

VARIATION IN COMPONENTS OF REPRODUCTIVE SUCCESS IN AN  
UNDERSATURATED POPULATION OF CORAL-REEF DAMSELFISH:  
A FIELD PERSPECTIVE

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Researchers have recently been greatly interested in reconciling the coarse population-level processes that concern population biologists with the more subtle processes affecting the behavior and reproductive success of individuals (e.g., Abrams 1984, 1986; Smith and Sibley 1985; May and Seger 1986). Historically, these processes have been kept separate in part because they function with quite different currencies. Population dynamics are determined simply by the net loss or gain of individuals (primarily through births or deaths), whereas many ecological and evolutionary processes are based on small differences in the reproductive success of living individuals and the resulting natural selection. Factors that limit the size of populations usually do influence the reproductive success of individuals, especially in populations regulated by resources. However, in large open populations regulated by disturbances or recruitment, factors that affect the reproductive success of individuals can often have little or no effect on the overall population size. For situations in which the factors operating at the population and individual level are not directly concordant, it is especially important to define and clarify their effects, particularly when knowledge of ecological processes is used to infer evolutionary processes.

Coral-reef fishes provide a good example of different factors operating at the population and individual level and the confusion that follows from not decoupling their effects. Observations of behavioral and morphological specializations among coral-reef fishes have led some researchers to presume that resources must generally be in short supply and, extrapolating to the population level, to reason that populations were at carrying capacity (the maximum number of reproductive individuals sustainable on the resources available). It was assumed that competition for these limited resources resulted in the specializations they observed, regulating both population sizes and individual reproductive successes (see, e.g., Smith and Tyler 1972, 1975; Luckhurst and Luckhurst 1978). This view was derived from one of the original assumptions of competition theory, which held that populations must be at an equilibrium directly determined by the supply of resources (MacArthur and Levins 1967; reviews in Wiens 1977; Grant 1986).

Recently, however, it has become apparent that some reef fish populations are generally undersaturated (below carrying capacity) as a result of chronically low rates of settlement of planktonic larvae (Williams 1980; Doherty 1983; Victor 1983, 1986; Wellington and Victor 1985). Within these extreme examples of recruitment-limited populations, resources may not be sufficiently scarce to affect mortality rates significantly, and population sizes may often be simply a direct product of the input of settling larvae. (Recruitment limitation requires not that there be zero density dependence in mortality rates, but rather that the rate of recruitment is a more important determinant of subsequent population sizes; Victor 1986.) Whether some individuals within these recruitment-limited populations consistently obtain different qualities or quantities of resources, which could eventually lead to niche specialization within a species or niche partitioning between species, has yet to be determined.

In this paper we discuss how the distribution of resources may affect the dispersion of populations of a single species, and how these patterns may lead to predictable variation in the reproductive success of individuals, even when populations are undersaturated (of course, we exclude the variation in reproductive success arising simply from sexual competition for mates). In support of our arguments, we document patterns in the distribution and abundance of a species of damselfish on a reef where the population appears to be limited by the availability of recruits. Results from removal experiments indicate that intraspecific competition for locally superior resources can lead to high variation in reproductive success, even though a surplus of less-preferred resources exists in adjacent areas. We believe that this approach to investigating questions of population and community ecology on coral reefs may be more helpful, especially from a field perspective, than the traditional approach of addressing questions from either an individual level or a population level alone. The data are presented primarily to confirm that a protocol such as ours is needed for more-integrative studies of coral-reef communities.

#### RESOURCE DISTRIBUTION AND VARIATION IN REPRODUCTIVE SUCCESS

How individuals in a population are distributed with respect to their resources depends on both the accessibility (the absence of barriers) and supply (quantity present) of the resource. When resources vary in their supply and are equally accessible, local population distribution reflects the supply of the resource and reproductive success varies little among individuals in the population (ideal free distribution). However, when resources vary in supply, either in quantity or quality, and are not equally accessible, reproductive success may vary greatly. This condition may result from the partitioning of heterogeneous habitats by behavioral interactions (territoriality) or by isolation (usually physical barriers limiting emigration and immigration) (fig. 1).

