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DEFERRED REPRODUCTION AS A RESPONSE TO SEXUAL SELECTION IN A CORAL REEF FISH: A TEST OF THE LIFE HISTORICAL CONSEQUENCES

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Ideally, individuals that initiate reproduction early in their lifetime gain the advantage of short generation time and reduced juvenile mortality. But in many species, males enter into reproduction much later than do females. This pattern is most common in species where a few larger or older males monopolize matings, and thus sexual selection is intense (Trivers, 1972; Warner, 1980). Theory in behavioral ecology suggests that in this situation younger males have little to gain from reproductive activity, since their probability of being successful is vanishingly small. Instead, they should avoid reproduction, maximize their foraging time, and channel their energy into growth, survival, or other factors likely to elevate their status (Caughley, 1966; Orians, 1969; Geist, 1971; Selander, 1972; Trivers, 1972; Wiley, 1974; Wittenberger, 1979). Life-history theory makes a similar prediction: when the returns in reproductive success are low over a broad range of reproductive effort, an organism should skip reproduction and allocate energy to growth and survival until a more favorable situation occurs (Williams, 1966; Gadgil and Bossert, 1970; Schaffer, 1974; Pianka and Parker, 1975; other references in Stearns, 1976).

These explanations of deferred reproduction assume that younger males have less competitive ability than older males. As Wiley (1981) points out, the fact that younger males avoid reproduction is not proof that they are competitively inferior, especially in animals with determinate growth. Other factors, such as the need for experience, could certainly contribute to selection for deferred repro-

duction. When older males are much larger, however, the potential trade-off between current reproduction and future growth assumes importance because larger individuals tend to win in contests (e.g., Rand, 1967; LeBoeuf, 1974; Howard, 1978; Warner and Hoffman, 1980b).

This suggests a general test of the supposed adaptiveness of deferred male reproduction: when male competitive ability depends on size, the reproductive activity of younger males should vary inversely with the intensity of sexual selection. When sexual selection is less intense, the current potential rewards for young males are increased and future prospects are decreased; they should therefore direct a larger proportion of their time and energy to reproduction. This should be true as long as mating success increases appreciably with investment in reproductive activities, and should be reflected in slower growth or increased mortality. In contrast, females should have time budgets and life histories that are much more insensitive to the intensity of sexual selection among males, because their reproductive success depends more on absolute size rather than on relative size (Schoener, 1971; Trivers, 1972).

These predictions have generally been investigated through comparisons between species that appear to differ in the intensity of sexual selection, but such comparisons are fraught with problems of uncontrolled environmental variables and differing phylogenetic histories (Stearns, 1977; Warner, 1980). Instead, I test the predictions within a single species by measuring the time budgets

and reproductive activities of young males and females under various naturally-occurring regimes of mate monopolization by larger males.

The predicted variation in young male mating activity is relatively trivial if small males are simply avoiding the aggressive attacks of larger males. However, life history theory suggests that the avoidance of current reproduction has a more fundamental result: growth and/or survival to a competitive size are enhanced. Virtually no information exists on whether deferred male reproduction has adaptive consequences in life history (Wiley, 1981). For that matter, the general idea of a cost of reproduction has been subject to surprisingly little experimental verification (Stearns, 1976), and the form of the relationship between various levels of reproduction and the associated costs is unknown for any species. This information is critical to predictions of adaptive allocations of time and energy to reproduction (e.g., Schaffer, 1974; Pianka and Parker, 1975).

Do future growth and survival vary inversely with reproductive output? Unfortunately, most studies (references in Stearns, 1976; Bell, 1980; Caswell, 1980) have simply shown a correlation between reproduction and a supposed cost, and thus admit the possibility of other causal covariables. These studies compare growth or survival (1) among individuals that vary naturally in reproductive output for unknown reasons; (2) among groups following year-to-year variations in overall reproductive output; (3) between breeding and non-breeding seasons; or (4) between different ages or sexes.

The results from controlled experimental studies provide conflicting evidence about the costs of reproduction. For effects on growth, one field study (Crisp and Patel, 1961) and one laboratory study (Hirschfield, 1980) indicated a definite negative effect due to reproduction, while another field study did not (DeSteven, 1980). A field experiment (Murdoch, 1966) and five laboratory studies (Clark and Sardesai, 1959;

Hirschfield, 1980; Partridge and Farquhar, 1981; Browne, 1982; Tallamy and Denno, 1982) demonstrate that reproduction can have a negative effect on survival. However, three other studies, one in the field (DeSteven, 1980) and two in the laboratory (Boyer, 1978; Munchilla and Loverde, 1981) indicated no such effect. Finally, two experimental studies have demonstrated a negative relationship between present and future reproduction, seemingly unrelated to growth or survival (Boyer, 1978; Munchilla and Loverde, 1981).

With one exception (Partridge and Farquhar, 1981), all of these studies deal with females or simultaneous hermaphrodites, even though it should be relatively easier to experimentally vary male reproductive effort through manipulations of the intensity of mate competition. In the light of these conflicting results, there is an obvious need to specifically test whether deferred male reproduction actually conveys the proposed longer-term advantages in growth or survival. I attack this problem by comparing the life histories of groups of males that initiate reproduction at different ages in response to the local social environment.

