a given species at least some are probably highly correlated. The importance of each of these criteria in selecting for patterns of female choice will be proportional to their predictable effects on the fitness of the offspring. These patterns of female choice will in turn be important in determining the degree of male-male competition for breeding sites, the relative levels of care given to individual offspring, and the degree of sexual dimorphism in the population.

The reproductive success of males in Malacoctenus hubbsi, a species with low levels of paternal care, was studied over two reproductive seasons. Attempts were made to gauge the relative importances of territory parameters, male size, courtship coloration, and mating status in determining the reproductive success of males. The results presented here are compared to other studies of paternal care in fishes where male mating success has been quantified and correlated with some of the above parameters.

Natural History

M. hubbsi is a small blennioid fish in the family Labrisomidae (formerly a subfamily of Clinidae, see George and Springer 1980). It is found throughout the central and lower Gulf of California and the Pacific side of Baja California but is most common in the central Gulf. It is a small fish, rarely exceeding 70mm standard length. It is found in shallow water (less than 8m) with its highest densities occurring just below the intertidal zone.

Malacoctenus hubbsi is common in the rocky subtidal and is the second most abundant fish found in the Gulf of California rotenone stations of Thomson and Gilligan (1983). The diet of M. hubbsi consists of a variety of small motile crustaceans, with amphipods being the most abundant single item in the diet (C. Ballard, unpublished manuscript). Both males and females defend feeding territories throughout the year. During the non-breeding season there are no significant differences in any territory parameters between males and females. In the breeding season, males are found in smaller, shallower territories that have a higher percentage of steep (>45 degrees) substrate than the territories of females (Table 5).

Table 5. Territory differences between males and females during the reproductive season of 1982. -- Males have smaller, steeper, and shallower territories. Mean, standard deviation, and significance (Wilcoxon two-sample test) are given. Sample sizes are in parentheses.

Sex	Territory size (m ²)		% Steep (>45°) incline		Relative tidal height (m)	
	mean	+1S.D.	mean	+1S.D.	mean	+1S.D.
males	0.54 (39)	+0.34	53.8 (39)	+24.5	0.13 (41)	+0.26
females	1.97 (12)	+0.92	25.6 (12)	+20.5	0.26 (23)	+0.21
	p<.01		p<.01		p<.05	

Breeding occurs from approximately April when the water begins warming until September. By October fish are between 30-55mm standard length and grow to 55-70mm by the beginning of the breeding season in April. Some fish that hatch early in the breeding season may begin spawning by the end of the same breeding season, but the typical adult pattern is an annual cycle with fish born one summer growing over winter, breeding the next summer, and dying. Before reproduction begins there appears to be no difference in the size of the sexes. During the reproductive season adult females are slightly larger than adult males ($p < .05$, females mean = 68.5mm, S.E.M. (standard error mean) = .57, $n = 40$, males mean = 65.9mm, S.E.M. = .96, $n = 64$; sample taken in July, 1982).

Spawning occurs in the territory of the male beginning at first light for approximately two hours. There is no apparent lunar periodicity in spawning. Females ready to spawn enter a male's territory. During spawning the female trembles while the male moves next to the female and makes a short push forward, apparently releasing sperm. This is repeated approximately 5 times a minute for the entire period the female stays in the male's territory, usually 40-55 minutes. Oviposition typically occurs on steeply angled rocks that have a turf of fleshy red or green algae (Gelidium, Valoneopsis), although eggs also are deposited on coralline algae (Jania). Females lay

approximately 200 eggs during a spawning period. Up to 5 females may be in the territory of a male at any one time. This is similar to the typical spawning pattern for most of the species of blennioid fishes studied to date (Breder and Rosen 1966, Wirtz 1978, Thresher 1984). Eggs are cryptic and cannot be counted without removing the algal turf and examining it under a low-power microscope.

Parental care in M. hubbsi involves maintenance of the oviposition site, tending eggs, and defending the site from potential predators. Preparation of the breeding site can include removing some algae from the algal turf, rubbing the site, or rostral nuzzling of the turf. The term "nest" will be used to describe the oviposition site although no obvious structure was built by either sex. Parental care of the eggs consists of the male picking at the nest (possibly removing dead or unfertilized eggs) and occasionally rubbing the nest with the ventral part of the body. No fanning of the nest was ever observed. When the eggs hatch after 5-7 days, the larvae immediately become planktonic, ending the period of parental care.

Male M. hubbsi defend oviposition sites from all potential egg predators. This group includes most of the small fishes in the area: Axoclinus carminalis, Axoclinus sp., Gobiosoma chiquita, Stegastes rectifraenum, Paraclinus sini, Thalassoma lucasanum, Halichoeres chierchiae, and

Pseudojulis notospilus, along with adult and juvenile conspecifics. Female territoriality consists primarily of defense of the feeding territory from other females and potential food competitors. Both sexes rarely defend their territories from heterospecifics during the nonbreeding season (Table 6).

Methods

The study was conducted in the vicinity of Bahia San Carlos, Sonora, Mexico, in the central Gulf of California. The study area was a shallow (<3m) area in a protected cove (Bahia Las Pintas) with a combination of solid rock and cobble bottom. Observations were made during June and July in 1981 and 1982 while snorkeling. Forty-three days of reproductive data was collected in the two years, 21 in 1981 and 22 in 1982. In addition, a total of 40 hours of behavioral data were collected during non-spawning periods of the day in the breeding season.

All males in the study and many of the females were marked for individual recognition. Individuals were captured, their standard length measured to the nearest millimeter, and all were tagged by clipping unique sequences of spines and rays from their dorsal or anal fins. The first three spines of the first dorsal fin were never clipped since they appeared important in intraspecific displays. These tags could be read

Table 6. Patterns of aggressive interactions in M. hubbsi. -- All data were taken during the non-spawning period of the day. Data were based on 200, 1010, and 440 minutes of focal animal observations for both sexes during the non-reproductive season, and for males and females during the reproductive season.

	Interactions /10min	
	with heterospecifics	with conspecifics

non-reproductive season*		
both sexes	0.10	0.65

reproductive season		
males	1.80	0.18
females	0.68	0.78

* Data collected January 1984

underwater without collecting the fish. Fin clipping was repeated before the fish had completely regrown the lost spines or rays, a process that took at least two weeks.

Territories were mapped after observing individual fish for several days during both non-spawning and spawning periods. Total substrate area, the angle of inclination of all rock surfaces, and the relative depth of each territory were recorded. Elevation of the territory was recorded as the tidal height relative to the lowest low tide observed in 1982 (negative numbers are below this mark, positive numbers above it).

The number of eggs in the territory of a male cannot be estimated by censusing nests during the non-spawning period of the day without destroying the oviposition site. As a nondestructive alternative, relative egg numbers were estimated as the total time females spent ovipositing in a male's territory. The time females spent in a given nest was estimated by censusing nests during the breeding period every 5 minutes in 1981 and every 10 minutes during 1982. This change allowed more nests to be censused during the same breeding period. The number of eggs laid in a male's territory could be estimated from the number of females in the male's territory at every census. This was an accurate estimate since egg-laying rates of females are independent of number of females in the territory. Females averaged between 45 and 50 minutes of spawning with one or more

males. To estimate daily male reproductive success, the number of females per census during the morning spawning period were summed. This number was divided by ten in 1981 and five in 1982 so the units of estimated male reproductive success could be given as the approximate number of female clutches received per day. When censusing male territories, the number of females and males in the territory and their identity, if known, were recorded in addition to the coloration of the male and any distinct behaviors that were observed. Coloration was scaled from 1 to 5, 1 representing the typical female coloration with no pink or red coloration visible and 5 representing males with solid bright red ventral body coloration, black dorsal barring, and a silver irridescent stripe along the midline and thru the lower part of the eye. Behaviors that were noted in addition to spawning included biting and rubbing in the oviposition area, courtship of nonspawning females, and aggressive interactions among neighboring males. Sneaking or pseudofemale behavior by males attempting to fertilize eggs in another male's territory was also noted. All males were censused until spawning had stopped in all of the territories.

The number of eggs in a territory was estimated from the egg laying that occurred over the past five days. If a day was missed, the missing day was estimated by

averaging the other four days. If more than one of the last five days was missing, the male on that day was omitted from the analysis.

To determine the effect of the presence of a spawning female on subsequent reproductive success of a male on that day, a single-female removal experiment was done in 1981. Males were paired according to similar reproductive success. On a day when each of the two males was beginning to spawn with a single female during the first 10 minutes of the spawning period, the female was removed from a randomly chosen male for the remainder of the spawning period. To control for possible effects of disturbing the male the other female was either removed and immediately released into the territory or harassed for an equivalent disturbance time. Males and released females began spawning within one minute of release and showed no effects of the short-term removals or harassment.

The effects of male size and territory parameters on male reproductive success were calculated in two ways. First, a multiple regression with male size and territory parameters versus estimated male daily reproductive success was performed. Second, paired observations were examined, either the same male in two different territories or different males in the same territory.

A total female removal experiment was conducted in 1982 to test for the effects of reproductive success on

site fidelity of males. Males were again paired according to relative reproductive success, and all females observed spawning with one male were removed. The control received similar harassment but was allowed to spawn with females. Each replicate continued until one male of the pair abandoned its territory.

A total of 213 and 394 male-spawning days were observed in 1981 and 1982, respectively. A total of 21 males and 15 females in 1981 and 63 males and 51 females in 1982 were fin clipped for individual recognition. In addition, territories were measured for 13 males in 1981 and 39 males and 12 females in 1982. For the regression analysis and estimated male reproductive success data, only those males that were observed on a territory for at least five days and were not part of an experimental manipulation were used.

Results and Discussion

Determinants of Male Reproductive Success

Estimated daily male reproductive success varied from 0-2.22 female clutch equivalents in 1981 (mean=.72, n=20 males) and from 0-2.26 female clutch equivalents in 1982 (mean=.63, n=38 males).

The amount of steep substrate in the territory of a male was a major determinant of a male's estimated

reproductive success in 1981 (Table 7). A linear regression of male size on estimated male reproductive success was not significant ($r=.36$, $n=20$, $p>.05$). However, when both steep territory area and male size were used in a multiple regression analysis, male size explained a significant amount of the unexplained variance after the effects of steep substrate area were removed (Table 7). Male size had a significant effect on the reproductive success of males, but the larger effects of steep territory area overshadowed the male size pattern. There was no significant correlation between the male's size and the amount of steep substrate in his territory (Table 8).

There was no apparent effect of the presence of a female spawning on a nest on the mate choice of other females. Males with one female removed did not differ significantly from control males in their subsequent estimated daily reproductive success ($p>.1$, $n=10$, Wilcoxon paired-ranks test).

In 1982, at the same site, the only variable that explained a significant fraction of the variance in estimated male reproductive success was the relative height of the territory (Table 7). Males with shallow territories attracted more females than did males with deeper territories. When male territories were divided into two classes, those whose oviposition sites were partially exposed at least once (intertidal) versus those that were

Table 7. Factors affecting estimated daily male reproductive success in Malacoctenus hubbsi, as indicated by stepwise multiple regression.

Year	Variable	order of inclusion	cumulative R ²	variance (r ²) accounted for	significance of r ²
1981	steep substrate	1	.65	.65	p<.01
	standard length	2	.77	.12	p<.05
	tidal height	3	.81	.04	n.s.
1982	tidal height	1	.20	.20	p<.05
	standard length	2	.28	.08	n.s.
	steep substrate	3	.29	.01	n.s.

never exposed (subtidal), the males with intertidal oviposition sites had a higher estimated reproductive success ($p < .005$, Mann-Whitney U-test). There was no significant difference in the size of males in these two areas ($p > .1$, Mann-Whitney U-test). In 1981, there was also a significant correlation between intertidal height of a male's territory and his estimated daily reproductive success (Table 8). However, this appeared to be due solely to the correlation between territory tidal height and the amount of steep substrate in the territory (Table 8). In a multiple regression, tidal height did not explain a significant amount of variance after the effects of steep substrate area had been removed (Table 7).

