



Numerical and Energetic Processes in the Ecology of Coral Reef Fishes

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I. Introduction

One of the most fundamental tasks in ecology is to explain why populations behave the way they do (Royama, 1992). Despite many years of research on population dynamics there is little consensus, not only over the answer to this question, but also as to exactly what the question is (Turchin, 1995, 1999; Wolda, 1995; den Boer and Reddingius, 1996; Murray, 1999). When populations are highly variable, researchers will naturally ask why they vary (Sissenwine, 1984). If they remain relatively constant, it is more likely that they will ask why they do not vary (Lack, 1954). In the rarer instances when populations exhibit cycles of abundance, then the challenge is to determine what generates

regular fluctuations (Boonstar *et al.*, 1998). The exact question we ask and our initial assumptions can have profound effects on the research programs that we establish, the variables we measure, and ultimately the processes we identify as important. Although population ecologists broadly seek an explanation of numerical patterns, the underlying processes may at first sight have very little to do with numbers at all. A comprehensive explanation of numerical patterns will require an assessment of all the processes that act directly or indirectly to determine the number of individuals in the population.

The lack of consensus among population ecologists is illustrated by the emergence of opposing schools of thought over the processes that regulate population numbers (Krebs, 1985). In historical context, dichotomous views highlight the search for generalizations based on single factors and the ultimate failure to find them. In hindsight, they serve to illustrate the variety of antagonistic processes that may be acting on populations at any one time. The first dichotomy in population ecology involved the existence and importance of density-dependent population regulation, a debate that continues to this day (see Murray, 1999; Sale and Tolimieri, 2000). It initially involved the dichotomy between researchers arguing that insect populations are limited by climatic or other density-independent factors (Andrewartha and Birch, 1954) and those arguing that they are regulated by density-dependent biotic interactions such as competition (Nicholson, 1954). Later, another dichotomy developed over whether intrinsic or extrinsic mechanisms are involved in the regulation of animal populations (Lidicker, 1978; Tamarin, 1983; Wolff, 1997). Intrinsic mechanisms that may regulate populations include territoriality, dispersal, and reproductive suppression, which reduce population growth

before extrinsic factors start operating. Alternatively, populations may be regulated by extrinsic factors that are external to the population, e.g., resource limitation, predators, disease, and weather. A more recent dichotomy has concerned the processes limiting demographically "open" populations that are linked by long-distance dispersal. The traditional view is that regional population size is limited by biological interactions occurring "within" populations. The more modern counterargument holds that they are limited by the supply of juveniles that have dispersed from other source populations (Roughgarden *et al.*, 1987). Although new alternative theories can expand our views and result in a flourish of research from both supporters and detractors, the resulting dichotomies unnecessarily polarize opinion over what are not essentially mutually exclusive processes.

None of the variations on the search for a single, all-encompassing explanation of what determines population numbers has been successful. Population ecologists now speak in terms of "pluralism" and the relative importance of many different processes (e.g., McIntosh, 1987; Olafsson *et al.*, 1994; Wolda, 1995; Caley *et al.*, 1996; Osenberg and Mittelbach, 1996; Schmitt *et al.*, 1999; Turchin, 1999). There are many processes that cause numbers to increase and many others that cause numbers to decline. A combination of processes may act to bring about stasis, while others will act to bring about change. Different factors may be important at different life history stages and different factors may operate over different spatial and temporal scales. Some processes may act directly and have immediate effects on the "quantity" of individuals in the population. Other processes act on population "quality," but in doing so, indirectly impact on population numbers in the future. That is, current population size and trends may not just be a product of current ecological processes, but may represent the lagged effects of historic conditions (Turchin, 1999). Comprehensive models to explain the behavior of populations must account for all the major direct and indirect effects that determine long-term trajectories in population size. In dispensing with single-factor theories, emphasis has shifted toward identifying predictable ecological circumstances or kinds of organisms whereby particular factors are relatively important (Wolff, 1997).