Natural History and Specific Tests

As discussed above, the value of present vs. future reproductive activity can change radically for males, depending on their size and the intensity of sexual selection. If a species has existed over evolutionary time in an environment that varies measurably and predictably in the intensity of sexual selection, then males may display reproductive activity budgets appropriate to the environment in which they find themselves. Furthermore, they may be expected to shift their budgets in predicted directions when the environment is experimentally altered. If we can then follow these males over time, we can measure the resultant growth and survival.

The bluehead wrasse, *Thalassoma bifasciatum*, occurs commonly over west

Atlantic coral reefs, and local populations vary in the intensity of sexual selection in a predictable and consistent manner. Adults do not leave the reef upon which they have settled, so the entire population is broken into small subpopulations connected only through larval dispersal. All adult interactions take place within these local groups (Warner and Hoffman, 1980*a*).

The species occurs in two color phases. Initial phase individuals can be either males or females. The less common terminal phase individuals are males, and tend to be the largest individuals in any local population (Warner and Robertson, 1978). Large females are able to change sex into secondary males (protogynous hermaphroditism, Warner et al., 1975). Females also tend to change into terminal phase coloration when they change sex. The great majority (91%) of initial phase males are primary males (not the result of sex change), and they transform into terminal phase coloration at about the same size as females (Warner and Robertson, 1978). Sex change and the transition to terminal phase coloration are controlled by local social conditions (Warner et al., 1975).

A mating period takes place every day, for about an hour in the midafternoon. Most females mate once each day, and the majority of matings occur on the downcurrent edges and projections of a reef. Females leave the feeding school at the upcurrent end of the reef, swim downcurrent, spawn, and return to the feeding school. Fertilization is external and there is no parental care of the pelagic zygotes.

During the mating period, the majority of males are located at the downcurrent end of the reef, where they attempt to mate with the arriving females. Only the largest terminal phase males maintain territories during the entire daily spawning period; smaller terminal phase males continue to feed or sporadically maintain territories in areas visited by relatively few females. Large males maintain territories at the same location on succes-

sive days, aggressively exclude other males, and spawn singly with females. Initial phase males are nonterritorial and usually spawn in multi-male groups with single females. They also interfere with terminal phase male matings, either by pair-spawning with females themselves or by rushing in to join a territorial male and a female at the apex of the upward spawning movement. Accordingly, terminal phase males direct most of their territorial defense toward initial phase males (Warner and Hoffman, 1980*b*).

Experimental increases in population density can lower the daily mating success associated with a particular territory because a territorial male must then spend increasing amounts of time in defense and thus has less time for courtship and mating (Warner and Hoffman, 1980*b*). As reef size increases, the proportion of initial phase males increases, and these males concentrate their activities at the major downcurrent spawning sites (Warner and Hoffman, 1980*a*). Terminal phase males position their territories in response to local conditions of initial phase male density, moving away from the prime downcurrent sites on larger reefs. The result is a large change with reef size in the strength of sexual selection (i.e., the variance in male mating success). On small reefs (less than 110 individuals), one or a few territorial males occupy all spawning sites and mate with nearly all females. On larger reefs (more than 120 individuals), a group-spawning aggregation of initial phase males occupies the major downcurrent spawning site, and male territories are located in peripheral areas upcurrent from the initial phase male group. Females appear to prefer downcurrent sites, so on larger reefs territorial males may mate with fewer than a third of the available females. Since mating success is thus more evenly distributed among males, sexual selection is correspondingly weaker on larger reefs (Warner and Hoffman, 1980*a*).

Since sexual selection is strong on small reefs but weak on large reefs, initial phase males on small reefs should spend less

TABLE 1. Sample totals for three periods of censusing of *Thalassoma bifasciatum* in the San Blas Archipelago, Panama. All tagged individuals were initial phase, between 50 and 75 mm SL. Large reefs have group-spawning aggregations, small reefs do not.

Period	Duration	Large reefs ($N > 120$)			Small reefs ($N < 110$)		
		Reefs (N)	Males (N)	Females (N)	Reefs (N)	Males (N)	Females (N)
I	7/7–8/29/79	1	52	45	2	11	54
II	8/25–12/24/79	4	122	143	2	41	144
III	3/3–7/24/80	6	203	262	4	57	155
Total		11	377	450	8	109	353

time and energy on reproduction than equivalent males on large reefs, but females should show no differences. Furthermore, if time or energy spent on reproduction carries a cost in reduced growth and/or mortality, the initial phase males on small reefs should grow faster and/or suffer less mortality than equivalent males on large reefs. These are the predictions tested here.

METHODS

All observations and experiments were carried out at the San Blas Field Station of the Smithsonian Tropical Research Institute, Panama. I ran three major series of observations (Table 1). In each series, I compared the behavior, growth, and survival of cohorts of initial phase males and females from large and small reefs. Individuals were captured by means of a lift net (see Roede, 1972) baited with sea urchins (*Diadema antillarum*), and tagged with unique combinations of small colored beads. Handling time was similar for all individuals.

The environmental variable of interest is the local intensity of sexual selection. This intensity, measured here as the variance in male mating success, was calculated for each reef using a formula provided by Wade and Arnold (1980). The data necessary for this calculation are the sex ratio, the proportions of different types of males, and the mating rates of different types of males. For simplicity, only three types of males were considered: initial phase males, nonterritorial terminal phase males, and territorial terminal phase males. Population parame-

ters were estimated using lift-net samples and visual censuses. Terminal phase male mating rates were already known (Warner and Hoffman, 1980a), and were verified during each series. Initial phase male mating rates were estimated as part of this study.