Under an ideal free distribution (Fretwell and Lucas 1970; Whitham 1980), individuals occupy habitats of the highest quality; but as the population density increases, the expected reproductive success of individuals in lower-quality habitats eventually equals that of those in the previously higher-quality habitats,

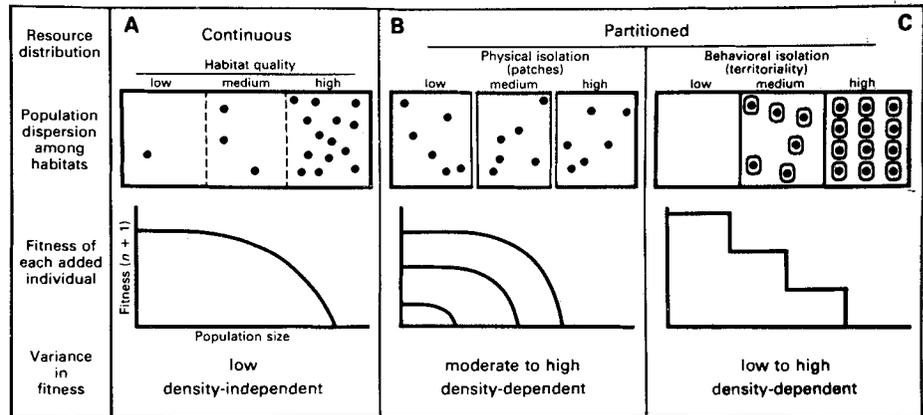


FIG. 1.—Predicted patterns of population dispersion, changes in fitness with population size, and variance of fitness for individuals with either continuous or partitioned resources. Patterns of population dispersion (upper panels) depict the distribution of individuals in an intermediate-sized population where movement between habitats is *A*, free (dashed vertical lines); *B*, partitioned by physical isolation (panels separated by vertical lines); and *C*, partitioned by behavioral isolation (single vertical lines between adjacent habitats). *Solid dots*, individuals; *open circles*, territorial limits. Fitness curves represent the effect of population size on fitness, in terms of reproductive success, of each added individual in these heterogeneous environments. *B*, The fitness curves show expected individual fitness as a function of population size in the three physically isolated patches. In this panel, changes in individual fitness in the low- and high-quality patches are represented by the curves nearest to and farthest from the origin, respectively.

and more individuals then begin to occupy lower-quality habitats. Population densities across habitats should adjust until individuals have approximately equal reproductive success (fig. 1). More-recent theoretical treatments of the concept of an ideal free distribution have demonstrated that if individuals are not considered equivalent in their abilities to garner resources, variation in individual success can arise within habitats even if the mean success among habitats is equal (as predicted by the original model for ideal free distribution). Differences in foraging efficiency or competitive abilities can contribute to variation in success even when individuals can move freely between patches of varying quality (Parker and Sutherland 1986). According to this view, the exclusive territoriality exhibited by damselfishes is an extreme case of differences in the competitive abilities of individuals enhancing the variation in success to a level comparable to physical separation of habitat patches.

Partitioning of heterogeneous resources, enforced through physical or through behavioral mechanisms, can lead to high variation in reproductive success among individuals in the population (fig. 1). Physical partitioning can occur if resources are distributed as discrete patches and are maintained as long as residents have low rates of immigration and emigration. The between-patch variation in reproductive success among individuals depends on two factors: the population sizes

and the differences in resource quality, particularly for species exhibiting a pattern of ideal free distribution within patches.

Behavioral partitioning through territoriality can also lead to high variation in reproductive success in an environment where resources vary in quality. Free access to resources is restricted by aggression, and the density within a habitat is limited by the number of territories it can support. If we assume that the quality of territories within habitats does not vary, individual reproductive success varies only across habitats and is proportional to the inequity of resources between habitats (Brown 1969). If territories were compressible or intruder pressure were sufficiently costly to the territory holders as density increased, then the quality of good habitats could be compromised to the point where reproductive success may vary little or not at all between habitats (functionally approaching an ideal free distribution; Schoener 1971). Within-habitat variation in reproductive success may occur when less successful nonterritorial individuals are able to coexist within the habitat (e.g., Riechert 1981).