The core of the debate in population ecology is still centered on the issue of "population regulation" and the relative importance of density-dependent and density-independent processes (Sinclair, 1989; Murdoch, 1994; Krebs, 1995; Wolda, 1995; Murray, 1999). Turchin (1999) distinguishes between exogenous factors (those that affect population change, but

are not themselves affected by population numbers) and endogenous factors (those that involve "dynamic feedbacks" affecting population numbers). A similar distinction has been drawn between "limitation" (the extent to which a process depresses population growth rate) and "regulation" (whereby a process leads to a local equilibrium through density-dependent effects) (see Osenberg and Mittelbach, 1996). Evidence for and against population regulation and the central role of density-dependent factors is still being compiled and continues to divide ecologists. However, Turchin (1999) emphasizes that both exogenous and endogenous factors affect population change, and their relative strength varies for different population systems. An additional problem is that the same factor may have both exogenous and endogenous effects, and therefore defy such classifications. Hence, rather than categorizing different processes as either density dependent or independent, it is more productive to identify processes that cause stasis or change in population numbers and determine the direct and indirect mechanisms by which these effects are manifest.

Dichotomous views over the processes limiting populations of coral reef fishes have been particularly extreme (see reviews by Doherty, 1991; Hixon, 1991; Jones, 1991). At first, all researchers assumed that space on coral reefs was a limiting resource. The ensuing debate centered on whether individual species were at the carrying capacity of the environment (Smith and Tyler, 1975) or whether chance recruitment patterns determined the population size of individual species (Sale, 1977). Subsequent research showed that there was not a lot of evidence for space limitation and the argument shifted to a debate over whether populations do not reach the carrying capacity because of recruitment limitation (Doherty, 1983a) or predation (Talbot *et al.*, 1978). Consistent with studies of other groups of organisms, modern theory and empirical research suggest that all of these processes, including recruitment, competition, and predation, can contribute to determine population size (Jones, 1987b, 1990, 1991, 1997; Forrester, 1990; Hixon, 1991; Caley *et al.*, 1996; Schmitt and Holbrook, 1999a,b; Schmitt *et al.*, 1999). These "multiple causes" may act independently, or may strongly interact to determine the patterns we see (Steele, 1997a). However, despite considerable research, the full extent of the interactions between recruitment, competition, and predation is only beginning to emerge.

Most local populations of marine organisms are demographically "open" and coral reef fishes are no exception (Caley *et al.*, 1996). By definition, local population changes will be to some degree driven by

variation in the supply of juveniles from the plankton, although this may be modified by postrecruitment interactions. It has been well recognized that factors influencing recruitment and adult reproductive output are “decoupled” in open marine populations such as coral reef fishes (Mapstone and Fowler, 1988; Wellington and Victor, 1988). Because factors affecting reproductive output could have little or no effect on population size, it has been argued that they should be disregarded in population studies (Doherty, 1991; Doherty and Fowler, 1994a). However, this assumes that (1) the survival of individuals in a population is totally unrelated to their historic or current condition, and (2) that the recruitment of individuals is at no scale in space or time related to the size and combined reproductive output of the parent stock. In this review we provide evidence to challenge these assumptions.

II. Integrating Numerical and Energetic Processes

A. The Numerical–Energetic Dichotomy

Although we have been critical of dichotomies, in the ecology of open populations it is constructive to distinguish between two potentially distinct patterns and processes that may be important in different ways. The first category concerns “numerical” patterns, or the “quantity” of individuals in the population. Numerical processes will be those that directly add individuals to the population (factors affecting recruitment) or those that subtract individuals from the population (factors affecting mortality). Recruitment variation and lethal factors will have immediate effects on population numbers. On the other hand, “energetic” processes concern the “quality” of individuals, either in terms of their size, condition, or reproductive success. These processes concern the acquisition, allocation, and expenditure of energy to different morphological, behavioral, or physiological functions (feeding rate, growth, condition, maturation, fecundity). At an individual level, energetic features represent important fitness parameters because they can be an important component of reproductive success. At the population level they do not directly cause numerical changes because they have only sublethal effects on population members. However, if energetic parameters affect the long-term probability of survival, they may contribute lagged effects on population changes as a result of indirect interactions.