In addition to the multiple regression analysis, the effects of individual differences between males and their territory parameters on reproductive success were also examined by comparing daily reproductive success of different males in the same territories and the same males in different territories in 1982. In ten paired comparisons of different males on the same territories, larger males had higher estimated daily reproductive success ($p < .05$, Wilcoxon paired-ranks test). In contrast, no territory parameters measured (intertidal height, steep substrate in territory, percent steep substrate in territory, territory size, order of occupancy) explained a significant amount of the variance in estimated

Table 8. Correlation coefficients among factors affecting estimated daily male reproductive success in Malacoctenus hubbsi.

Variable	vertical substrate	intertidal height	standard length

1981			
reproductive success	.806**	.628*	.338
vertical substrate		.638*	.063
intertidal height			.098
1982			
reproductive success	.016	.449*	.252
vertical substrate		.288	.076
intertidal height			.052

*p<.05
**p<.01

reproductive success of the same individual male on different territories ($p > .1$, Wilcoxon paired-ranks test).

There were no apparent differences in spawning coloration in males at the beginning of the spawning period that were correlated with reproductive success that day. Males that did not acquire mates changed to non-spawning coloration sooner, but this appeared to be a result rather than the cause of lower success in attracting females. Males began the spawning period with the brightest coloration (5 on a scale of 1 to 5) in over 98 percent of the spawning days.

The effect of differences in male parental ability on female choice patterns was not examined in this study. Since females did not wander from their territories during the non-spawning period, any assessment of males by females must occur primarily during the spawning period. Males did not appear to differ in their abilities to chase potential egg predators. Nest maintenance appeared to be energetically inexpensive and accounted for only a small percentage (<2%) of a male's time. The number of bites on the nest by the male increased with the number of eggs estimated to be on the nest ($r = .67$, $n = 11$, $p < .05$). This increase must be due at least in part to the number of eggs actually in the territory, since when males with equal past reproductive success were paired and females were restricted from spawning with one male, the male with fewer

eggs in his territory has a lower nest bite rate. The possibility that females based their choice of mates on differences in male parental care appears slight, but cannot be completely ruled out.

Differences Between Years

The factors affecting estimated daily male reproductive success changed from steep substrate and size of the male in 1981 ($R^2=.77$) to intertidal height of territory in 1982 ($r^2=.20$). This shift may be due in part to differences in the effects of spring tides in the two years. In 1981 only 2 of 22 territories were partially exposed, while in 1982, 16 of 22 territories observed during a spring tide series were exposed. During long periods when no territories are exposed, the territories that receive the most eggs may be consistent, but during periods of extreme tides patterns of territory success may be highly variable. Shallow territories may attract more females, but run a higher risk of being exposed.

Shallow Versus Deep Sites

If the general pattern of shallowness and the amount of steep substrate are aspects of territories that females use to choose oviposition sites, why is female choice based on these parameters? Within a territory, females oviposit on steep rocks with algae. Steep

substrates in shallow water have the least problem with siltation and should have the highest levels of water movement. This may be important for sufficient aeration of eggs in such species as M.hubbsi, which shows little direct care of eggs and no fanning.

The disadvantages of having a shallow territory are twofold. First, the site may become exposed, increasing egg mortality and, if exposure occurs during the spawning period, limit spawning opportunities. Second, if the site is abandoned, males will have to find a new territory that may be of lower quality, and may suffer increased predation while searching. In this study male reproductive success was estimated as the daily average of the number of females spawning in the territory. Shallow territories are more prone to exposure, potentially increasing the probability of egg mortality and male abandonment. This may have resulted in an overestimation in the male reproductive success of shallower males relative to deeper males. However, intertidal males were no more likely to permanently abandon their territories than subtidal males ($p > .1$, Mann-Whitney U-test) and territories were only exposed in the early morning when desiccation would not be as severe and may not have caused substantial egg mortalities.

Site Fidelity

In both 1981 and 1982, males that stayed on their territories longer had higher estimated daily reproductive success. In 1982, when all females entering a territory were removed, the resident male always abandoned his territory within three days and always before a paired control male (n=5). Two reasons for this pattern are apparent. Males that have higher-quality territories should benefit more by staying on them. If the ability of a territory to attract females can change in a very short time, males might use only their recent reproductive success as a measure of territory quality. At the same time that territories are becoming poorer at attracting females, the number of eggs on the territory is decreasing, reducing the cost of abandonment. Both of these factors favor male desertion when females reduce or stop depositing eggs in the territory of the male.

Temporal Variance in Spawning Success

Mating success of male M. hubbsi appears to vary on a daily basis. There is either a marginal or no significant correlation between a male's estimated reproductive success on consecutive days, depending on the year (Table 9). Females spawned on approximately 50% of the days and usually spawned on alternate days, so if

Table 9. Predictability of a male's estimated daily reproductive success based on his estimated reproductive success from previous days.

Days previous (reproductive success)	1981	1982
1	r=.16 (124)	r=.16* (181)
2	r=.36** (129)	r=.40** (172)
3	r=.09 (116)	r=.08 (140)
4	r=.47** (93)	r=.33** (115)
5	r=.23* (81)	r=.19* (105)

r= correlation coefficient
sample sizes are in parentheses
*p<.05
**p<.01

individual females exhibited specific male preferences an overall pattern between male success at two-day intervals might give a more accurate estimate of the consistency of a male's performance on a territory. Females return to the same males more often than would be expected if they selected mates randomly (7 of 23 returns to the same male, expected 1.41 returns based on 16 males observed in an average spawning period, $p < .01$, G-test with Yates correction). Because of alternate-day spawning of individual females, reproductive success two and four days ago was a better predictor of current reproductive success than one, three, or five days ago (Table 9). These patterns of female choice are not due simply to female preferentially spawning with nearby or adjacent males. Females typically travel over several meters and past the territories of several males to spawn with a particular male. Although specific choice patterns of individual females account for the lack of correlation on consecutive days, they do not help in understanding why more females tend to choose particular males or territories.

Male Size, Female Choice, and Sexual Selection

Larger males were not positively associated with more successful territories, either because they could not predict the location of those territories or because they could not displace established smaller territorial males

from those sites. Males were only observed moving into the territories of neighbors after they had been abandoned, even when the neighbor was a smaller individual and was spawning with more females. Only one fight was ever observed between a territory owner and an intruder. The territory owner retained ownership but it appeared to suffer severe injuries from the encounter with a larger intruder and disappeared two days later. The territory remained empty for the remainder of the study.

Larger males do not obtain higher estimated daily reproductive success than smaller males. In the two years of this study using a multiple regression analysis male size had either no correlation with estimated male reproductive success (1982) or was only significant only in regard to explaining the residual variance after territory parameters had been factored out (1981). Larger males may stay on territories for a longer time and in general have longer survivorship than smaller males, giving them higher lifetime reproductive success. This would result in the acceptance of a null hypothesis that no difference in short-term reproductive success existed between different sized males when there were important differences in lifetime reproductive success between males. Male size had no effect on site fidelity, although the current study was not specifically designed to look at this aspect of male

success.

In both years, there was evidence that when the effects of territory quality were held constant, larger males were preferred by females. In 1981, the multiple regression analysis had a significant male size component after the effects of steep substrate were removed. In 1982, when two males occupied the same territory at different times, the larger male had a higher estimated daily reproductive success. However, any effects of female preference for larger males were confounded by the inability of larger males to be positively associated with the preferred territories.

Depending on the species, studies on fishes with paternal care have found either male size (Downhower and Brown 1980, 1981, Schmale 1981, Cole 1982) or territory quality (Sargent 1982, Gross 1982) to be important predictors of male mating success. Typically, larger males were associated with the better territories. When good oviposition sites are predictable, it might be expected that male size and territory quality to be highly correlated. This is not the case with M. hubbsi. The low levels of parental care, the unpredictability of preferred spawning sites, and the low variation in adult size of this annual species may have led to male size being of secondary importance to characteristics of territories in female choice of mates.

Female choice should be based on those parameters that predictably confer reproductive success. Thus, the extent to which females rely on a specific parameter should be proportional to its variance in nature, the ability of females to assess it reliably, and the extent to which offspring fitness is correlated with that parameter. This makes it difficult to extrapolate the results of female choice in laboratory experiments where characteristics of territories and male themselves may be quite different than those in natural populations, and emphasizes a major advantage of field studies over laboratory studies.

The inability of larger males to find and maintain the most successful territories may help to explain the pattern of sexual size dimorphism in M. hubbsi. It is the only one of the four species examined from the central Gulf of California where adult females are slightly larger than adult males. Of the other common congeners in the central Gulf of California adults are the same size in M margaritae and M gigas while males are larger in M. tetranemous. These species exhibit similar spawning and parental behavior but occur in different habitats. Closer examination of ecological differences that affect reproductive success in these species might explain the different patterns of sexual dimorphism in size.

Fecundity has been observed to increase with size in females of M. hubbsi (Y. Maluf, unpublished data). The absence of increased estimated daily reproductive success in larger males and the maximum lifespan of one year in both sexes may be the major force selecting the slightly larger female size in M. hubbsi. An interesting prediction from this would be that in similar species with males larger than females, the ability of larger males to find and hold preferred territories should be higher. This could be tested against an alternative explanation that differences in size dimorphism patterns were due to the differing energetic demands of parental investment and courtship by the two species or to differential mortality between the sexes. These types of comparative studies could be useful in understanding patterns of sexual dimorphism in fishes in general. The genus Malacoctenus, with its variation in size dimorphism patterns among species, may be a good candidate for such a study.

CHAPTER 4

MATING STRATEGIES AND GENDER ALLOCATION IN SERRANUS FASCIATUS, A HERMAPHRODITIC REEF FISH

Tropical reef fishes show a variety of gender patterns, including gonochorism (populations with separate sexes), sequential hermaphroditism (both protogyny and protandry), and simultaneous hermaphroditism. Simultaneous hermaphroditism in reef fishes is restricted to several genera in the family Serranidae. The role of ecological factors in the evolution of simultaneous hermaphroditism in these fishes is not currently understood. The species appear to have little in common ecologically, varying from solitary and group predators to gregarious planktivorous fish in groups of up to 300 individuals (Fischer 1980, 1981, 1984a, 1984b, Pressley 1981b).

All simultaneously hermaphroditic reef fishes studied to date demonstrate some type of reciprocal fertilization, often in the form of "egg trading" (Fischer 1980, 1981, 1984a, 1984b, Pressley 1981b, Lejeune et al. 1980). Egg trading is defined as the alternation of sexual roles by a spawning pair of fish several times during a spawning period, with each fish releasing only a portion of its daily egg production at a time. In Hypoplectrus

nigricans, the one species studied in depth by Fischer (Fischer 1980, 1981), the continued release of eggs by an individual was contingent upon the release of eggs by its partner. Fischer hypothesized that egg trading and a long courtship period functioned to reduce additional mating opportunities by the partner during the relatively short spawning period. Egg trading, long courtship, and a restricted breeding period appeared to prevent individuals from specializing as males and maintained simultaneous hermaphroditism as an evolutionarily stable strategy (ESS) in these species of fishes (Fischer 1981, 1984). Fischer (1980) predicted that some form of egg trading would probably occur among most or all other simultaneously hermaphroditic reef fish.

Recently a new form of gender allocation in fishes has been found in the barred serrano, Serranus fasciatus (Jenyns). Individuals start life as hermaphrodites but lose female function at larger sizes to become functional males (Hastings and Petersen ms.). The transition from hermaphrodite to male appeared to be abrupt since all hermaphrodites devote the greater part of their ovotestis to ovarian tissue. Reciprocation or "egg trading" has never been observed in this species (Hastings and Petersen ms.). No other reports of this sexual allocation pattern are known from a natural population of animals, although Serranus baldwini, may have the same or a similar pattern

(Petersen and Fischer in prep.). Harrington (1971, 1975) has reported a transition from hermaphrodite to male in the cyprinodontid fish Rivulus marmoratus, but he was only able to obtain these previously hermaphroditic males (secondary males) by maintaining individual fish in aquaria for long periods of time, and he did not observe secondary males in the field. Males have been observed in natural populations of R. marmoratus by Kristensen (1970) but these fish appear to have been males from birth.