Behavioral responses to the intensity of sexual selection were estimated by the proportion of time spent in reproductive activity. In contrast to seasonal breeders, it is unlikely that *Thalassoma* stores energy over long periods for eventual use in reproduction, since it mates every day. In addition, individuals spend nearly all of their non-reproductive time feeding (see Results). For these reasons, it was assumed that time devoted to reproductive activities represented a significant decrement in energy input. It would be very difficult to measure the actual energy budgets of this mobile planktivore. As Bell (1980) points out, the critical question is how changes in reproductive expenditure affect fitness, and an exact measure of reproductive effort may be unnecessary.

In each observational series, a randomly chosen subsample of individuals of both sexes were observed for 30-min periods in and out of the mating period, with time allocations and mating success recorded on small waterproof cassette recorders. The mating period was defined as the time interval during which spawning was actually occurring; this averaged 57 min (114 observations), and began between 1115 and 1530 EST each day.

For the purposes of this paper, only two major categories of activity need be

described. Reproductive activity in initial phase males consisted of chasing females at spawning sites, lurking at the periphery of terminal phase male territories, courting females, and actually spawning. For females, reproductive activity consisted of being chased or courted, waiting at territorial spawning sites, and spawning itself. Foraging activity for both sexes consisted primarily of feeding on plankton in the water column at the upcurrent end of the reef. Other activities, which formed a small proportion of total time, consisted primarily of transit between different sites on the reef.

Estimates of total amount of time spent in reproductive activity per day were calculated by multiplying the estimate of the proportion of time spent in reproductive activity during the mating period times the average length of the spawning period for a particular reef. Time spent in reproductive activity was used to compare the reproductive output of different classes of males.

Mating success for males was measured in pair-spawning equivalents, estimated by summing the total number of spawns in which the individual participated, each divided by the total number of males involved in each spawning (Warner et al., 1975). Female matings require no such discounting.

It was important to establish that reproductive activity expenditures were short-term responses to the local reef environment. To do this, I transplanted males from large reefs to small reefs, and vice versa. Tagged individuals were first observed on their home reefs to document their normal activity budgets, then transferred and subsequently observed up to 20 days at their new reef location. Controls were treated identically, except that they were either transferred to a reef similar in characteristics to their home reef (transplanted controls) or they were replaced on their home reef (nontransplanted controls). These experiments were conducted from July 20 to September 1, 1979, and from January 13 to March 3, 1980.

In order to monitor the longer-term

effects of current reproductive activity, I traced the growth and survival of marked cohorts of males and females from a range of reef sizes. Regardless of the time budgets of the resident individuals, reefs may have direct effects on growth and survival, depending on such things as position in the current, density of predators, shelter availability, etc. I attempted to adjust for these intrinsic effects by using females as controls. The results show that female reproductive activity budgets were similar on all reefs and therefore I assumed that any differences seen in female growth or survival rates were due to intrinsic properties of the reef. I then used the rates for females in multiple regression analyses to remove the effects of intrinsic reef differences on the same rates for males. For illustrative purposes in Figures 4 and 5, I used the female rates to normalize male growth or survival rates. If the mean female rate for all reefs is R_{mf} , and R_{if} and R_{im} are the mean rates for females and males on a particular reef i , then the normalized male rate was calculated as $(R_{mf}/R_{if}) \cdot R_{im}$. Note that none of these procedures assumes that male and female rates are similar, only that reef characteristics affect male and female rates by a similar factor.

Growth rates were estimated by monthly recapture and measurement of tagged individuals. The mean growth rate for a cohort on a particular reef was weighted by the duration of the available sample for each individual. Average duration of the sample was 49 days ($N = 470$). All lengths are given as Standard Length (S.L.).

Survival rates were estimated from weekly visual censuses of tagged individuals. Two observers swam in a grid pattern over the reef, recording tagged fish, until no further individuals were added in a complete pass of the reef. A given week's surviving population number was adjusted on the few occasions when unrecorded individuals were seen in subsequent samplings. Rate of survival was based on the decay in numbers of tagged individuals. Censuses continued up until 120 days after the initial day of tagging.

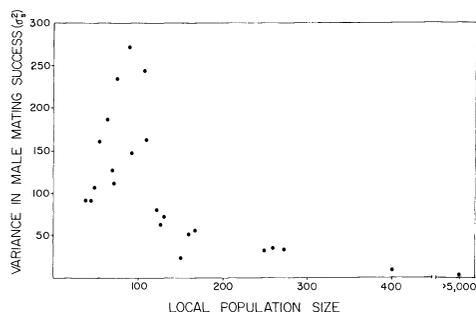


FIG. 1. The intensity of sexual selection, measured as the estimated variance in male mating success, for *Thalassoma bifasciatum* on reefs of increasing initial phase population size. Data are from 19 reefs in the census periods (see Table 1) and four small reefs used in the transplantation experiments.