#### BEHAVIORAL PARTITIONING IN THE ACAPULCO DAMSELFISH

The Acapulco damselfish, *Stegastes acapulcoensis*, is one of the most abundant resident fishes on coral reefs in the eastern tropical Pacific and provides a clear example of the behavioral partitioning discussed above.

The study site is a shallow fringing reef (1–12 m in depth) on the southwestern corner of Contadora Island (Perlas Archipelago) in the Gulf of Panama (8°37'23"N; 79°02'31"W). The reef (3 ha in extent) overlies a series of juxtaposed sandstone ridges running parallel to the shoreline, with coral development extending to 100 m offshore. Dead and live colonies of the branching coral *Pocillopora damicornis* (Anthozoa: Scleractinia) contribute 80%–85% of the cover. A more complete physical and biological description of the study site can be found elsewhere (Wellington 1982).

The Acapulco damselfish, like most benthic damselfishes, is largely herbivorous and highly territorial, and it cultivates mats (or gardens) of algae on rock and dead-coral surfaces. The territories of both sexes include a defended area about 1 m in radius from the algal mat, which covers about 0.25 m<sup>2</sup> (Wellington 1982). Damselfish defend their algal mats against intrusion by other grazers. Since defended areas outside the mats are shared by conspecifics, the potential maximum population size is determined by the total number of sites for algal mats (with adjacent shelter sites) rather than by the number of entire territorial areas available (i.e., the algal mat and adjacent defended areas) that could fit in the available habitat.

In addition to providing food, the territory also functions as a shelter from predatory fish and serves as a nesting site for males. Females attach their eggs to the algal mat of the male where they are brooded and guarded against egg predators for a number of days. Upon hatching, larvae disperse into the plankton and after a period of weeks return to the reef, where they settle in or adjacent to habitats occupied by adults.

### *Sampling Methods and Experimental Procedures*

Densities of coral cover were estimated along linear transect lines placed parallel to depth contours on the reef flat and slope. The proportions of living- and dead-coral substrates were calculated from the linear distances covered by each substrate in contact with a 30-m fiberglass tape that was draped over the substrate. Transect surveys conducted in 1979 (before El Niño) were compared with those taken in November 1984 and December 1985 (after El Niño).

Since adult damselfish maintain discrete, nonoverlapping algal mats (one mat per fish), densities were estimated by counting the number of algal mats that occurred partly or entirely within a band 0.5 m on either side of the transect line (Wellington 1982). Recently settled juveniles ( $\leq 20$  mm standard length), which were easily spotted because of their bright blue coloration, were counted along these same transect lines.

We visually estimated the standard lengths of all damselfish encountered along a transect line passing through the shallow habitat (1–2 m in depth) and a transect line through the deep habitat (7–10 m in depth). Initially, 20 fish were measured in this manner, then speared and measured with a rule, showing that our visual technique was accurate to within  $\pm 5$  mm in standard length. To compare gonosomatic indexes of female damselfish from deep and shallow habitats, we speared a series of adult damselfish from each habitat. Each fish was weighed, measured, and dissected. Sampling was conducted over a period of 3 wk during the peak period of reproduction (D. Robertson, pers. comm.). We detected no differences in the degree of maturity of female gonads between fish in deep-water and shallow-water habitats during the sampling period.

To test whether fish competed for territories, we removed the damselfish from three 10-m<sup>2</sup> quadrats at both shallow-water and deep-water sites. The territory of each damselfish within the quadrats was mapped, and most of the resident damselfish were subsequently speared, removed, measured, and weighed. After 48 h, the number of damselfish that had relocated into the cleared quadrats was recorded.

### *Results and Interpretation*

What is the evidence that populations of *Stegastes acapulcoensis* exist below their carrying capacity? The unusually intense 1982–1983 El Niño oceanographic event resulted in higher than average sea surface temperatures that led to massive mortality of reef corals in the eastern Pacific (Glynn 1984). Before 1982 a negative correlation between the percentage of cover of the predominant coral, *Pocillopora damicornis*, and damselfish abundance indicated that in some areas the local abundance of damselfish was limited by live-coral cover (Wellington 1982). Damselfish apparently cannot maintain an algal mat on the skeleton of living colonies of this coral, even though topographic complexity at high coral density is generally adequate to meet their requirements for shelter (Wellington 1982). Since damselfish can readily establish algal mats on dead-coral surfaces (Wellington 1982), the die-off resulting from the El Niño event represented a substantial increase in available resources.