Warner (1984) summarized the work of several authors and hypothesized that these specific gender allocation patterns, and especially sex change, were evolutionary responses to specific mating systems, which in turn were determined by a host of ecological factors. If gender allocation patterns represent adaptive responses to particular social and mating systems, then S. fasciatus should differ from other reef fishes in some important aspects. The primary aim of this chapter is to examine the social and mating system of S. fasciatus to determine the factors that have led to its unique gender allocation pattern. The second aim is to determine which factors other than reciprocation could lead to the persistence of a simultaneously hermaphroditic phenotype in a population of reef fishes. Alternatively, the gender allocation pattern in S. fasciatus may be evolutionarily unstable and S.

fasciatus is in transition from simultaneous hermaphroditism to protogynous hermaphroditism or vice versa. These alternatives were examined by estimating male and female reproductive success values, intraspecific interactions, and behavior for a group of hermaphrodites and males in a natural population.

Materials and Methods

The study was conducted at Punta Santa Inez, approximately 45 kilometers southeast of Santa Rosalia, Baja California Sur, Mexico, in the central Gulf of California. The study site consisted of a shallow (1-4m in depth) area with a mixture of sand and rock substrate adjacent to rocky outcrops. Data were collected from 28 June to 30 July, 1983. In this region S. fasciatus appears to spawn during the months of higher water temperatures (May-October).

Individuals were captured using a hand-held dropnet, anesthetized using 2-Phenoxyethanol (Barton 1981), measured for standard length, and tagged with unique sequences of colored beads using the methods of Pressley (1981b). Fifty individuals were tagged and subsequent behavioral data were collected on 41 fish. Males and hermaphrodites were distinguished by a series of white ventral bars found only on hermaphrodites. At the end of

the study all remaining tagged individuals in the study area were captured and preserved.

Home ranges were mapped after a minimum of three ten-minute observation periods had been performed. In addition, mapping of home ranges was preceded by 10-20 minutes of observations. A territory was defined as the subset of the home range of an individual that was normally defended against conspecifics of the same gender as the focal fish. Home ranges and territory boundaries were checked during subsequent observations of focal animals and modified as necessary. Territory areas were measured from maps using a planimeter and calculated by assuming a flat, horizontal substrate.

For analysis of activity budgets, daylight hours were divided into four time periods: nonreproductive, pre-reproductive, reproductive, and post-reproductive. From first light until 1600 hours was listed as the nonreproductive period. No spawning has ever been observed during this period (Hastings and Petersen in prep.). The pre-reproductive period started at 1600 hours and ended at the last 10 minutes before any local spawning activity was observed. This period ranged from 20 to 80 minutes in duration. The reproductive period consisted of all the observational periods starting with the first one when spawning activity was observed and ending with the last such period, and lasted from 20-90 minutes. The final

period of the day, the post-reproductive period, was the shortest and went from the end of the reproductive period until all activity ceased. No more than three ten-minute activity budgets were ever taken during this period on one dive.

All individuals in the study were observed for five ten-minute periods during the non-reproductive period except for three individuals that disappeared before five periods were taken. These ten-minute periods were taken throughout the non-reproductive period, and whenever possible on different days for the same fish. Because adjacent fish were not observed at the same time, this data represents 100 minutes of potential interaction time between any two fish.

Starting at approximately 1630 hours, but always before spawning activity began, individual fish were observed until the reproductive period appeared to be over. While observing a fish, a record of the frequency and duration of specific behaviors was kept. Six mutually exclusive behavioral categories were differentiated: patrol, stalk, perch, hide, and two types of intraspecific interactions. The first four are listed in order of decreasing activity and were defined as follows:

Patrol. Fast directional swimming usually at least 25cm above the substrate with no interruptions for foraging.

Stalk. Any hovering or slow swimming near the bottom.

This is a common foraging behavior, with intermittent slow forward movement and hovering.

Perch. Body resting on top of a rock or on sand in the open, without moving pectoral fins.

Hide. Under a rock ledge or in a small cave. The fish is either not visible or only partially visible.

Intraspecific interactions were divided into spawning and non-spawning interactions, defined as follows:

Non-spawning interactions. One fish initiating an encounter with a second fish, leading to a head=down posturing, a retreat, no response, or rarely an aggressive response by the second fish, but never an S=curve or a spawn. In order of increasing intensity, behaviors included lateral displays with median fins erect, opercular flares, dorsal rubs (chin of the initiating fish rubbed along the back of the second fish), pushes (snout of initiating fish pushed into abdomen of second fish), chases, and bites. In most encounters one of the two fish was clearly dominant based on its more aggressive behavior and its more intense display. Often the subordinate individual retreated from the dominant fish or exhibited a submissive head=down posture, although draws sometimes occurred. A male dominance index was computed for each male to represent the proportion of male=male encounters in

which an individual was dominant. Draws were treated as half=dominant, half=subordinate interactions.

Spawning interactions. Spawning in S. fasciatus consists of a pair quickly rising to 0.5-2 meters above the substrate, after an S-curve display by one of the individuals. The eggs and sperm presumably are released at the apex of the spawning rush. Fertilization is external in S. fasciatus and there is no parental care of the pelagic eggs or larvae. I assume that in the spawning rush eggs are released by the fish performing the S-curve behavior, and that sperm are released by the partner, although gametes cannot be observed. Fish adopting these two roles will be referred to respectively as the female and pair-spawning male. Occasionally, a third fish that was hiding nearby would join the spawning pair. This fish is assumed to release sperm and is referred to as a sneak male. Sneak males did not exhibit pseudofemale behavior, but instead attempted to hide from dominant males and join the spawning rush (a behavior that will be referred to as streaking). A detailed account of the spawning act and evidence for the gender assignments for each fish are given in Hastings and Petersen (in press).

Estimation of Reproductive Success

The gonad of S. fasciatus consists of discrete testicular and ovarian sections, which can be teased apart

and weighed separately. Reproductive success through female function was estimated for the hermaphrodite as directly proportional to "ovary" weight (weight of the ovarian portion of the ovotestis). This calculation assumed that female egg production was proportional to "ovary" weight and that the percent of eggs fertilized was independent of the number of eggs released in any spawn.

Male reproductive success for males and hermaphrodites in a given spawn was estimated by dividing the fecundity of the female=role fish by the number of male=role fish in the spawn. If only one male was involved, the reproductive success of the fish assuming the male role equaled that of the female. If two or three males were involved, each male received $1/2$ or $1/3$ of the female reproductive success for that spawn. This is a rough approximation of male spawning success, since the pair=spawning male is in better spatial position to fertilize eggs, but males assuming the sneak role in many species have larger testicular mass and appear to release more sperm per spawn. This method of assigning male reproductive success evenly to all male=role fish in a spawn has been used in previous studies of fishes with alternative male strategies and sperm competition between individuals (Warner and Hoffman 1980a, 1980b).

Results

Behavioral data were collected on 41 individuals: 8 males, 32 hermaphrodites, and one in transition from hermaphrodite to male. For all comparisons the transitional fish was included with the males. Males were larger than hermaphrodites (male mean standard length=73mm, N=8, range 75-89.5mm; hermaphrodite mean standard length=64mm, N=29, range 45-75mm).

204 spawns were observed during the study. In all cases the pair-spawning male was larger than the female-role fish. The frequency of spawns throughout the spawning period is given in Figure 1.

Space Utilization

The population consisted of socially distinct groups that were delineated by the territory of a male and contained from 1-8 hermaphrodite territories. Spawning took place within the territory of the female-role hermaphrodite. Males defended these groups of hermaphrodites or harems from other males but not from other hermaphroditic individuals. All hermaphrodite territories partially or completely overlapped the territory of only one male. The size of a hermaphrodite's territory was therefore much smaller than the average male's territory (hermaphrodites $\bar{x}=10.7m^2$, range 2.8-27;

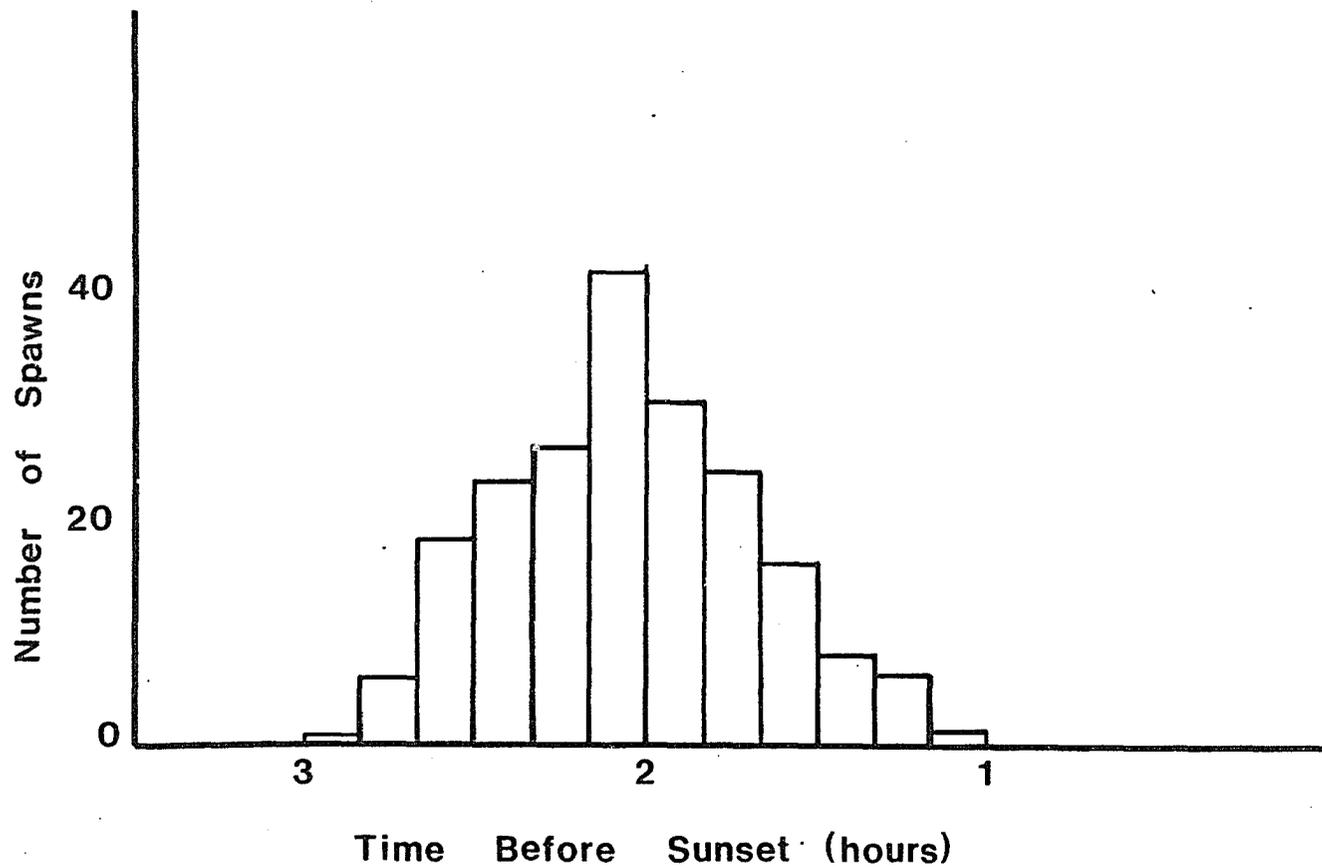


Figure 1. Spawning activity as a function of time of day relative to sunset in Serranus fasciatus. -- N=180

males $\bar{x}=80.6\text{m}^2$, range 21-199). Eight harems were observed in this study.

Hermaphrodites typically defend territories from conspecific hermaphrodites (mean= 10.7m^2 , $N=26$), but occasionally two or more hermaphrodites foraged together within the home range of one of the individuals. There is a weak, but significant, positive correlation between territory size of hermaphrodites and individual length ($r=.40$, $N=26$, $p<.05$). A hermaphrodite territory does not overlap with the territory of any other hermaphrodites. Territories varied from very flat sandy areas to areas with rocks up to 0.8m high and up to 50% rock cover.