No claim is made that the growth and survival rates measured by these methods accurately reflect normal rates of untagged individuals. Tagging is traumatic, and may introduce some significant effects of its own. For this reason, comparisons were only made among tagged individuals. However, to discuss the effects of differences in growth rates on expected lifetime mating success (see Discussion), it was necessary to estimate natural mortality rates. This was done by removing all the recruits and juveniles (individuals less than 25 mm S.L.) from two small reefs, and then monitoring the decline in numbers of adults. Initial removals and adult censuses were performed from June 20 to July 1, 1981. New recruits were removed periodically as needed and adult censuses continued

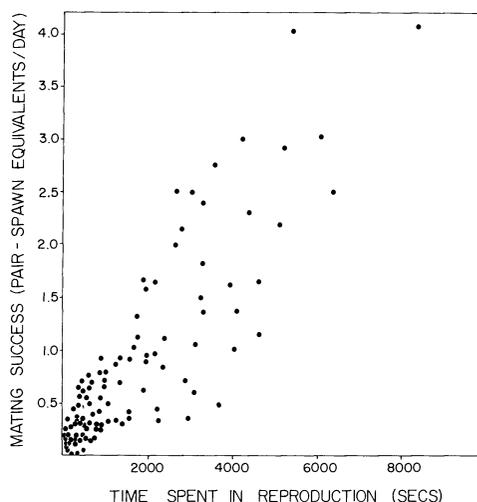


FIG. 2. Returns in mating success for observed time spent in reproductive activity for initial phase males on large reefs.

until November 9, 1981. This technique assumes that the removal of recruits and juveniles does not affect the survival rate of resident adults. Since *Thalassoma* population sizes appear to be below reef carrying capacity under normal conditions (Victor, 1983), such an assumption is probably justified.

RESULTS

Local Intensities of Sexual Selection

Because increasing male density at the mating site reduces the effectiveness of terminal phase male territorial defense, large males accrue a progressively smaller share of the total daily matings as reef

TABLE 2. Returns in mating success to initial phase individuals for time spent in reproductive activity. Rates are expressed as the mean \pm 1 S.E. PSE is pair-spawn equivalent, explained in text.

	N	Total observation time (min)	Total time in reproduction (min)	Spawning rate (spawns/min)	Mating success rate (PSE/min)
Small reefs	8				
Males (transplants to 4 reefs)	14	4,337	25	0	0
Females	31	2,252	50	10.37 \pm 2.11	10.37 \pm 2.11
Large reefs	11				
Males (resident)	91	15,359	4,101	.73 \pm .05	.08 \pm .01
(transplants to 2 reefs)	9	916	122	.86 \pm .17	.09 \pm .03
Females	17	2,768	55	14.99 \pm 2.47	14.99 \pm 2.47

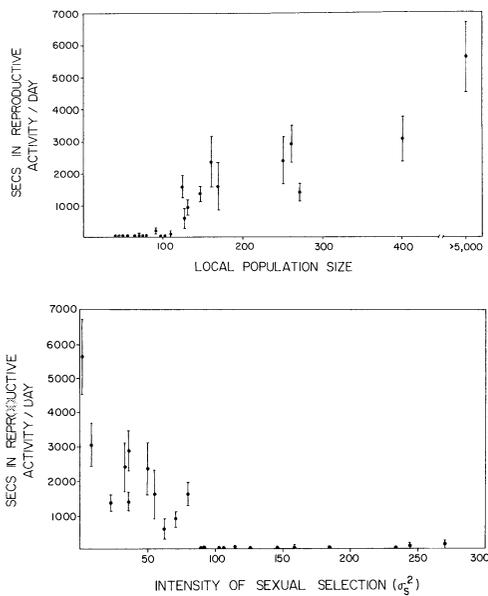


FIG. 3. A. Time spent in reproductive activity per day by initial phase males relative to reef population size. B. Time spent in reproductive activity per day by initial phase males as a function of the local intensity of sexual selection. Data are from 19 reefs used in the census periods and four used in the transplantation experiments. Shown are means and their 95% confidence intervals.

size increases, the remainder going to initial phase males (Warner and Hoffman, 1980a). Initial phase males do not attempt to aggressively exclude each other from mating, but spawn in groups, so it is assumed that there is relatively little variation among them in mating success on a particular reef. The overall result is that as reef size increases, mating success becomes more evenly distributed among males, and thus the local intensity of sexual selection is diminished (Fig. 1).

The among-male variance in mating success reaches a maximum at local population sizes of about a hundred individuals. Above this level, the ability of terminal phase males to control the mating sites begins to break down. Below this level, there are progressively fewer deprived males and thus the variance is less. This reaches its logical extreme on the smallest of reefs ($N < 25$), where a single

TABLE 3. Summary of time allocations of tagged initial phase individuals of *Thalassoma bifasciatum*.

	N	Days	Observation time (min)	Proportion of total time spent in	
				Foraging	Reproduction
Within spawning periods					
Small Reefs	8				
Males	45	104	5,478	.982	.002
Females	31	46	2,252	.967	.022
Large Reefs	11				
Males	91	163	15,359	.701	.267
Females	17	37	2,768	.964	.020
Outside spawning periods					
Small Reefs	8				
Males	35	61	2,842	.990	.000
Females	24	32	1,116	.989	.000
Large Reefs	9				
Males	52	77	2,867	.973	.015
Females	14	25	791	.979	.000

secondary male garners all spawnings and initial phase males are absent (Warner and Hoffman, 1980a). No reefs of this size were used in this study.