In this review we argue that both numerical and energetic processes, and their interactions, are critical

in explaining long-term patterns in population size and structure in coral reef fishes. Our main thesis is that fundamentally different processes affect numerical and energetic parameters, but each one can have important indirect effects on the other. We do not deal specifically with evidence for and against density dependence and population regulation in coral reef fishes (see Caley *et al.*, 1996; Schmitt *et al.*, 1999; see Chapter 14, this volume, for discussions). Here we are concerned with identifying particular processes and determining if they primarily limit numerical or energetic parameters, and whether there are indirect effects that have secondary consequences for other demographic patterns. Discussions of the relative importance of different processes such as recruitment, competition, and predation are meaningless, unless the parameters they affect are clearly measured over appropriate time scales. An integrated model of reef fish populations will require a separate understanding of the two suites of processes affecting numerical and energetic patterns and their interactions.

Although counterintuitive, it is particularly important to consider energetic processes, such as growth and reproductive condition in open populations. Open populations are expected to exhibit greater phenotypic plasticity in these life history traits than are closed populations, because the environment experienced by offspring will be less predictable (Warner, 1997a,c). Indeed, the growth, maturation, and fecundity of marine fishes are extremely flexible, resulting in considerable spatial and temporal variation in these parameters. Thus open populations tend to be “size structured” (*sensu* Werner and Gilliam, 1984; Ebenman and Persson, 1988; Olson, 1996), meaning that shifts in ecological relationships and between life history stages appear to be more closely related to size than to age. Even though recruitment may not be related to adult stock, actual numbers of individuals reaching particular life history stages (e.g., breeding population) can be directly linked to “bottlenecks” affecting growth and condition during previous life history stages (Jones, 1984; Bystrom *et al.*, 1998). The potential roles of both numerical and energetic processes in reef fish populations will not be understood unless we examine the dynamics relating to both age and size.

B. A Model Linking Numerical and Energetic Processes

In this review we put forward and assess a model that links numerical and energetic processes in the ecology of reef fish populations (Fig. 1). Initially we examine the potentially independent effects of processes