Males maintained large territories (mean= 80.6m^2 , $N=8$) and defended them from other males. There was no significant correlation between male size and territory size ($r=.37$, $p>.05$). Male territories were significantly larger than hermaphrodite territories ($p<.001$, Mann-Whitney U-test) and contained at least part of one to eight hermaphrodite territories. No hermaphrodite territories overlapped into two male territories, so each male had an exclusive group of hermaphrodites within his territory.

Activity Budgets

Non-reproductive period. Males and hermaphrodites showed extreme differences in their partitioning of time into different behavioral categories (Figure 2). Males

● Hermaphrodites

N=28 (9A, 9B, 9C)

N=27 (9D, 9E)

○ Males

N=8 (9A, 9B, 9C)

N=7 (9D, 9E)

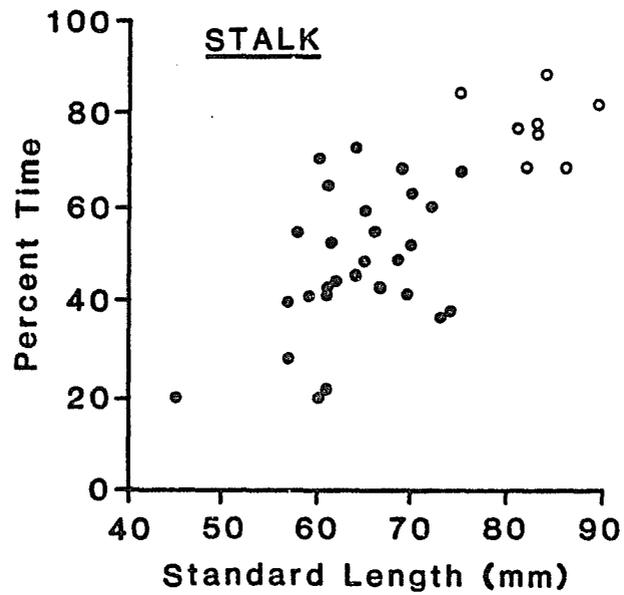
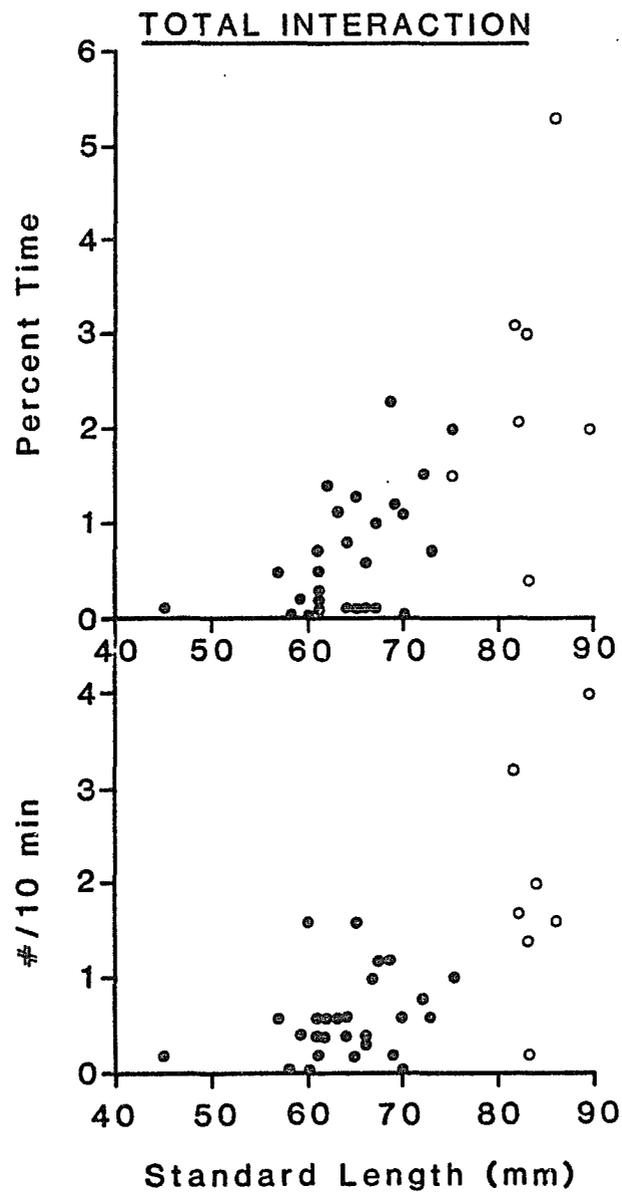


Figure 2. Individual behaviors versus standard length for hermaphrodites and males

Figure 2. Individual behaviors--Continued

spent significantly more time patrolling, stalking, and in social interactions while hermaphrodites spent significantly more time perching and hiding ($p < .05$, Mann-Whitney U-tests), the less active behaviors. Patrolling was not included in Figure 2 since most hermaphrodites were never observed patrolling and male patrol rate was low during the non-reproductive period (mean=2.1, range 0.0-9.0%). Stalk was the only behavior that exhibited a significant trend within a gender, increasing with hermaphrodite size ($r = .41$, $p < .05$, $n = 28$). In general, males were both more active and spent much more time in the open and in social interactions than did hermaphrodites.

Daily changes in behavior. Changes in behavior occur not only between genders, but also within a gender throughout the day. In general, the discrepancies between genders were accentuated during the reproductive period. The changes in behavior of both sexes are summarized in Figure 3.

The most distinct change occurs in male patrolling behavior. It increases as the reproductive period nears, peaks at the reproductive period, and then declines after reproduction ends (Fig. 3). Hermaphrodites rarely exhibit this behavior. Stalking decreases in both genders during the reproductive period. In hermaphrodites this resulted in a net decrease in activity because animals spent more

○ Males
 ● Hermaphrodites
 ○ Mean \pm 1 S.E.
 * $p < 0.05$

NON Non-reproductive
 PRE Pre-reproductive
 R Reproductive
 POST Post-reproductive