TABLE 1

POPULATION DENSITY OF THE ACAPULCO DAMSELFISH, *STEGASTES ACAPULCOENSIS*, AND THE PERCENTAGE OF LIVE-CORAL COVER AT CONTADORA REEF, PANAMA, FROM CENSUSES BEFORE AND AFTER THE EL NIÑO SOUTHERN OSCILLATION

	Before El Niño, 3/79 (n)	18 mo after El Niño, 11/84 (n)	30 mo after El Niño, 12/85 (n)	P (Kruskal-Wallis)
Population density (per m <sup>2</sup> ) of <i>S. acapulcoensis</i>	0.35 ± 0.04 (12)	0.42 ± 0.03 (17)	0.39 ± 0.05 (10)	>0.20
% live-coral cover	79.8 ± 13.4 (8)	3.9 ± 1.9 (11)	4.6 ± 2.5 (10)	<0.001

NOTE.—Values are means ± 1 standard error of the mean with sample sizes representing 30-m<sup>2</sup> transects. Data indicate no short-term or longer response in fish abundance despite a large increase in available resources.

Comparisons of damselfish densities before (1979) and after (1984, 1985) El Niño showed that despite a nearly fivefold increase in substrate available for territories with algal mats (i.e., dead-coral surfaces surrounded by high topographic complexity), the overall population density did not increase significantly (Wellington and Victor 1985). Additional data collected at the end of 1985, some 30 mo after the death of corals, indicate that the damselfish population density still had not increased significantly, despite the continued low cover of live coral (table 1). It appears, then, that these damselfish populations may exist chronically below carrying capacity. Probably, sufficient time has elapsed for a numerical response to this augmentation of resources to have occurred, since these damselfish have high fecundity (several thousand eggs per clutch), reproduce several times over an extended season, and produce larvae that spend only about 1 mo in the plankton (pers. obs.).

The lack of a response to a fivefold increase in the supply of resources, combined with the paucity of newly settled recruits in censuses taken during the peak recruitment periods of 1984 and 1985 (0.01 recruits per square meter ± 0.005 standard error of the mean [SEM],  $n = 10$  10-m<sup>2</sup> transects, and 0.02/m<sup>2</sup> ± 0.006 SEM,  $n = 10$ , respectively) and a size-class frequency distribution skewed toward larger and older individuals (fig. 2), clearly suggests that these populations are limited by recruitment rates.

Do the resources used by individuals in this population vary predictably in their quality, and if so, do these qualitative differences result in variable reproductive success among individuals? Although damselfish are distributed over the entire reef from -1 to -12 m in mean lower low-water depth, densities in shallow-water habitats (mean = 0.6 individuals per square meter at -1 to -6 m) are twice that of the reef slope (0.3/m<sup>2</sup> at -6 to -10 m) and six times that at the reef base (0.1/m<sup>2</sup> at -10 to -12 m). In the shallower habitat, the ratio of adults to juveniles is greater than on the reef slope, and adults are 20% larger (table 2; fig. 2). In addition, the gonosomatic index ([wet gonad weight/wet body weight] × 10<sup>2</sup>) of females is significantly higher in shallow-water populations than in deep-water

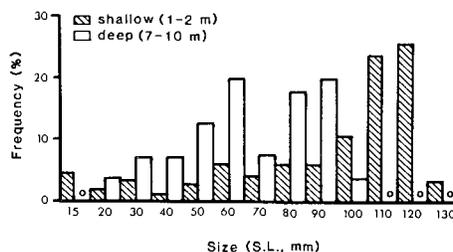


FIG. 2.—Size-frequency distribution of the Acapulco damselfish, *Stegastes acapulcoensis*, at shallow- and deep-water sites at Contadora Reef, Panama. These data were collected on December 15, 1985, 30 mo after 1982–1983 El Niño. The mean standard lengths (SL) in millimeters are  $100.8 \pm 3.6$  standard error of the mean (SEM),  $n = 84$ , and  $74.0 \pm 2.8$  SEM,  $n = 55$ , for shallow- and deep-water populations, respectively (Wilcoxon two-sample test with continuity correction,  $z = -5.67$ ,  $P \ll 0.0001$ ).