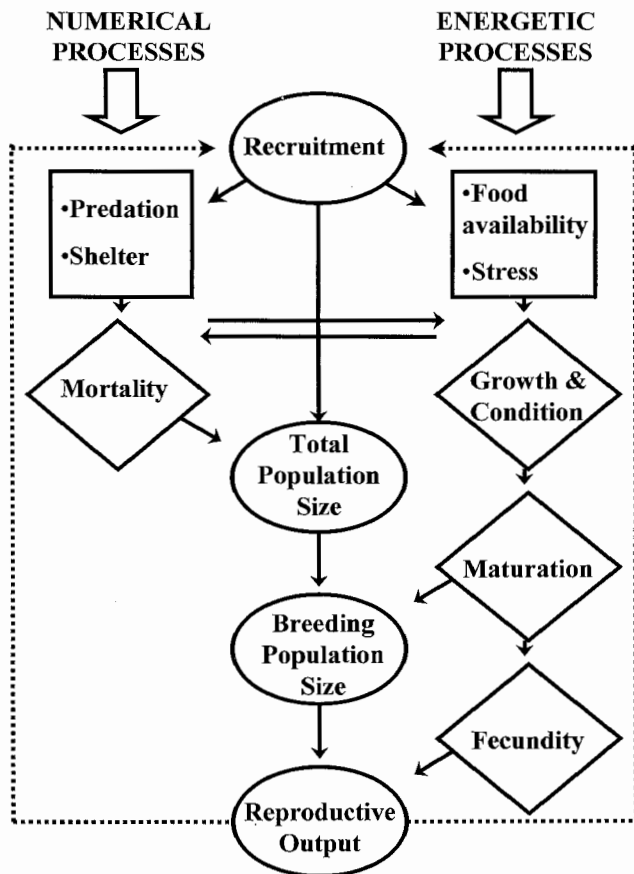


FIGURE 1 Model illustrating linkages between numerical and energetic processes and their consequences for the ecology of reef fish populations. Numerical processes (e.g., predation) directly determine the “quantity” of individuals in the population (Section III); energetic processes (e.g., competition for food) determine their “quality” (Section IV). Predator pressure can indirectly determine many energetic parameters (Section V); conversely, competition and behavioral interactions can have an indirect effect on mortality rates (Section VI). Habitat selection may be a trade-off between the numerical and energetic costs of living in different habitats (Section VII). Population structure and breeding population size will be determined by a combination of numerical and energetic processes (Section VIII). The size of the breeding population and the interaction between numerical and energetic processes in the larval phase will determine the recruitment into the reef-based population every generation.

affecting numerical and energetic parameters in reef fishes. We assess the predictions that recruitment, predation, and competition for shelter play can play important roles in determining absolute population size and the short-term dynamics of reef fish populations, and that competition for food and behavioral interac-

tions can play a major role in determining parameters. We also review the evidence that the reciprocal interactions between numerical and energetic processes (indirect effects) are vital to an understanding of reef fish population dynamics (Fig. 1). We examine the hypotheses that recruitment and predation indirectly affect the acquisition and allocation of energy, as a result of predator avoidance, restrictions on foraging, and predator-induced stress. We also examine how food resources and competition may indirectly affect recruitment and mortality, and thus produce lagged effects on long-term population changes. The evidence that energetic effects in the early life history can subsequently determine the numbers of individuals reaching adult life history stages will be evaluated. That is, we determine whether numerical and energetic processes can interact to produce the secondary characteristics of reef fish populations, such as population size and age structure, biomass, adult population size, and the reproductive output of local populations. Finally, we examine the potential for numerical and energetic links between the adult population and the subsequent recruitment of reef fishes.

C. Where Does Movement Fit in?

There is increasing evidence that movement after settlement can have a major influence on local population size (Robertson, 1988a; Lewis, 1997; Ault and Johnson, 1998a). Whether movement is considered an energetic process or a numerical one depends on the scale at which a local population is defined. Immigration and emigration will have direct numerical effects, but these may become less important at larger spatial scales. Also, movement is associated with a risk of predation and so may result in a reduced life expectancy. However, movement is fundamentally an energetic process, because it exacts a cost in terms of energy expenditure. The energy gains associated with movement depend on the quality of the habitat that is being selected. Clearly, both numerical and energetic processes will be of importance in explaining the patterns of movement of fish populations to and from reefs.

D. Recruitment versus Postrecruitment Processes

Our model of reef fish populations begins with recruitment, the parameter that determines the initial size of each cohort entering the reef-based population

(Fig. 1). Recruitment, defined here as the number of juveniles settling out of the plankton into the reef-associated population, is the major factor replenishing populations. Its theoretical role in determining local population size in open systems, as a result of variations in larval supply, has been well documented (Doherty, 1991; Caley *et al.*, 1996). In support, there is ample empirical evidence that recruitment can be a major factor affecting population size (e.g., Jones, 1990; Doherty and Fowler, 1994a,b). Unless density-dependent mortality is so strong that there is complete compensation (i.e., one death for every new recruit), variation in recruitment will lead to a change in population size (Caley *et al.*, 1996). However, there is also considerable evidence that patterns established at the time of recruitment can be substantially modified by postrecruitment processes (Jones, 1990, 1991, 1997; Forrester, 1990, 1995; Hixon and Carr, 1997; Steele, 1997a,b, 1998; Holbrook and Schmitt 1999; Schmitt *et al.*, 1999). Some of these act almost immediately after recruitment (e.g., Holbrook and Schmitt, 1999), whereas others are noted only after several years of observation (Jones, 1991; Robertson, 1996). Both predation and competition have been implicated, but a general understanding of where and when each process will be important has not been reached. In our model a general understanding of how recruitment is modified requires two clear distinctions to be drawn. First, direct and indirect effects of the actions of predation, competition, and other processes need to be clearly distinguished. Second, competition cannot be treated as a single cohesive process. Competition for shelter or refuges from predators has a fundamentally different effect compared to competition for food. Hence, to achieve an understanding of the effects of competition on predation rates, it is critical to identify the resources that are the object of competition.