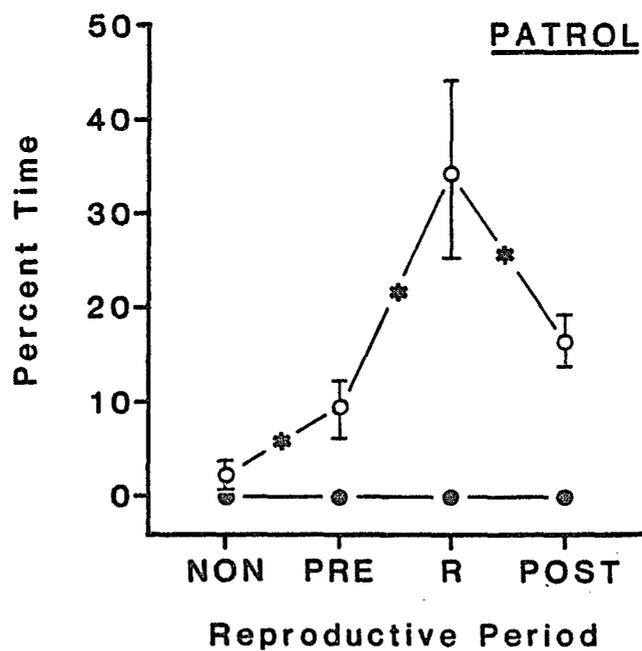


Figure 3. Changes in behavior during the day for hermaphrodites and males

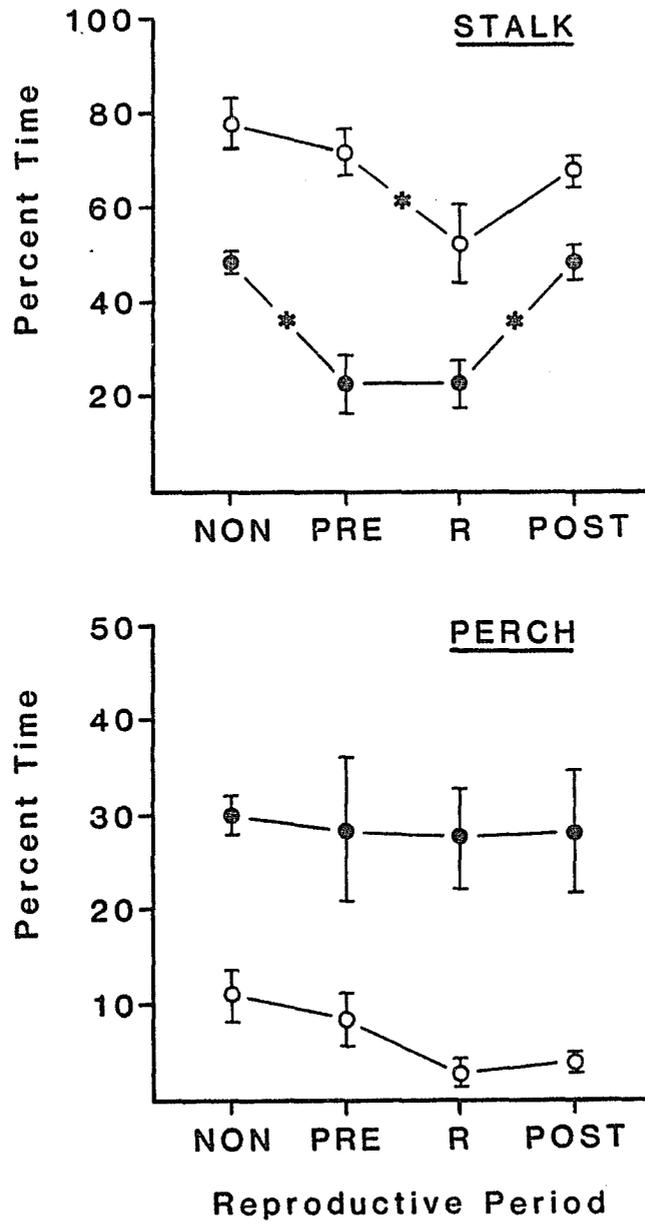


Figure 3. Changes in behavior--Continued

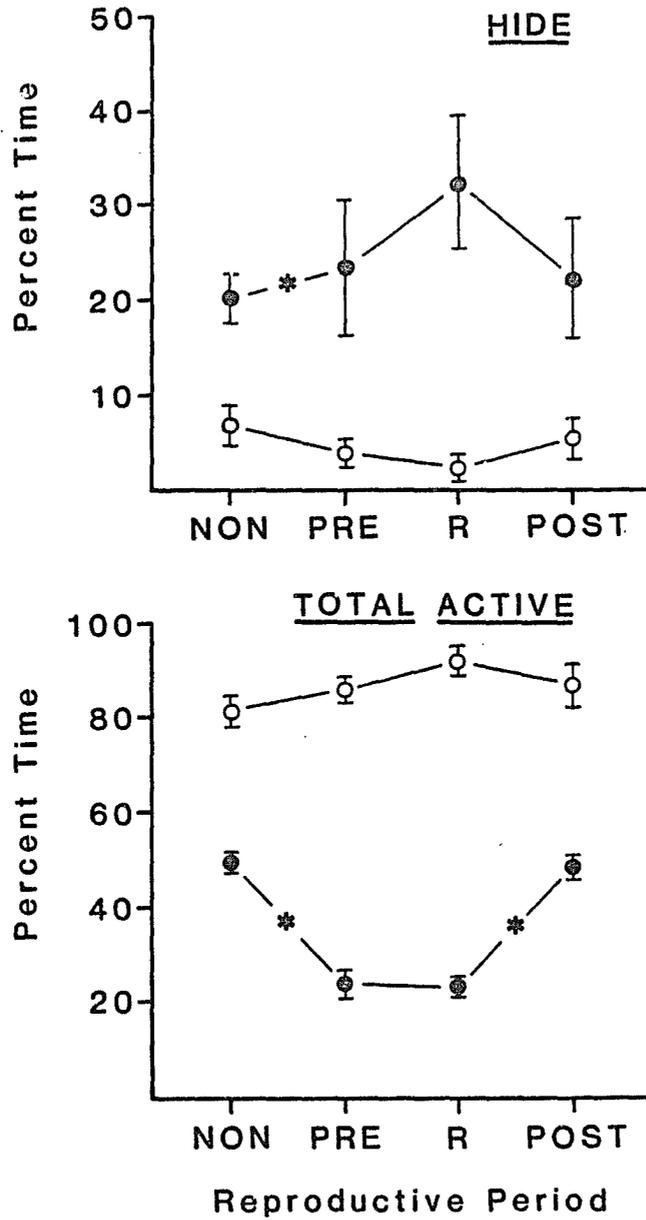


Figure 3. Changes in behavior--Continued

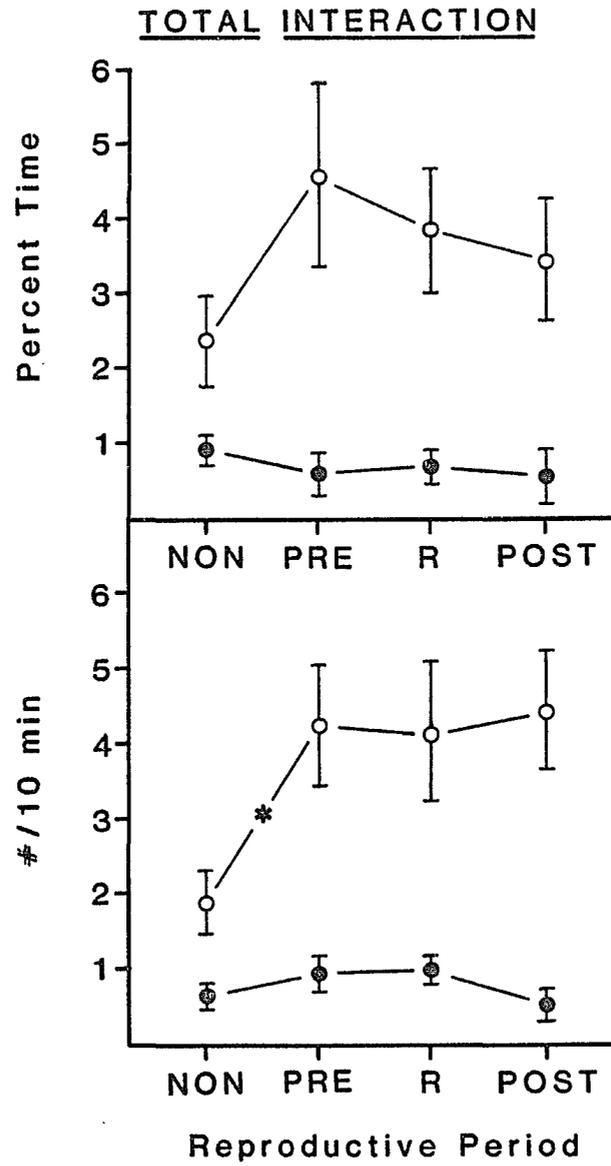


Figure 3. Changes in behavior--Continued

time hiding (Figure 3). In males, the percent of time spent in "active" behaviors remained relatively constant, but during the reproductive periods the least active of these behaviors (stalk) decreased while the more active behaviors (patrol, social interaction) increased. Males were much more active than hermaphrodites, especially during the reproductive period.

Social interactions. During all four time periods males interacted at higher rates and for a larger percentage of the time than hermaphrodites ($p < .05$, Mann-Whitney U-test). The total interaction rate of males was much higher for the reproductive periods compared to the non-reproductive period (Figure 3, Table 10). However, the time males spent in interactions was not significantly different for sequential time periods ($p > .05$, Wilcoxon paired-ranks test). Although male-male interactions were relatively constant between the two periods, male-hermaphrodite interactions significantly increased during the spawning period (Table 10). This was in striking contrast to hermaphrodite-hermaphrodite interactions, which decreased to near nonexistent levels during the spawning period (Table 10).

Patterns of aggression immediately prior to spawning were analyzed to determine if aggression by the male of the spawning pair or by the hermaphrodite decreased the success of sneaks. Although hermaphrodites did not

Table 10. Total number of aggressive encounters for different combinations of genders during non-spawning and spawning periods in Serranus fasciatus. # Numbers in parentheses represent sample size (number of individuals). Comparisons between time periods were done using a Wilcoxon paired signed-ranks test. Sample sizes used for the statistical tests were 8,7,14, and 14 respectively.

	Time of day		significance
	non-spawning period	spawning period	

Focal fish: Male			
Male=male	.29(8)	.38(8)	ns
Male=hermaphrodite	1.54(8)	3.67(7)	p<.05
Total	1.83	3.94	
Focal fish: Hermaphrodite			
Hermaphrodite=male	.35(26)	1.05(14)	p<.05
Hermaphrodite=herm.	.21(26)	.014(14)	p<.01
Total	.56	1.06	

show aggression towards sneaks, males often interacted with hermaphrodites near a hermaphrodite about to spawn as a female. One hundred forty of the 204 spawns observed were complete enough to analyze for pre-spawning patterns. Of the 39 spawns with male-hermaphrodite interactions within two minutes of a spawning attempt, sneaks were eventually successful in joining the spawning rush in only three of these cases. In 20 of 23 successful streaks no pre-spawning aggression was seen. Although hermaphrodites did not chase sneaks, they often stopped their vertical rise in the water column prior to releasing eggs. This behavior was followed by searching behavior by the male, who would act aggressively toward any nearby hermaphrodite.

Sneak rates were not correlated with harem size. Seven hermaphrodites were identified that successfully took part in spawns as sneaks. Males did not direct more aggression towards sneaks than similarly sized individuals that were never observed successfully sneaking for any activity period ($p > .1$, Mann-Whitney U-test). This pattern existed even though sneaks were commonly chased immediately after a successful streaking attempt. Successful sneak hermaphrodites differed from other similarly sized unsuccessful male-role hermaphrodites only in their increased number of hermaphrodite-hermaphrodite interactions during the non-reproductive period (Table 11).

Table 11. Behavioral comparisons between successful hermaphrodites and other similar sized hermaphrodites.

	sneak		non-sneak
Non-spawning period	N=7		N=20
Herm.=Herm. interactions /10 minutes	.67	**	.18
% Move	56.4		48.9
% Perch	29.6		30.0
% Hide	12.5		21.2
Spawning period	N=6		N=8
% Move	27.5		26.0
% Perch	34.9		30.3
% Hide	36.2		40.7

**p<.01 Mann-Whitney U

Female Reproductive Success

Hermaphrodites were observed as focal individuals during the spawning period 22 times. Additional data on hermaphrodites were derived from the 44 reproductive periods where males were followed. With two exceptions, the hermaphrodite spawned in the female role once a day during the reproductive period. The first exception was that hermaphrodites rarely spawned on the day they were tagged. This was probably due to stress caused by the tagging procedure and lasted only one day. The second exception was an individual that appeared to be in transition from hermaphrodite to male at the beginning of the study period and spawned as a female on 4 of 8 nights observed. Subsequently, this individual established a harem and defended it from males. At the end of the study this fish was collected and found to have only a minute portion of ovarian tissue. Focal observations on this fish were not included in the hermaphrodite sample size.

The relationship between standard length and weight of the ovarian portion of the ovotestis of hermaphrodites is shown in Figure 4. Large hermaphrodites had significantly more ovarian tissue than smaller ones. Because all hermaphrodites normally spawned as females once daily during the study period, the reproductive success of a hermaphrodite spawning in a female role was assumed to be proportional to the weight of its ovarian tissue. To

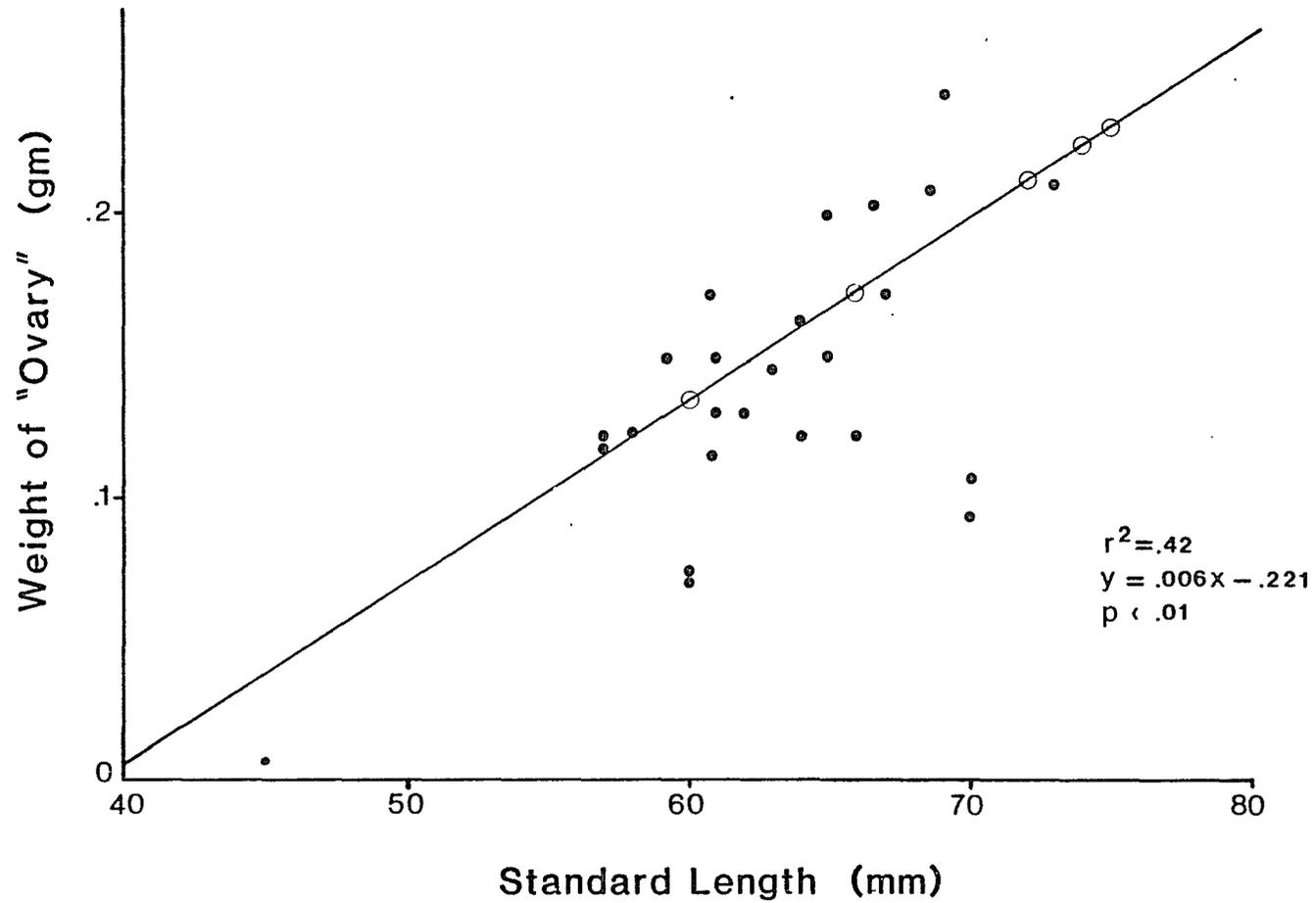


Figure 4. Size of ovarian portion of ovotestis ("ovary") versus size for hermaphroditic Serranus fasciatus. -- Estimated ovotestis weights are shown as open circles

facilitate comparisons between and within genders, this estimate of female reproductive success was scaled so that the female reproductive success for a hermaphrodite with the mean amount of ovarian tissue equaled one.

Male Reproductive Success

Average male reproductive success values from sneak and pair-spawning male-role fish are given for males and hermaphrodites in Figure 5. In all but two instances (same fish involved both times) the male-role fish of the spawning pair was a male (Table 12). Males spawned once nightly with every hermaphrodite (the hermaphrodite acting as a female) in their respective harems. Occasionally, hermaphrodites joined the spawning pair by streaking (21 of 204 or 10.3% of all spawns, with two sneaks in one spawning rush).