Returns in Mating Success for Reproductive Activity

Unfortunately, the observed variance in male mating success among reefs says nothing about the potential mating success of a young male who attempts to breed. His actual mating success may be low because he never tried to mate. When sexual selection is intense, it is usually assumed that any effort spent on reproduction by smaller males is doomed to failure. This is equivalent to assuming that a situation exists in which the observed behavior would be adaptive, a circular argument in the context of the present hypothesis (cf. Wiley, 1981). Unfortunately, it is often difficult to induce individuals to vary their reproductive behavior in order to detect the consequences.

I circumvented this problem by transplanting 14 initial phase males from large reefs (where they were sexually active, see

TABLE 4. Reproductive time budgets of tagged initial phase males transplanted from large reefs to small reefs. Transplanted controls were moved to other large reefs. Number of observations are shown in parentheses.

Proportion of time in reproduction within spawning period			
Premanipulation	.326 (72)		
	Nontransplanted controls (N = 13)	Transplanted controls (N = 9)	Experimentals (N = 14)
Postmanipulation			
1-5 days	.347 (6)	.053 (11)	.011 (36)
6-10 days	.263 (7)	.140 (9)	.001 (27)
11-15 days	.345 (4)	.153 (6)	.003 (10)
16-20 days	—	.249 (5)	.000 (7)

below) to small reefs. These males attempted to mate with females for a few days, chasing and courting females as they had on their home reef. This allowed an otherwise unavailable assessment of returns in mating success for reproductive activity on small reefs (Table 2). These initial phase males were never successful during 25 min of observed reproductive activity.

On large reefs, the measurement of mating success rate was more straightforward. For resident initial phase males, mating success increased with time spent in reproduction (Fig. 2). Furthermore, the nil return for males on small reefs was not an artifact of transplantation: males from large reefs transplanted to other large reefs enjoyed a mating success rate similar to resident males (Table 2; $t_s = .294$, 98 *d.f.*, $P > .50$).

Compared with males, females have a very high rate of mating success per unit of time spent in reproduction (Table 2). In accord with the initial predictions, this high rate of success does not appear to be affected by the local intensity of sexual

TABLE 5. Reproductive time budgets of tagged initial phase males transplanted from small reefs to large reefs. Transplanted controls were moved to other small reefs. Number of observations are shown in parentheses.

Proportion of time in reproduction within spawning period		
Premanipulation	.000 (36)	
	Transplanted controls (N = 5)	Experimentals (N = 11)
Postmanipulation		
1-5 days	.001 (10)	.028 (27)
6-10 days	.002 (4)	.092 (16)
11-16 days	.000 (6)	.164 (16)

selection. Mating success rates for resident females on large and small reefs did not differ significantly from one another ($t_s = 1.426$, 46 *d.f.*, $P > .20$).

Time Expenditures on Reproduction

Given the returns in mating success outlined above, it is not surprising that there were striking differences in the time spent in reproduction by initial phase males on reefs of different sizes (Fig. 3a). As the intensity of sexual selection diminished, small males spent an increasing amount of time in reproductive activity (Fig. 3b).

A broad comparison can be made by pooling the data into two reef size classes (Table 3). As predicted, females have nearly identical time budgets on large and small reefs. An average female spends less than a minute in reproductive activity each day (means of 53 and 44 sec for small and large reefs, respectively). In contrast, initial phase males on large reefs spend an average of 28.5 min a day in spawning attempts. The equivalent males on small reefs spend virtually none of their time in reproductive activity (mean of 9.1 sec/day).

Outside of the spawning period all types

TABLE 6. A. Effects of male reproductive activity (measured in seconds/day) and female per capita daily mortality rate on male per capita daily mortality rate. B. Effects of male reproductive activity (measured in seconds/day) and female growth rate (mm/day) on male growth rate (mm/day).

	<i>d.f.</i>	Sum of squares	<i>F</i>	<i>P</i>	<i>r</i> ²
A. Model	3	.0013	3.95	.0294	.441
Male reproductive activity	1	.0000	.31	.5852	
Female death rate	1	.0011	9.62	.0073	
Interaction	1	.0002	1.91	.1877	
Error	15	.0017			
B. Model	3	.0266	13.60	.0003	.758
Male reproductive activity	1	.0073	11.12	.0054	
Female growth rate	1	.0163	25.04	.0002	
Interaction	1	.0030	4.65	.0505	
Error	13	.0085			

of individuals feed nearly constantly (Table 3). However, initial phase males on large reefs continue to display low levels of reproductive activity (Table 3).

Verification of Short-Term Responses in Time Allocation

Before we can safely ascribe differences in growth and survival to the effects of the time allocations displayed by the various groups, it is necessary to eliminate the possibility that males on large and small reefs are distinct genetic morphs that settle preferentially on particular reef types. If this were the case, then any long-term differences in growth and survival could conceivably represent evolved characteristics completely unrelated to their reproductive expenditures.

To ensure that I was dealing with a homogeneous population of males responding to a heterogeneous distribution of local sexual selection intensities, I transplanted initial phase males from large reefs to small, and vice versa. The results clearly show that males adjust their reproductive activity to the reef upon which they find themselves.