III. Direct Effects on Numerical Parameters: Predation and Competition for Shelter

A. Predation

Since Hixon (1991) reviewed the role of predation in coral reef fish communities, evidence has continued to accumulate showing predators can have a major influence on the abundance of reef fish (Caley, 1993; Carr and Hixon, 1995; Beets, 1997; Beukers and Jones, 1997; Steele, 1998, 1999; Steele *et al.*, 1998;

Connell, 1998a, 2000). For example, removal of the predatory squirrelfish *Holocentrus adscensionis* in the United States Virgin Islands has had a significant effect on the juvenile densities and adult abundance of other species (Beets, 1997). The effects of predators on juvenile densities or adult numbers can be directly attributed to an increase in mortality rates (Carr and Hixon, 1995; Hixon and Carr, 1997; Beukers and Jones, 1997; Connell, 1998a; Steele, 1999; Forrester and Steele, 2000; Emslie and Jones, 2001). Connell (1998a), for example, showed that juvenile *Acanthochromis polyacanthus* survived substantially better when predatory fishes were excluded by cages (Fig. 2). Small reef fish species may be particularly susceptible to predation, exhibiting generally higher mortality rates as compared to large species (Munday and Jones, 1998).

It is almost considered a general rule that juvenile mortality rates in fishes increase in relation to density, whereas adult mortality is density independent (Myers and Cadigan, 1993a; Valiela, 1995; Bjornstad *et al.*, 1999). Mechanisms put forward to account for this include increased predation (including cannibalism) at high densities and competition for food and habitat. However, there is little evidence that competition for food causes mortality directly. In coral reef fishes, juvenile mortality rates are density dependent, and this can largely be attributed to the effects of predation (Forrester, 1995; Beukers and Jones, 1997; Hixon and Carr, 1997; Steele 1997a,b; 1998; Connell, 1998a, 2000). However, the role of predation in population regulation has yet to be tested via long-term predator removals. That is, we do not know if populations in the long term reach a carrying capacity in the absence of predators.

B. Availability of and Competition for Shelter

Coral reef fishes frequently take refuge from predators in the branches of corals or in holes in the reef matrix. Under conditions of high predation pressure, the availability of shelter or predator-free space will often influence the abundance of reef fishes through effects on mortality rates (Fig. 1). Recent manipulations of shelter availability have been shown to affect reef fish abundance (Hixon and Beets, 1989, 1993; Connell and Jones, 1991; Buchheim and Hixon, 1992; Caley and St. John, 1996; Holbrook *et al.*, 2000; Syms and Jones, 2000; Schmitt and Holbrook, 2001). In addition, orthogonal manipulations of both shelter and predators (e.g., Beukers and Jones, 1997; Eggleston *et al.*, 1997;