Male size was not correlated with territory size ($r=.40$, $N=8$, $p>.05$), but larger males had more hermaphrodites in their harem (Fig. 6) and had higher estimated reproductive success than did smaller males (Fig. 7). Streaking rates were highly variable between harems but were not correlated with harem size, so adding another hermaphrodite did not tend to change the percentage of spawns with streaking in the harem. Larger males are able to defend an area with more hermaphrodites, and thereby obtain higher reproductive success than smaller males.

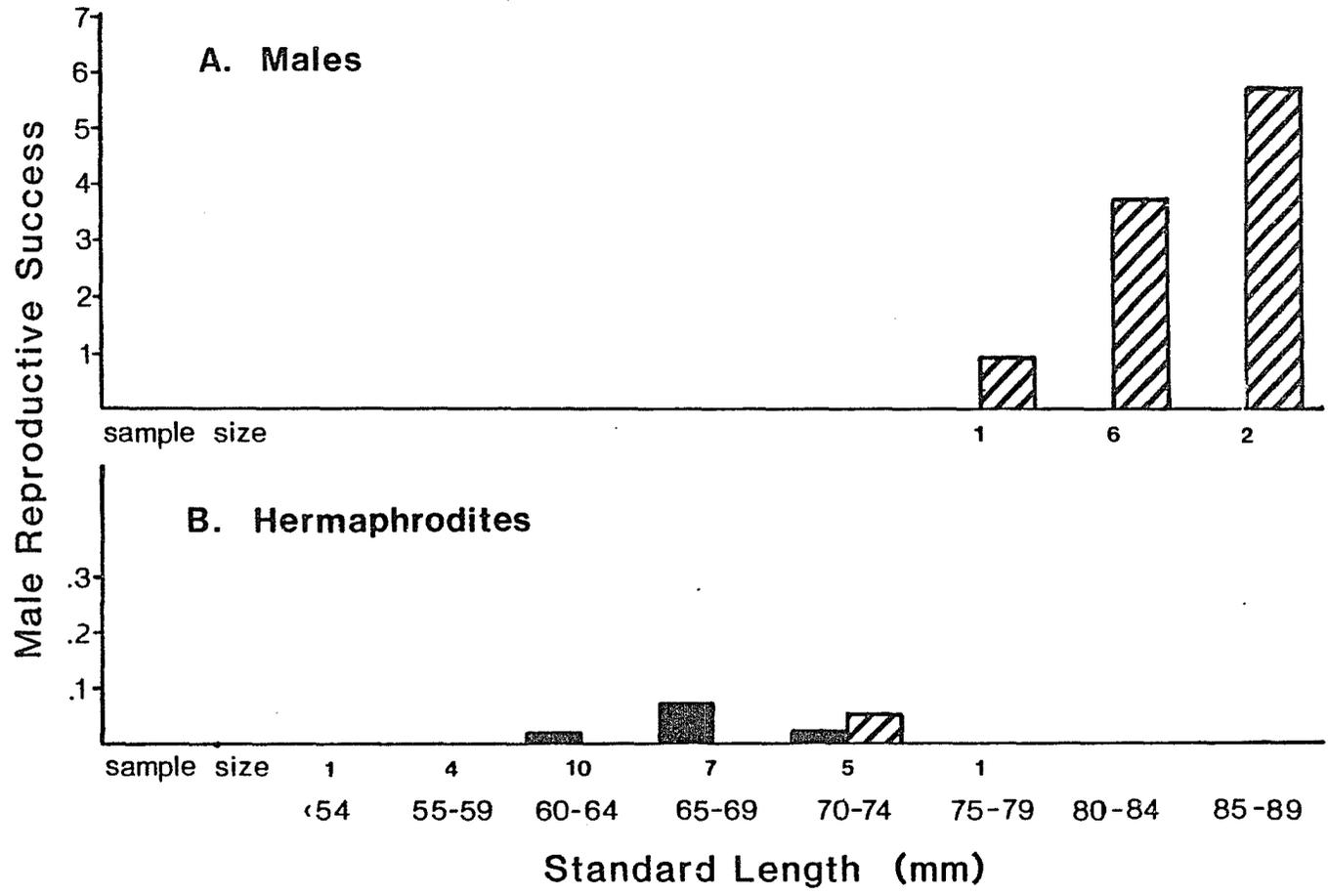


Figure 5. Male reproductive success as a function of size and gender type in Serranus fasciatus. -- Male reproductive success can be obtained by either pair spawning (hatched bars) or streaking (solid bars)

Table 12. The distribution of male spawning roles between males and hermaphrodites of Serranus fasciatus.

	Pair-spawning male	Sneak
Male	185	0
Hermaphrodite	2	22

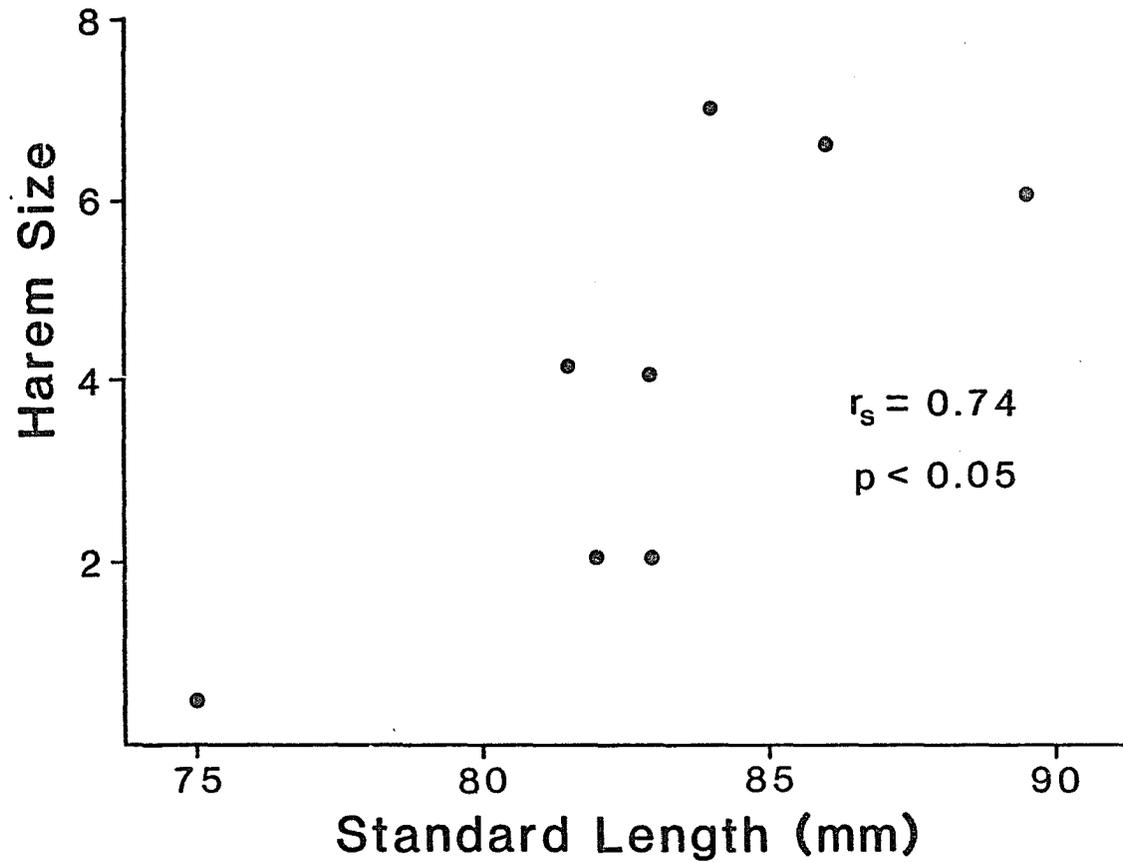


Figure 6. Harem size for different sized male *Serranus fasciatus*

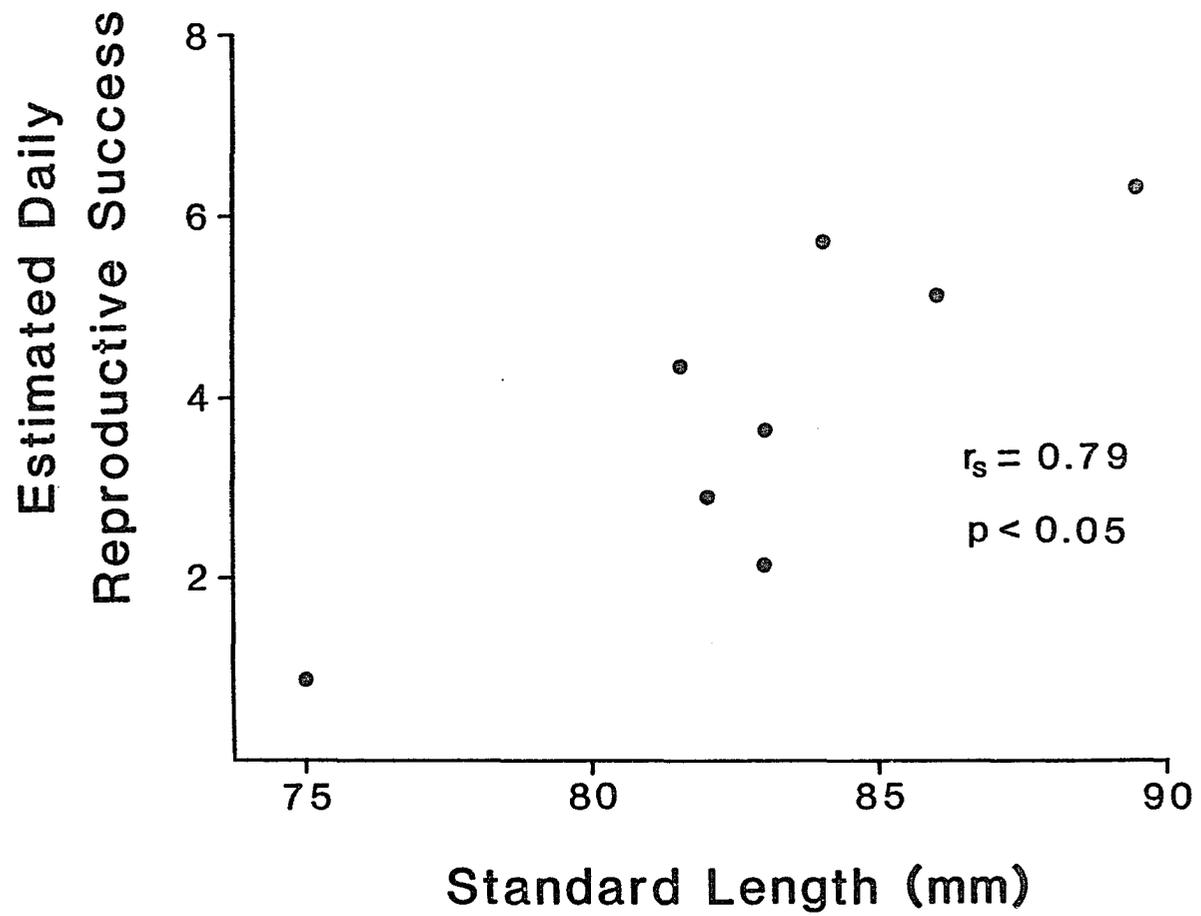


Figure 7. Estimated daily reproductive success for different sized males

All of the streaking behavior was performed by hermaphrodites. Streaking rate was not significantly correlated with hermaphrodite size, but the low streaking rate made the detection of any patterns difficult. Male reproductive success of hermaphrodites was not correlated with individual size ($r_s=.25$, $N=28$, $p>.1$) In 12 of the 14 cases in which the streaking fish were identified, the sneak came from within the harem.

The absolute amount of testicular tissue in hermaphrodites is less than the amount in males (Hastings and Petersen ms.). However, because hermaphrodites spawn as males much less frequently, the amount of testicular material per spawn is 20 times higher in hermaphrodites than in males. A larger relative testicular size per spawning act is common in animals with more intense sperm competition (Smith 1984). Hermaphrodites encounter sperm competition in over 90% of their spawns, while males have sperm competitors in only 10% of their spawns. This result suggests that an even division of fertilizations between a pair-spawning male and sneak male may be a conservative estimate of the sneak male's reproductive success. Although the pair-spawning male is probably in closer association with the released eggs, the sneak male maybe releasing much more sperm.