TABLE 2

POPULATION PARAMETERS FOR THE ACAPULCO DAMSELFISH, *STEGASTES ACAPULCOENSIS*, IN SHALLOW- AND DEEP-WATER HABITATS AT CONTADORA, PANAMA, COLLECTED IN DECEMBER 1985

Depth	Adult:Juvenile Ratio (n)	Adult Size (n)	Female Gonosomatic Index (n)
Shallow (1–2 m)	4:1 (84)	$115.1 \pm 1.88$ (67)	$3.7 \pm 0.004$ (11)
Deep (6–8 m)	1:1 (55)	$92.2 \pm 0.97$ (28)	$2.9 \pm 0.004$ (11)
<i>P</i>		$<0.001$	$<0.05$

NOTE.—Adult size is the standard length in millimeters. The female gonosomatic index is (gonad weight/gutted weight)  $\times 10^2$ . Values for body size and the gonosomatic index are means  $\pm 1$  standard error of the mean. Probabilities are based on the two-tailed *t*-test statistic. Sizes were transformed to natural logs to obtain homogeneous variances.

populations (table 2). These differences in components of reproductive success may be due to the higher productivity of shallow-water algal mats. Important qualitative differences in the algal species composition may also exist. A study of the Caribbean three-spot damselfish (*S. planifrons*) reported not only that shallow-water territories contain a higher algal biomass than territories on the reef slope, but also that shallow-water territories are dominated by preferred filamentous green and red algae that are largely absent from the deep-water territories (Brawley and Adey 1977). Although we did not sample the algal mats, our observations indicate that the density of the preferred red and green filamentous algae is much higher in the shallow-water mats than in mats in deeper water. The lower densities and smaller sizes of damselfish in the deep habitat may also be a product of higher predation rates. Although this would not account for

TABLE 3  
RESULTS OF DAMSELFISH-REMOVAL EXPERIMENTS AT CONTADORA REEF

Depth and Replicate No.	No. Present	No. Removed	Size	No. Replaced after 48 h	% Recovery
Shallow (1-2 m)					
1	20	18	114.2 ± 11.3	16	89
2	12	8	110.9 ± 14.5	7	87
3	13	10	108.2 ± 7.9	6	60
Deep (7-10 m)					
1	8	5	84.7 ± 9.8	1	20
2	8	5	74.4 ± 5.5	0	0
3	9	8	75.6 ± 17.8	0	0

NOTE.—Territory-holding individuals were removed from 10-m<sup>2</sup> areas. Size is the standard length ± 1 SD, in millimeters.

the observed differences in gonosomatic indexes, it could certainly be a contributing factor to the lowered quality of deep habitats.

It should be emphasized that despite the apparently depth-related differences in habitat quality, the deep habitat is still quite adequate for damselfish growth and reproduction. Indeed, our collections indicate that although adults may be smaller in the deep habitat, they reached sexual maturity at about the same size (67.5–70.0 mm in standard length in shallow habitat vs. 69.8–74.7 mm in standard length in deep habitat) and continued to be reproductive into adulthood (table 2).

In areas that were cleared of damselfish, conspecific adults at shallow-water sites replaced the damselfish almost completely and usually within 24 hours, whereas at deep-water sites, removals were followed by few or no replacement individuals of any size (table 3). Thus, it appears that competition for territories exists in shallow water but not in the deeper habitat. The replacements observed at shallow-water sites were adults that appeared to have relocated from areas adjacent to the removal sites. Even though the removals were conducted during the peak recruitment season (Wellington and Victor 1985), no larvae or small juveniles were observed recruiting to the cleared sites. These results not only suggest the presence of competition for apparently higher-quality sites in shallow water but also provide some further evidence that resources do not limit population size. If the population were limited by resources, we should have also observed replacements at deep-water sites, at least small juveniles ready to establish a territory (juvenile damselfish typically move into territories as they grow larger).