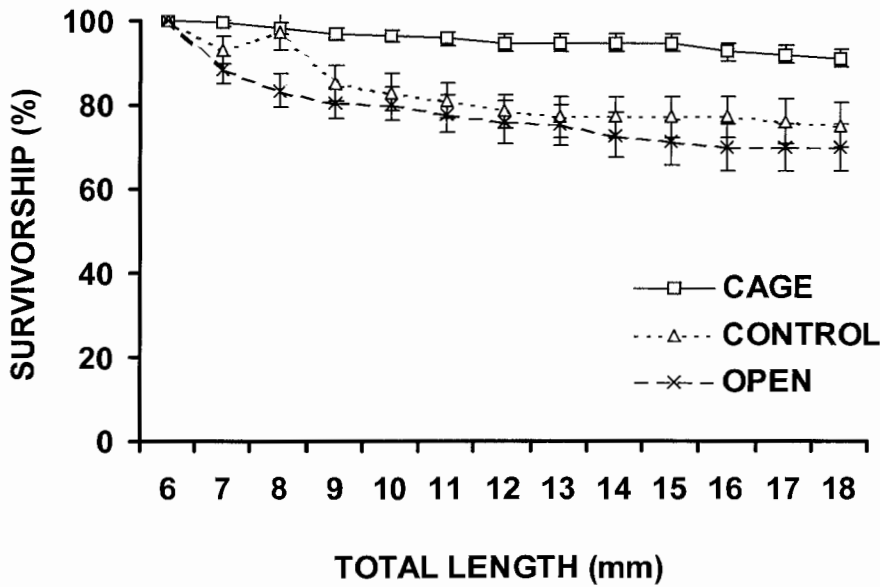


FIGURE 2 Effects of piscivore exclusion on the survival of juvenile *Acanthochromis polyacanthus* at One Tree Reef, Great Barrier Reef (with permission from Connell, 1998a).

Steele, 1999) have shown that survival varies with shelter treatments when fishes are exposed to predators, but less so when predators are reduced or absent (e.g., *Pomacentrus moluccensis*; Fig. 3).

There is a close relationship between predation and competition for shelter. When shelter from predators is in short supply, individuals are expected to compete for shelter, provided that predation pressure is sufficient to lead to greater mortality when shelter is poor or absent. Conversely, in the absence of predation pressure, competition for shelter may not occur at all. Thus we might expect competition for shelter to occur at a threshold below which there is ample shelter for all individuals in the population.

There is increasing evidence that competition for shelter, both within and among species, directly affects mortality rates and population size, particularly in species that are highly dependent on specialized shelter sites. Anemone fishes exhibit strong competition for anemones, both within and among species, although competitive hierarchies do not appear to explain differences in anemone use among species (Srinivasan *et al.*, 1999).

Schmitt and Holbrook (1999b) measured strong density-dependent mortality in *Dascyllus* species associated with both anemones and live coral heads in Tahiti. The effect of predation appeared to be mediated through competition for shelter, with behavioral

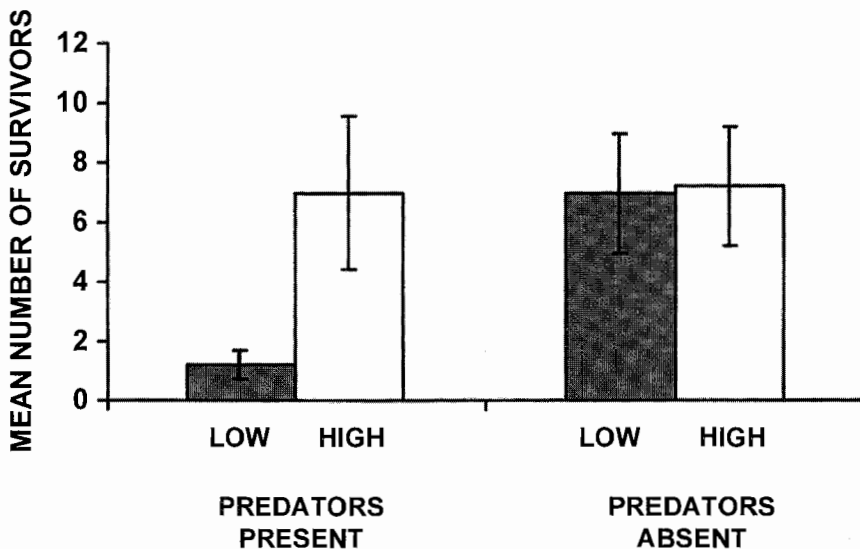


FIGURE 3 Interaction between predator pressure and habitat quality in determining the survival of the damselfish *Pomacentrus moluccensis* at Lizard Island, Great Barrier Reef. The graph shows the mean number surviving 2 months on patch reefs made from low shelter (*Acropora nobilis*) and high shelter (*Pocillopora damicornis*), both in the presence of two predatory fishes (*Cephalopholis boenak* and *Pseudochromis fuscus*) and where they were absent (from Beukers and Jones, 1997).