Is the Gender Allocation Pattern
in *S. fasciatus* an ESS?

An evolutionarily stable strategy (ESS) is any strategy that, if adopted by most members of a population, would give higher fitness than any "mutant" strategy (Maynard Smith 1982). For the hermaphrodite-male pattern of *S. fasciatus* to be stable, it must resist invasion by pure male, pure female, and pure simultaneous hermaphroditic phenotypes. "Pure" means that the individual maintains its sexual type (male, female, or hermaphrodite) for its entire lifetime. Growth and survivorship will be assumed to be equal for the real and hypothetical phenotypes compared below.

In any population where large males obtain most of the matings, a simultaneous hermaphrodite strategy that is maintained throughout life appears to be less successful than one that allows a transition from hermaphrodite to male. In *S. fasciatus*, only the smallest male that was unsuccessful at maintaining a one-female harem and then disappeared from the study site had a lower estimated reproductive success than its hypothetical reproductive success as a hermaphrodite (using the regression equation from Figure 4 to estimate female reproductive success and the mean sneak rate to estimate its male reproductive success). By reallocating all of their reproductive time

and energy into male function, large fish are able to obtain much greater total reproductive success (Figure 3).

Similarly, an individual with a pure female strategy would suffer decreased reproductive success compared to one that changes to a male at large size. As long as the harem social system is maintained, this strategy does not appear to be capable of achieving reproductive success comparable to the current hermaphrodite-to-male progression.

A third possible gender type is a pure male phenotype. Alternative male mating strategies have been reported for many species, including fishes (Barlow 1967, Wirtz 1978, Gross and Charnov 1980, Dominey 1980, Rubenstein 1980, Gross 1982). Small males can delay reproduction and direct energy into increased growth or increase survivorship probability. However, they can also adopt an alternative mating strategy, either a short-term strategy until they become dominant males, or as a lifetime strategy.

The most likely pure male strategy in this situation would be to spawn as a sneak male early in life and eventually become a dominant male. The estimated reproductive success of this hypothetical male phenotype was calculated as follows. The reproductive success per streak attempt was calculated by multiplying the percent of streaks that are successful (successful streaks/total

streak attempts observed, 23/59) by the proportion eggs in the spawn that the sneak could fertilize (0=100%). This gives a range of average reproductive success per sneak attempt of 0.00=0.39. Since hermaphrodites have an average daily reproductive success of 1.05 (1.00 as a female, 0.05 as a male), a male would have to engage in over 2.7 sneak attempts per spawning period to have a higher reproductive success than the hermaphrodite=when=small strategy. If streaking males only fertilized half the eggs, they would have to engage in more than five sneak attempts per spawning period to invade the population. The combination of spatial unpredictability and temporal synchrony of spawns and the probable agonistic behavior of large males toward small males in harems makes the pure male strategy highly unlikely.

It is more difficult to determine if a protogynous hermaphrodite could invade this population. A protogynous hermaphrodite would invest all of its early reproductive allocation into female function, and later change into a male. For the hermaphrodite=when=small strategy to be stable against invasion from a female=when=small strategy, the male reproductive success of hermaphrodites must be greater than their increase in female reproductive success if they shunted all of their male allocation to female function. Hermaphrodites obtain only an estimated 0=9% of

their reproductive success through male function, so their investments in male-related structures and behaviors must be minimal for hermaphroditism to be stable. This appears to be the case.

Although the percent of gonad devoted to testicular tissue could not be calculated for this population, these data were determined for a similar population with comparable streaking rates studied during 1981 and 1982 in San Carlos, Mexico and for specimens from the fish collection at the University of Arizona (Hastings and Petersen ms.). From these samples the average fraction of gonadal wet weight devoted to testicular material was 6.7% (N=19, range 1.5%–24.1%; no significant change in allocation with hermaphrodite size). If it is assumed that male and female tissue are equally expensive to produce and maintain energetically per gram of wet weight, by converting 6.7% of the gonad from male to female tissue an individual would raise its female reproductive success from 1.00 to 1.07. This gain in female reproductive success of 0.07 is within the range of estimated male reproductive success for hermaphrodites (0.00–0.09). The amount of error produced by assuming equality of male and female tissue production and maintenance costs per unit weight is unknown. Hermaphrodites appear to invest only slightly in male function, but whether this amount is low enough to

allow for the evolutionary stability of this gender pattern is equivocal based on these data alone.

Hermaphrodites may have a benefit in future reproductive success over small females because the transition to a functional male is faster for hermaphrodites. Unlike harem-forming protogynous hermaphroditic fishes, which apparently require one to three weeks to become functional males (Robertson 1972, Shapiro 1979, Hoffman 1980, Moyer and Zaiser 1984), Serranus fasciatus does not have this delay since males are derived from simultaneous hermaphrodites that are already capable of sperm production. This benefit would increase the lifetime reproductive success of the hermaphrodite-male strategy over the protogynous strategy. However, the possible benefits of faster gender change may be slight when compared to the lifetime reproductive success of individuals. Individuals appear to spawn for several months and probably more than one season as hermaphrodites before becoming large enough to change gender.

The most likely path for the evolution of a protogynous Serranus fasciatus would be through the gradual loss of male tissue in hermaphroditic individuals. In Serranus baldwini, a closely related species, small fish rarely spawn as males (1-2% of the days based on field observations from a Belize population, compared to 10% in S. fasciatus). The ovotestis of small hermaphrodites in a

S. baldwini population studied contained such a small amount of testicular tissue it could not be separated from the ovarian tissue (Petersen and Fischer in prep.). If hermaphroditic S. fasciatus are not obtaining adequate male reproductive success, the pattern of gender allocation should be expected to move toward that reported for S. baldwini.

In summary, hypothetical pure male, pure female, and pure simultaneous hermaphroditic phenotypes do not appear capable of invading this population. A hypothetical protogynous hermaphroditic phenotype appears to obtain daily reproductive success comparable to the hermaphrodite-male pattern observed in S. fasciatus. When two possible gender patterns give similar reproductive success, the ancestral gender pattern may be crucial in determining the gender pattern that evolves. Serranus fasciatus belongs to a genus composed entirely of simultaneous hermaphrodites, and the evolution of the current gender pattern instead of a protogynous pattern may thus be due to the past evolutionary history of this lineage. However, the possible benefits of faster gender change and the lower testicular allocation in a similar species with a lower sneak rate suggest that the testicular allocation in Serranus fasciatus is adaptive and that the hermaphrodite-

male gender allocation pattern observed in S. fasciatus is an ESS when compared to a protogynous phenotype.

Discussion

Gender Allocation and the Mating System

The observed spatial, behavioral, and reproductive patterns of S. fasciatus combine both resource and harem-defense polygyny, except that males guard hermaphrodites instead of females. Hermaphrodites maintained long-term territories and were a predictable resource that males could monopolize by limiting its access to other fish, especially during the spawning period (Table 10). Large fish maximize reproductive success by defending as many hermaphrodites as possible and by allocating all of their reproductive effort to male function. Conversely, male reproductive success in hermaphroditic S. fasciatus is mainly obtained through streaking, an alternative male reproductive tactic. Although males may lose some reproductive success to hermaphrodite sneaking, this loss is always outweighed by the increase in eggs provided by the addition of a female-role hermaphrodite.

Alternative male reproductive tactics such as streaking are rare in other harem reef fishes (Robertson and Choat 1974, Robertson and Warner 1978). Robertson and Choat (1974) hypothesized that in a harem social system, dominant males can identify all of the nearby conspecifics

and will not allow any known males to become established in the harem. In S. fasciatus, males should not attempt to permanently exclude any hermaphrodites from the harem since the gain in eggs fertilized is greater than fertilizations lost due to increased sperm competition, even if it is assumed that males fail to fertilize any eggs on spawns with sneaks. However, this should not preclude a male from chasing a sneaking hermaphrodite, which in fact often occurs.

Activity Patterns

Distinct behavioral differences exist between males and hermaphrodites and can be attributed to the change in gender exclusive of size. Only one behavior (stalk) showed a significant increase with size among hermaphrodites. The much higher levels of male activity are due to a distinctly different time allocation strategy, and not just an allometric relationship of increasing activity with individual size. However, general activity levels increase slightly with hermaphrodite size and may account for some of the increase in activity. Both the increased social interactions and time spent in active behaviors by males are due to the higher level of territory defense and social interactions, both within the harem and towards adjacent males.

During the pre-reproductive, reproductive, and post-reproductive periods, males greatly increased their levels of general activity, especially the number of interactions and time spent patrolling the territory. Patrolling peaked during the reproductive period, when the total number of interactions (both non-spawning and spawning) was also highest.

The increase in male activity coincided with a decrease in hermaphrodite activity during the reproductive period. This decrease in hermaphrodite activity has not been reported in other harem fish species, where females appear to behave normally except for the short time that they spawn with the male. The decrease in activity does not appear to be related to a general decrease in activity near dusk, since post-reproductive activity levels return to non-reproductive levels (Figure 10). This is the only behavioral difference that appears to distinguish hermaphrodites in S. fasciatus from females in all other harem fish species, save their occasional spawning in as males.

The decreased activity levels of hermaphrodites during the reproductive period in S. fasciatus could be due to either of two factors. First, hermaphrodites may decrease activity to be more successful as sneak males. Hermaphrodites had very little success at sneaking if located by the male immediately before spawning. However,

the activity budgets of successful sneaks during the reproductive period did not differ from individuals that were never observed successfully sneaking (Table 11).

A second possible explanation is that hermaphrodites decrease activity levels during the reproductive period in response to increased male aggression. Males show increased aggression towards hermaphrodites during the reproductive period (Table 10). This may be a male strategy to decrease hermaphrodite movement during reproduction and to restrict sneaking opportunities by male-role hermaphrodites. This second aspect appears more consistent with the general patterns of male-hermaphrodite interactions observed.

Larger males also had higher dominance indices than smaller males. However, the correlation of dominance index with male size may be an artifact of the higher rate of movement of small males outside their normal territories. Within their territories males acted aggressively towards all intruding males.

In some protogynous harem-forming fishes, males direct either more aggressive interactions (Hoffman 1980, Moyer and Nakazano 1978) or more intense aggression (Robertson 1972, Kuwamura 1984) toward the largest females in their harems. These patterns have been interpreted by the authors as a male response to a potential threat to its

future reproductive success. In S. fasciatus there are no differences in aggression based on hermaphrodite size within the harems. This difference could be due to either: 1) the increased threat of simultaneous hermaphrodites to the current reproductive success of the male, or 2) the presence of dominance hierarchies in many sequentially hermaphroditic species that do not exist in S. fasciatus.

If male aggressive behavior toward hermaphrodites appears to be a response to a current reproductive threat, then males might be expected to behave differently towards individuals that have been observed successfully sneaking. This is not the case in Serranus fasciatus. The only differences between sneaks and non-sneaks in their activity levels were their hermaphrodite=hermaphrodite interaction rates (Table 11).

Hermaphrodites do not appear to set up dominance hierarchies within harems in S. fasciatus, as do females in Labroides dimidiatus (Robertson 1972, Robertson and Choat 1974, Robertson and Hoffman 1977, Kuwamura 1984), Bodianus rufus (Hoffman 1980, 1983), Centropyge interruptus (Moyer and Nakazano 1978), and possibly Dasyllus aruanus (Fricke and Holzberg 1974, Coates 1982). However, dominance hierarchies and increased interaction levels between males and larger females are not the rule in all harem species, so this difference cannot be attributed to the presence of

hermaphrodites instead of females. Dominance hierarchies do not appear to exist in the gonochore Pseudobalistes fuscus (Fricke 1980), the sequential hermaphrodite Malacanthus plumeri (T. Baird, personal communication), or Serranus baldwini (Petersen and Fischer in prep.). No data on female-female interactions were presented in the other studies of harem reef fishes (Barlow 1975, Moyer 1979, Thresher 1979, Lobel 1978, Robertson 1981, Neudecker and Lobel 1982, Tribble 1982, Moyer, Thresher, and Colin 1983). The factors that produce dominance hierarchies in some harem species and not in others are unknown.