For 14 males transplanted to four small reefs, all had ceased their reproductive activity within two weeks (Table 4). Control individuals transferred to other large reefs showed an initial depression of breeding activity, but were reproductively active at a rate approaching that of residents by three weeks post-transplant.

The converse experiments had similar results (Table 5). When transplanted to large reefs, males from small reefs gradually increased their time spent in reproduction. Within 20 days of transplantation their activity budgets were comparable to resident males. Concurrent controls showed no changes.

Long-Term Effects on Survival and Growth

I now turn to the question of whether the short-term responses of a male's time budget have any effects on lifetime fitness. Since large territorial terminal phase males are highly successful at mating on all sizes of reefs (Warner and Hoffman, 1980a), smaller individuals should benefit by raising their probability of reaching terminal male status. This can be achieved by increasing survival during the initial phase, by growing at a faster rate and thus reaching large size more quickly, or both.

Upon removal of the effects of intrinsic reef differences (estimated by female death rates), there was no detectable relationship between the mortality rates of tagged males and time they spent in reproductive activity (Table 6A, Fig. 4). This is also apparent when reefs are classified into two size classes as before: mortality rates are essentially identical for males and females from both large and small reefs (Table 7).

Natural mortality rates for untagged

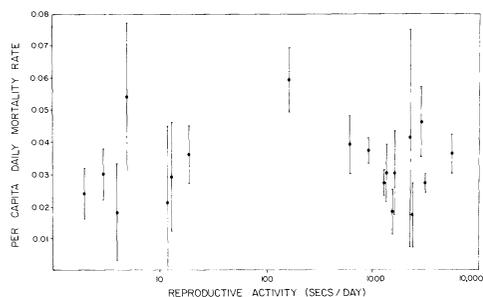


FIG. 4. Per capita daily mortality rates of initial phase males on each census reef relative to time spent in reproduction per day. The male mortality rate for each reef was normalized by the female rate (see Methods). Shown are means and their 95% confidence intervals based on weekly censuses of marked cohorts.

initial phase individuals were very similar on the two experimental reefs. After accounting for the transformations of some individuals to the terminal phase, the initial phase per capita daily death rates were .0034 and .0030 for the two reefs, about an order of magnitude lower than for tagged individuals (initial cohort sizes: 129 and 94 individuals; durations: 132 and 131 days).

In contrast to the survival results, the analysis of growth rates indicates that time spent in reproduction is associated with a substantial cost for initial phase males (Table 6B, Fig. 5). The significant curvilinear regression in Figure 5 suggests that a large reduction in growth occurs if males enter into reproduction, but the cost of time spent in reproductive activity beyond the initial investment may be minimal. When the reefs are divided into two size classes, it appears that males who avoid reproduction enjoy about a twofold increase in growth over those males who do not (Table 8).

DISCUSSION

As predicted, small males appear to reduce their reproductive efforts in response to the intensity of sexual selection, while females do not. Initial phase males are not reproductively active on small reefs, while they may spend over an hour a day in active pursuit of females

TABLE 7. Overall means for per capita daily mortality of tagged initial phase males and females on small and large reefs.

	N (Reefs)	Mean initial cohort size	Mean du- ration (weeks)	Mortality rate (daily) $\bar{x} \pm 1 \text{ SE}$
Small reefs	8			
Males		10.4	6.0	.033 \pm .005
Females		32.3	10.2	.032 \pm .008
Large reefs	11			
Males		25.8	12.7	.029 \pm .004
Females		33.2	11.0	.026 \pm .003

on larger reefs. The transplantation experiments demonstrate that these time budgets are short-term responses to the local environment rather than fixed behaviors. Of course, the existence of fixed behavioral morphs that settled onto reefs appropriate for their time budgets would not have invalidated the first prediction. However, it would have allowed the possibility that life-history differences are due to effects within the distinctive genotypes that are unrelated to time budgets. By ensuring that the male population is homogeneous, differences in allocations to reproduction can be assigned a more causative role in shaping life history.

The Cost of Reproduction

The longer-term studies indicate that initial phase males who forego reproduction grow significantly more rapidly than those who do not. This should have some adaptive value in increasing the probability of attaining terminal phase male status (see below). On the other hand, there appears to be little or no cost of reproduction in terms of survival. This was somewhat unexpected, since most of the predation events we have witnessed have been attacks on group-spawning aggregations (55 out of 64 recorded events). However, since these aggregations often consist of hundreds of individuals, the per capita rate of attacks received may be no higher than elsewhere.

The concave shape of the relationship between growth and reproductive activity (Fig. 5), combined with the linear in-

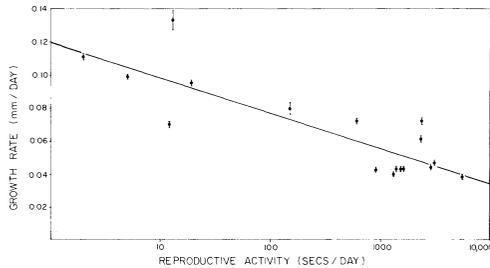


FIG. 5. Census reef means of initial phase male daily growth rates relative to time spent in reproduction per day. The male growth rate for each reef was normalized by the female rate (see Methods). Shown are means and their 95% confidence intervals of the growth rates of tagged individuals recaptured monthly. The growth rate was weighted by the duration of the available sample for each individual. The regression equation is $G = .1203 - .0213 \log S$, where G = growth rate and S = seconds in reproductive activity ($r = -.845$; significance of regression, $F_{1,15} = 15.52$, $P < .005$; slope different from zero, $t_{15} = 4.467$, $P < .001$). A linear regression of the same data was not significant ($F_{1,15} = 4.07$, $P > .05$).

crease in mating success with time spent in reproductive activity on large reefs (Fig. 2), suggests that males on larger reefs should spend the maximum amount of time possible in reproduction. The reasoning is identical to that of Schaeffer (1974) and Pianka and Parker (1975): when the initial cost of reproductive investment is large, but further investments incur only marginally more costs, then the investment should be maximized if it is made at all. In this case, the maximum time investment should be the total spawning period. Why do initial phase males spend only about a quarter of the spawning period in reproductive activity (Table 3)?