#### DISCUSSION

Although numerous population studies of coral-reef fishes have been conducted (many of which are primarily concerned with potential interspecific interactions), few have attempted to correlate patterns in the dispersion of individuals within a population in relation to resource abundance or quality. We found no reports for or against the existence of ideal free distributions, although the candidates most

likely to conform to this pattern would be large, free-ranging species such as predators or planktivores whose food resources are not easily defended.

For several reasons we believe that patterns of dispersion in reef fish populations probably reflect either physical or behavioral partitioning of resources. Physically, coral reefs are a mosaic of patchy environments. Patchiness can exist over a distance as small as that between adjacent coral colonies or as great as that between reef systems separated by thousands of miles. Probably in response to this patchiness, virtually all coral-reef fishes have a widely dispersing planktonic larval stage, during which they are capable of settling onto reefs some distance from the parental population. After settlement, however, most reef fish do not move far and avoid migrating across open spaces where they are vulnerable to predation. As a result, coral-reef fishes are divided into isolated yet open subpopulations (by "open" we mean the source of recruitment to local populations comes from planktonic immigration and is mostly, if not entirely, independent of local stock). If the quality of the patches occupied by these subpopulations is variable, this system can provide the opportunity for high and predictable variation in reproductive success within the overall population simply as a product of physical isolation. This inequity would be maintained as long as larvae continue to settle into habitat patches of unequal quality. Studies on habitat selection by juvenile coral-reef fishes indicate that settlement does occur at a variety of habitats of different quality (Thresher 1983; Sale et al. 1984; Sweatman 1985; Victor 1986).

Many sessile marine invertebrates have much in common with coral-reef fish populations. They share a widely dispersing larval phase, and their populations are similarly divided into open subpopulations physically isolated into habitat patches that may confer varying reproductive success on their occupants (e.g., Keough 1984*a,b*; Gaines and Roughgarden 1985). Roughgarden and Iwasa (1986) have modeled the population dynamics of a metapopulation composed of subpopulations in which settlement is a function of the proportion of available space (called a "space-limited" population, although there is a surplus of free space and physical factors control the actual rate of settlement, which is the major determinant of population size in the barnacles upon which the model is based; Gaines and Roughgarden 1985; Gaines et al. 1985). This system is somewhat analogous to that of damselfish; however, reef fish do not appear to have the added complication of density-dependent settlement rates (Doherty 1983; Victor 1983). Nevertheless, the occurrence of physically partitioned subpopulations with varying reproductive success may be more the rule than the exception for patchily distributed marine organisms.

Behavioral partitioning of habitats through territoriality is also particularly characteristic of coral-reef fishes. Territoriality is especially common among herbivorous reef fishes, presumably because of intense grazing pressure in shallow-water habitats (Randall 1961; Sammarco et al. 1974; Vine 1974; Hay 1981; Hixon and Brostoff 1983). Our removal experiments indicate that for Acapulco damselfish, habitats of higher quality are saturated with territorial individuals. The rapidity with which these territories are reoccupied following the removal of residents further suggests that competition for high-quality sites is intense, even

though large areas of less-preferred habitat (although certainly adequate for reproduction) are available. Myrberg (1972) and Itzkowitz (1977, 1978) have demonstrated that, within a species, damselfish territories are distributed on the basis of a size-mediated dominance hierarchy. In addition, Jones (1987) has recently shown that the juveniles of an Australian damselfish, on experimentally manipulated artificial patch reefs, experience reduced growth rates in the presence of conspecific adults and when juvenile density is increased.

Other removal experiments have yielded similar results. To test for habitat specificity, Waldner and Robertson (1980) performed several sequential removals of *Stegastes dorsopunicans* adjacent to habitats dominated by a closely related congener, *S. planifrons*. They observed rapid replacements (within 24 h) by *S. dorsopunicans*. The new residents were, however, significantly smaller, suggesting that better territories were held by larger individuals. The larger fish were found in elkhorn-coral habitat in high densities, whereas smaller individuals occupied low-density and presumably less-preferred habitats. Furthermore, large expanses of habitat that the authors presumed suitable below a depth of 10 m were only sparsely occupied by small damselfish. Along a similar line, Brawley and Adey (1977) reported that territories of *S. planifrons* were contiguous in shallow water but separated by some distance in deeper areas of the reefs. It has also been demonstrated that some habitats containing adult *S. planifrons* do not appear to be saturated. Robertson et al. (1981) removed half the volume of some small patch reefs and found that displaced damselfish relocated to the remaining half and established new territories without apparent loss in any components of reproductive success. It thus appears that the distribution of individuals within populations of several of the common damselfish species in the Caribbean and eastern Pacific regions may be determined by intraspecific territorial interactions, even though overall population sizes are below the carrying capacity of the entire habitat.