Successful sneaks interacted at much higher rates with neighboring hermaphrodites during the non-reproductive period. These hermaphrodites may have better knowledge of the location of neighboring hermaphrodites because of their increased interaction rates. This would facilitate sneaking during the reproductive period, when both their movements and hermaphrodite-hermaphrodite interactions are severely restricted. However, whether the increased interaction rates facilitate higher sneaking rates, or if some individuals have higher sneaking tendencies and show more interactions, is unknown. Many fish that were never observed successfully sneaking were observed attempting to sneak. Hence, given the opportunity all hermaphrodites will attempt to sneak.

Gender Allocation in S. fasciatus

Figures 8A and 8B represent the hypothesized relationships of reproductive success versus gender allocation for hermaphrodites and males, respectively. This type of graph was first used by Charnov (1979, 1982) to determine how non-fixed reproductive allocations (allocations to gametes and behaviors that can alter the reproductive success of an already functional sex) could be distributed between male and female function. The female curve is depicted as a direct relationship with energy devoted to non-fixed female structures. This curve is derived from two assumptions: that female reproductive success is determined by energy devoted to reproduction (Bateman's principle, Bateman 1948), and that this relationship is linear. The male curve, drawn with a negative second derivative, quickly asymptotes at a level much lower than the maximum female reproductive success. The difference between overall male and female reproductive success of optimally allocating hermaphrodites is due to large dominant males obtaining most of the male reproductive success in the population. Initially, the male reproductive success curve increases quickly, since small levels of investment provide gametes for occasional streaking and male-role pair spawns by hermaphrodites. As energy devoted to male function increases, spawning

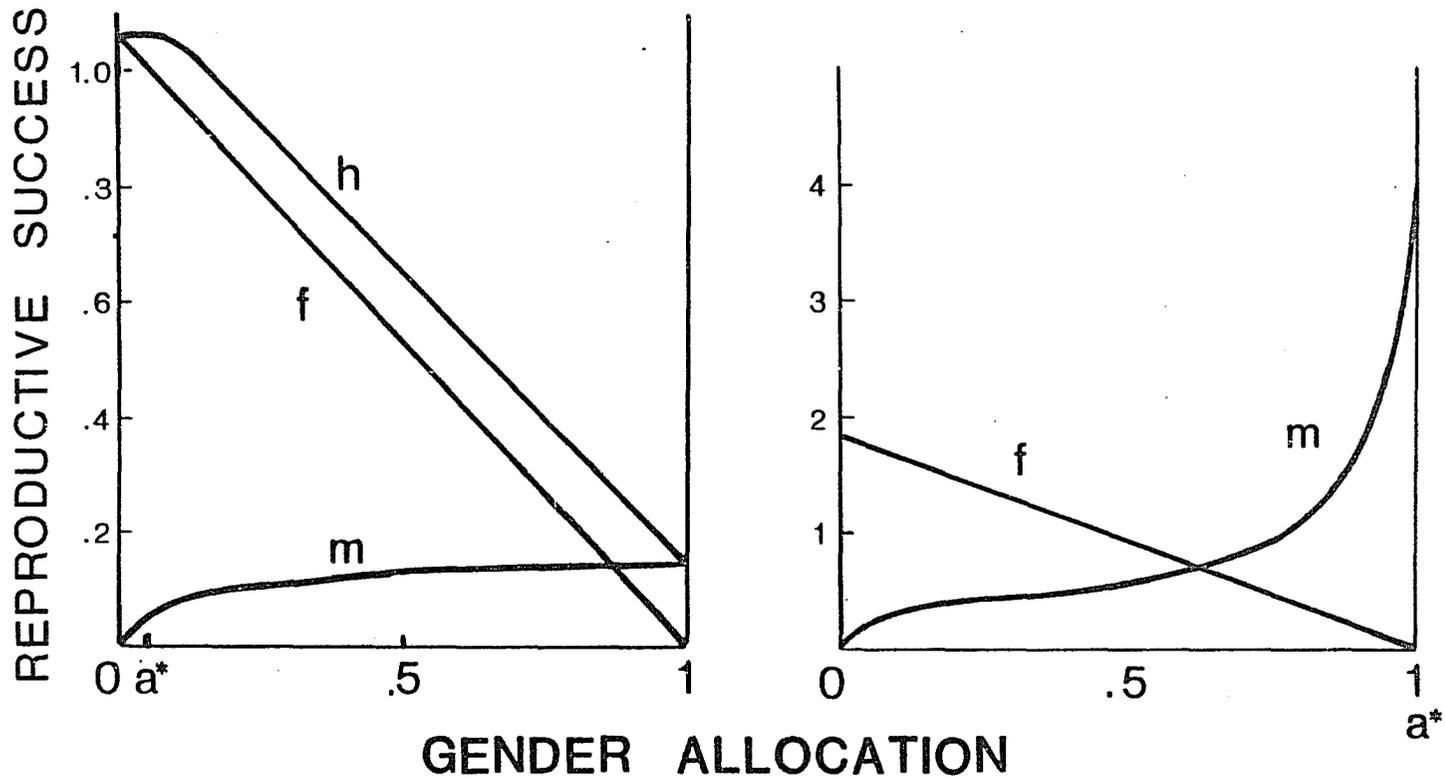


Figure 8. Hypothesized relationship of reproductive success versus gender allocation for hermaphrodites and males in Serranus fasciatus. -- The left graph (8A) represents the allocation for a small hermaphrodite, the right graph (8B) represents the allocation for a male

attempts do not increase proportionately due to time and predictability constraints.

Two conditions that will stabilize hermaphroditism are low fixed costs for male function and a rapid asymptoting of male reproductive success with investment. Both of these conditions should be occurring in S. fasciatus hermaphrodites. This species exhibits external fertilization and no specialized male reproductive structures other than sperm sinuses and sperm ducts, thus fixed male reproductive costs are probably low. Hermaphrodite reproductive success as a male should also asymptote quickly with increasing investment. Because male mating opportunities for small individuals are limited, the temporal synchrony and spatial variability of spawning prevents the number of sneaks an individual can obtain from being greatly modified by changes in individual behavior. The only way small individuals could increase reproductive success is by releasing more sperm per sneak. This would increase the number of eggs fertilized by the sneak's sperm, but at decreasing rates, resulting in diminishing returns for increased allocation to male function.

Why Is This Gender Pattern So Rare?

If this gender allocation pattern is stable, why has it not been observed before in a natural population? Two possible reasons exist. The endocrinological

differences between sequential and simultaneous hermaphrodites are unknown. Early endocrinological work done by Reinboth (1962) points to responses of hermaphrodite gonads to androgens and estrogens that differ from those observed in gonochoristic and sequentially hermaphroditic species. For example, females in many protogynous species will change to males when injected with testosterone, while in at least one simultaneous hermaphroditic fish both male and female tissue were apparently stimulated when testosterone was injected (Reinboth 1962). In many species with similar social systems, the ability to evolve hermaphroditic individuals may not exist, but the constraints involved, if any, are unknown.

Males in many species of reef fishes and other animals exhibit alternative mating strategies. However, in all other species studied to date, small males exhibit this behavior rather than hermaphrodites. What factors in these other species allows for the coexistence of these males? In most fishes that release pelagic eggs, spawning occurs at specific sites on the reef (Robertson and Hoffman 1977, Johannes 1978, Loiselle and Barlow 1978, Sale 1978). This spatial predictability may provide sufficient opportunities for small individuals to specialize as males using alternative mating strategies. Serranus fasciatus does not travel to specific locations on the edge of reefs to spawn.

This may be because: 1) S. fasciatus already occurs in the rock-sand habitat at the margins of reefs, where egg predation is less frequent; 2) it is a relatively small species compared to others that release pelagic eggs and so may be limited in its movements by potential predators; 3) unlike many labroids, it maintains a specific territory. Whatever the reason, nonlocalized spawning of S. fasciatus has restricted the evolution of a "full-time" sneak male strategy, but has allowed individuals to become "part-time" sneaks, with the sneak strategy embedded in a hermaphroditic individual that obtains most of its current reproductive success through female function. Unlike other harem fish, these facultative males are able to coexist in a harem in close contact with a larger male. These potential sperm competitors are tolerated within the harem because they exist in predominately female individuals. The presence of a hermaphrodite always increased the male's reproductive success, since additional eggs fertilized more than compensated for the increased sperm competition.

What factors have led to the evolution of reciprocation in Hypoplectrus and other simultaneously hermaphroditic Serranus and a polygynous system in S. fasciatus? Serranus fasciatus tends to occur at higher densities than most other simultaneously hermaphroditic reef fishes. This higher density may be important in

allowing large individuals to sequester several mates. In Serranus tortugarum, the only simultaneously hermaphroditic reef fish that occurs at higher densities than S. fasciatus, defense of mates or resources may not be possible. Serranus tortugarum is a planktivore found in large aggregations above coral heads. Planktivorous fishes tend to change location relative to currents, which may make it impossible for males to defend the resources necessary for smaller individuals. The constant change in location by smaller fish would also reduce their predictability in time and space by larger conspecifics. Serranus fasciatus appears to have the most conducive conditions for polygyny of any species of simultaneously hermaphroditic reef fish studied to date. Serranus baldwini, which is ecologically similar to S. fasciatus, appears to have a harem social system. Its social system is currently under study (C. Petersen and E. Fischer in prep.).

Warner (1984) noted that although certain types of gender patterns were good predictors of specific social and mating systems, the reverse prediction, that specific social and mating systems should result in a specific type of hermaphroditism or separate sexes, was much weaker. Of the species that have separate sexes, many may have hormonal or morphological factors restricting the evolution of hermaphroditism. Similarly, in some sequential

hermaphroditic species there may exist some factor restricting the evolution of simultaneously hermaphroditic individuals. Thresher (1979) hypothesized that small males exhibiting alternative mating strategies did not exist in Halichoeres garnoti because spawns were not spatially predictable. It is not clear why a hermaphrodite-when-small strategy has not invaded this protogynous species. Labrids appear to have no specialized morphological adaptations that would make simultaneous hermaphroditism too expensive energetically, but this gender pattern is not known to occur in this family.

When the benefits from specializing as a sneak outweigh losses due to diminishing returns in male fitness with investment, then sneak males and females should evolve instead of small hermaphrodites. In Serranus fasciatus the decreasing return for increasing male function in a small individual appears to outweigh any benefit from specializing as a pure male when small. In species with constraints preventing simultaneous hermaphroditism and with similar social systems to S. fasciatus, protogyny or other polygynous systems should be the evolutionarily stable strategy.

Summary

In the hermaphroditic bass Serranus fasciatus, individuals are first simultaneous hermaphrodites but later

lose female function to become males. Males (i.e., large individuals) establish territories containing several hermaphrodites that they defend from other males and spawn with on a daily basis during the reproductive season. Hermaphrodites obtain small amounts of reproductive success through male function by joining hermaphrodite-male pair spawns in a behavior identical to those employed by males in other reef fishes. This gender allocation pattern appears to be uninviable by protogynous individuals, thus making it an ESS, although the results obtained are equivocal.

In general, this social system appears remarkably similar to harems in gonochoristic and sequentially hermaphroditic fishes. Both male-hermaphroditic interactions and hermaphrodite behavior are similar to other harem species lacking established ranks among females. Males interact with most hermaphrodites at similar rates, but actively chase fish that are about to sneak on pair spawns. The one difference observed in activity patterns between this and all other harem species was the reduced activity of harem members (hermaphrodites) during the reproductive period, which may reflect increased aggression by males to reduce sperm competition or an alternative male mating strategy by hermaphrodites.

The absence of this gender allocation pattern in socially similar species of reef fishes may be due to restricted spawning locations, which can favor distinct small-male mating strategies. However, the rarity of this complex pattern is probably also due to evolutionary constraints on its development in other species.

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