interactions reducing the access of smaller fish to shelter, making them more susceptible to predation. Competitive interactions between two species inhabiting the same coral species, *Dascyllus aruanus* and *Dascyllus flavicauda*, were asymmetrical. *Dascyllus flavicauda* appeared to be a superior competitor where the two species cooccurred, having a greater effect on the mortality of *D. aruanus* than vice versa. Munday *et al.*, (2001) have shown that interspecific competition is a major determinant of the population densities of *Gobiodon* species, which are the specialized inhabitants of certain acroporid corals. The larger, dominant species *Gobiodon histrio* has a major influence on the recruitment and survival of other species with similar habitat preferences, and excludes these species from preferred shelter sites. However, effects of competition for shelter are not universal. Steele (1997a,b), for example, detected no effect of interspecific competition for shelter in two temperate reef gobies. Species that evolve either specialist or generalist shelter requirements may be trading off the risks of predation and competition. That is, adaptation to specific shelters may reduce the risk of predation, but increase the likelihood of competitive interactions over shelter or other resources.

IV. Direct Effects on Energetic Parameters: Competition for Food, Behavioral Interactions, and Stress

A. Food Availability and Competition for Food

There is ample evidence that food availability and competition for food can have major effects on growth rates and the onset of key life history events in fishes from a variety of habitats (Abbott and Dill, 1985; Metcalfe, 1986, 1993; Thorpe, 1989; Simpson, 1992; Levin *et al.*, 1997b). The actual amount of food energy available for maintenance, growth, and storage will be determined by the absolute amount of food available and how many individuals are sharing that resource. When food declines and/or densities of fishes increase to a point at which the supply of food does not meet demand, competition will affect the growth of individuals. As a consequence, growth is typically density dependent in fishes, especially prior to maturation, when individuals are growing most rapidly (Valiela, 1995). Evidence also suggests that, after settlement, food availability and competition for food seldom cause mortality directly (Brown *et al.*, 1989; Jenkins *et al.*, 1999).

It appears that fishes are resilient to variation in the acquisition of energy that might arise from fluctuations in food abundance or population density.

Studies on coral reef fishes appear largely to support these generalizations. When juvenile densities have been manipulated, growth is almost always negatively related to density, which may be explained by competition for food (Doherty, 1982; Jones, 1987b, 1988b; Forrester, 1990; Booth, 1995; Webster and Hixon, 2000). However, density-dependent growth may also result from behavioral interactions or may be an indirect response to predation pressure, if predators aggregate at sites of high density (see Section VI). One obvious way density influences growth is through food limitation to less competitive parts of a group or population. For example, Jones (1987b) manipulated the densities of recruited *Pomacentrus amboinensis* in small patch reefs from natural to three times natural densities and found that growth was slower at high densities. In addition, juvenile growth was considerably slower in the presence of adult individuals. In these experiments, mortality did not decline in relation to density, suggesting that individuals can survive a food reduction associated with high fish density. Among coral reef fishes there are no documented examples of competitors directly killing one another in the process of acquiring food resources. Observed declines in the abundance of food seldom lead directly to increased mortality rates, except in rare instances when starvation results from dramatic environmental perturbations (e.g., Tsuda and Bryan, 1973).