Variation in reproductive success imposed by physical or behavioral partitioning of habitats could, under some circumstances, have important effects on the evolution of a species. If certain genotypes are predictably associated with habitats of a particular quality (Underwood et al. 1983), variation in reproductive success will be translated into differing fitness, and assuming that the traits are heritable, an evolutionary response should occur. The action of selection on populations physically divided into isolated habitats would tend to promote habitat selection or any niche specialization associated with habitats that confer higher reproductive success (e.g., parasites that specialize on hosts to promote the probability of finding mates; Rohde 1979). Without the physical isolation of habitats, the advantages of selecting better habitats would be diluted by migration, and ultimately habitat selection would not be advantageous (ideal free distribution). In behaviorally partitioned populations, strong selection for traits associated with aggressiveness or territory-holding ability could occur. Although our study has dealt exclusively with interactions within a species, the concepts can be extended to interspecific interactions as well. Rates of coevolution among interspecific competitors might also be influenced in an analogous manner. If the quality of habitats is determined by the presence or absence of another species, then selection for habitat selection and other specializations could result in in-

creased niche displacement and niche partitioning (Jackson 1977; Grosberg 1981; Keough 1984b).

These results have implications for the current controversy over the factors that structure communities of coral-reef fishes. The traditional view among coral-reef fish ecologists emphasizes the role of competition and niche partitioning (reviewed in Roughgarden 1986). Whereas the preponderance of evidence to date strongly suggests that populations of coral-reef fishes are typically well below carrying capacity (Williams 1980; Doherty 1983; Victor 1983, 1986; Wellington and Victor 1985), there is no such consensus on whether competition for resources has played a role in the evolution of coral-reef assemblages. A number of studies have concluded that particular groups of reef fishes exhibit some niche partitioning (Roughgarden 1974, 1986; Anderson et al. 1981; Gladfelter and Johnson 1983; Ebersole 1985), but other workers have either taken issue with these interpretations (Sale and Williams 1982; Findley and Findley 1985) or documented other groups of reef fishes that clearly do not display niche partitioning (Roughgarden 1974; Sale 1977, 1978).

Studies of community ecology have often implicitly linked individual processes with population dynamics. In our view, theories dealing with competition and the evolution of specialization and niche partitioning require not that populations be at their carrying capacity, but only that the reproductive success of individuals show a predictable variation associated with habitat quality. To gain a complete ecological and evolutionary understanding of the mechanisms that structure and organize communities (particularly in the marine environment), future studies should be designed to clarify and separate the contributions of individual and population processes.

#### SUMMARY

The main issue we have attempted to address in this paper is whether resource-based variation in reproductive success (excluding competition for mates through sexual selection) among individuals in a population necessarily arises only when populations approach their carrying capacity. We describe conditions under which differential reproductive success can develop within and between local populations even when available resources do not limit overall population size. We contend that if resource quality varies spatially and predictably, as is probably the case for most natural systems, then significant variation in the reproductive success of individuals can arise through behavioral mechanisms (territoriality) or through physical isolation. Behavioral mechanisms could result in selection for attributes to enhance competitive ability; isolation should promote habitat selection and concomitant specializations.

In support of our argument, a study of a territorial coral-reef damselfish, *Stegastes acapulcoensis*, in Panama shows that significant habitat-related differences in the components of reproductive success (body size and female gonad size) can occur in a population limited by recruitment. In areas cleared of damselfish, conspecific adults rapidly and almost completely replaced damselfish at shallow-water sites, where components of reproductive success are high. In

contrast, at deep-water sites, where these parameters are lower, few or no replacement individuals of any age moved in after removals. We interpret these results as evidence for the existence of intraspecific competition in a population whose size is not limited by resources.

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