Initial phase males may not be active for the entire spawning period because females are not continuously available, so some foraging activities represent feeding with the spawning group at the mating site during intervals when no females were present. But most initial phase males that were followed spent time feeding away from the active mating site, and would join the group spawn for only a portion of the spawning period.

TABLE 8. Overall mean daily growth rates for initial phase males and females from large and small reefs. Each individual's growth rate was weighted by the duration of the available sample for that individual.

	<i>N</i> (Reefs)	Mean sample size (individuals)	Growth rate (mm/day) $\bar{x} \pm 1 \text{ SE}$
Small reefs			
Males	6	3.9	.1091 \pm .0234
Females	7	11.4	.0500 \pm .0110
Large reefs			
Males	11	14.3	.0483 \pm .0062
Females	11	15.2	.0519 \pm .0052

A reasonable (but by no means tested) explanation for this behavior is sperm depletion. Due to external fertilization, the extent of paternity accrued by a male in a particular group spawn is related to the proportion that his sperm makes up of the total sperm output of the participating males. This sperm competition is reflected in the very high testis weights of initial phase males (Warner et al., 1975; Warner and Robertson, 1978), and high sperm output per spawning is expected. It is possible that a male participates in as many spawnings as possible given his sperm supply that day, and then abandons that day's reproductive activity in favor of feeding.

If this is the case, then the relationship between growth rate and time in reproductive activity (Fig. 5) is easier to explain. The costs incurred by mating males would lie not so much in time spent away from feeding (which diminishes energy input), but in the expenditure of gametes (which increases energy output). Thus even males with short reproductive bouts may still be allocating a large proportion of their available energy to gamete production, and this allocation can be reflected in diminished growth. A study of the allocations of energy rather than of time could potentially give clearer results and resolve these questions, but the difficulties of measurement are enormous in this system.

A point that should be stressed about the growth and mortality study is that at no time was it assumed that males and females with similar time budgets should have similar growth or mortality rates. Energy allocation can be vastly different between the sexes. The relevant comparisons were between male groups differing in time budgets, controlled by comparisons between female groups with time budgets that were similar to each other. The fact that males and females on large reefs have quite similar life histories (Tables 6 and 7) suggests that both their current energy expenditures on reproduction and their prospects for future reproductive success are similar. Because initial phase males are in sperm competition, their energy output to gametes may well match that of females (see Fig. 1 in Warner et al., 1975). Also, since females in this species are fully capable of becoming terminal phase males, future prospects are likely to be similar as well.

The problem of distinguishing causation from mere correlation in the relationship between current reproductive output and retarded growth is not entirely solved in this study. Causation is strongly suggested, however, because (1) females acting as controls showed no relationship of growth or survival with reef size; (2) transplants indicate that male behavior patterns are short-term responses to the local environment; and (3) the local environments are naturally heterogeneous in the intensity of sexual selection, and thus the responses of small males are not experimental artifacts.

Reproductive Compensation

So far, we know only that the avoidance of reproduction by initial phase males on small reefs is potentially adaptive because increased growth should raise the probability of attaining terminal male status. But can these small males fully compensate for the early losses of reproduction? It is possible that these males are merely making the best of a bad situation, raising their fitness somewhat, but not to the level of males on large reefs.

The resolution of this question has importance, because it addresses a currently unexplained phenomenon: the frequency of initial phase males increases dramatically with reef size, from essentially none on reefs with less than 25 individuals to about 50% on the largest reefs (Warner et al., 1975; Warner and Hoffman, 1980a). One explanation is that the fitness of primary males on small reefs is low, and they avoid them, if possible, while settling (Warner et al., 1975; Warner and Robertson, 1978). The few males unable to do this comprise the low frequencies found on small reefs. An alternative explanation proposes that each local reef is in an evolutionary stable state (Charnov, 1982a, 1982b). In the latter scenario, the proportions of males on various reefs have been set by specific settlement choices or through locally influenced sex determination, and the fitnesses of all males are equalized. That is, initial phase males on small reefs should fully compensate for lost early reproduction through growth.

If one assumes that the population is not growing or declining, the net reproductive rate, R_0 , is an adequate measure of fitness. It is simply the sum of the expected reproduction at every age, i.e., the summation of each age's fecundity multiplied by the probability of living to that age (Mertz, 1970). For comparisons among male types, a similar measure can be calculated in which each age's expected mating success is weighted by the appropriate expectation of survival. A primary male's reproductive life can be divided into four stages (Table 9). For initial phase males, reproductive activity can begin at about 35 mm in size, and individuals transform to the terminal phase at about 75 mm ($\bar{x} = 75.02$ mm, $N = 57$ tagged individuals). Terminal phase males are nonterritorial to begin with, and they engage in little reproductive activity. At about 95 mm, they begin to sporadically defend territories in marginal breeding sites, and accrue a small amount of mating success. Only after the attainment of quite large size (> 100 mm)

TABLE 9. Estimated life history parameters for mature primary males on small and large reefs.¹

Male stages	Size range (mm S.L.) (<i>l</i>)	Daily mating success (pair-spawn equivalents/day) (<i>b</i>)	Growth rate (mm/day) (<i>g</i>)	Per capita daily death rate (<i>q</i>)	Duration in days (<i>D</i> = <i>l/g</i>)	Expected mating success in stage $\sum_{x=0}^D (1 - q)^x b$	Probability of survival to next stage $(1 - q)^D$	Mating success discounted by expected mortality	
								Large reef ♂♂	Small reef ♂♂
<i>Initial phase</i>									
Small reefs	35-75	0	.109 (27)	.0032	367	0	.31		0
Large reefs	35-75	1.34	.048 (129)	.0032	833	387	.07	387	
<i>Terminal phase</i>									
Nonterritorial	75-95 (57)	.28 (18) (35 days)	.074 (46)	.0062 (39)	270	37	.19	3	11
Sporadically territorial	95-100 (12)	3.70 (12) (23 days)	NA	.0129 (9)	68	165	.41	2	10
Permanently territorial	>100 (21)	25.21 (44) (218 days)	NA	.0109 (28)		2,287		<u>12</u>	<u>55</u>
						Expected lifetime mating success of a newly mature male		= 404	76

¹ The initial phase male mortality rate is assumed to be similar on all reefs and equal to the mean rate measured for untagged individuals (see text). The growth rate of sporadically territorial terminal phase males was not measured, and for the purposes of computation was assumed to be equal to non-territorial terminal phase males. Many of the mortality rate data for terminal phase males were supplied by M. Schildhauer (pers. comm.). The last two columns represent the expected mating success in successive male stages, viewed from the perspective of a newly mature primary male. These quantities are calculated by multiplying the expected mating success within a particular stage by the cumulative probability of surviving to reach that stage. For example, a primary male on a small reef expects to have a mating success of 165 spawnings during its sporadically territorial stage, but has only a .06 (= (.31)(.19)) probability of surviving to that stage. Thus the discounted expectation is 10 spawnings (= (.06)(165)). Estimates are based on the number of individuals shown in parentheses. NA = data not available.

does an individual secure and maintain a highly successful territory.

Although initial phase males on small reefs are about four times more likely to attain terminal phase by virtue of their increased growth, they do not appear to be able to fully compensate for losses in early reproduction (Table 9). In fact, initial phase males on large reefs have about five times the expected mating success as that of equivalent males on small reefs.

Using ESS arguments, the frequency of initial phase males has been predicted quite accurately for the species overall (Warner and Hoffman, 1980a), and for large reef populations where males and females grow and die at similar rates (Charnov, 1982a). Charnov (1982a, 1982b) has also provided a formula which predicts the ESS frequency of primary males on small reefs, where their advantage lies only in increased growth or sur-

vival. If a male is α times more likely to reach terminal phase than a female, a stationary population has an ESS frequency P of initial phase males, where

$$\frac{P}{1 - P} = 1 - 2/\alpha \quad (\alpha \geq 2).$$

Since the growth and mortality of females on all reefs is similar to that of males on large reefs (Tables 7 and 8), we can use Table 9 to calculate that $\alpha = .31/.07 \sim 4$. This gives a predicted P of .33, about three times as high as the actual value of .10 on the small reefs used in this study ($N = 8$, $SD = .04$, range .04-.15).

These calculations are based on field estimates, and so are subject to problems of compounded errors, but the differences in reproductive expectations are so large that it is unlikely that all reefs are in an evolutionary stable state. The differences also suggest why so few primary

males are found on small reefs. However, when primary males do settle where the intensity of sexual selection is high, they can substantially increase their fitness by avoiding reproduction while small and thereby attain dominant male status more quickly.

SUMMARY

In the bluehead wrasse *Thalassoma bifasciatum*, small reefs are characterized by a large amount of sexual selection: larger, older males have complete control of the spawning sites. On larger reefs, the population density at the mating site is such that large males cannot monopolize mating. Several hypotheses in behavioral ecology suggest that when return for reproductive effort is low, and the rewards of attaining large size are great, individuals should postpone reproduction and direct energy into survival and growth. In accord with the prediction, smaller males on small reefs spend much less time in reproduction than do equivalent males on large reefs, and females show no differences. The behavior was experimentally shown to be a short-term response to local conditions. The same hypotheses assume that time spent in reproduction carries a cost in reduced growth and/or mortality. Through long-term marking, censusing, and recapture, it was determined that (i) no differences in mortality are detectable and (ii) males on small reefs grow about 100% faster than males on large reefs, while females, acting as controls, again show no differences among reefs. This is the first direct demonstration that deferred reproduction can result in a more rapid attainment of a successful reproductive size. The increased growth and rapid approach to large size by males on small reefs do not appear to fully compensate for losses in early reproduction, and these males may simply be making the best of a bad situation.

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