Food is obviously going to be important for growth, but is it in short supply and therefore a resource that will be competed for? One source of circumstantial evidence suggesting that food is at a level that limits growth comes from studies of planktivorous fishes. Several studies have shown that the abundance and growth of planktivores are correlated with current speed, and hence the supply of food to reefs (Thresher, 1983a,b; Kingsford and MacDiarmid, 1988; Anderson and Sabado, 1995). Food availability may also be important to the growth of reef fishes in other trophic groups. A unique study by Clifton (1995) suggested the overwhelming importance of food to the Caribbean parrot fish, *Scarus iserti*. He examined two populations, separated by only 3 km, that were exposed to very different patterns of seasonal food availability. Both growth and reproduction tracked the availability of food and were very different for the two populations. Similarly, Stewart (1998) showed that the growth of small piscivorous fishes on the northern Great Barrier Reef was correlated with the abundance of prey.

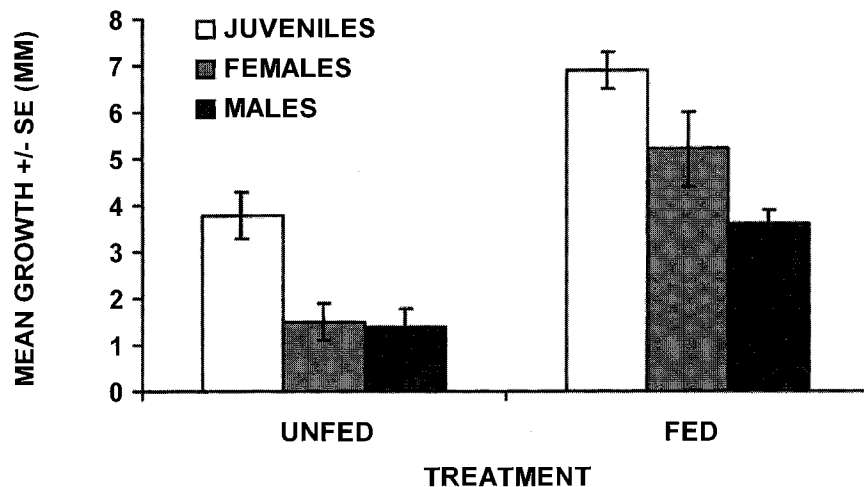


FIGURE 4 Influence of supplemental feeding on the growth of subadult juveniles, adult females, and adult males of *Pomacentrus amboinensis* in field populations at One Tree Reef. Fish were fed on freeze-dried euphausiids, twice a day over a 6-week period. Growth is compared to fish exposed to natural prey levels.

Studies that have directly manipulated food availability on coral reefs provide the strongest evidence that it influences juvenile growth rates (G. P. Jones, 1986; Forrester, 1990; Kerrigan, 1994). G. P. Jones (1986) manipulated the diets of recently settled *Pomacentrus amboinensis* transplanted to patch reefs at two depths in One Tree Lagoon, using daily zooplankton supplements. Food supplementation was found to increase growth rates, regardless of depth, but did not influence mortality rates. Kerrigan (1994) manipulated food availability to social groups of the same species in mesocosms and found that growth tracked food availability. Similarly, Forrester (1990) found that supplemental feeding enhanced the growth of *Dascyllus aruanus*. G. P. Jones (unpublished data) has provided supplemental food to older individuals of *P. amboinensis* and found that it promotes growth throughout the life cycle, impacting large juveniles, mature females, and mature males (Fig. 4).

Food availability and competition for food may affect other life history parameters that are closely related to growth, such as time to maturity and fecundity (Jones, 1984, 1987b; Ma *et al.*, 1998; Wootton, 1998;

Ali and Wootton, 1999). In size-structured populations this has major implications for determining the size of the breeding population and the reproductive output of the population (Fig. 1). Because the attainment of sexual maturity in reef fishes is often size based, time to maturity is often found to be density dependent, as a consequence of growth rates and ultimately food consumption. Booth (1995) found that juvenile *Dascyllus albisella* took longer to reach maturity in larger groups. Alternatively, Jones (1987b) found that numbers of *Pomacentrus amboinensis* reaching the size of maturity were not related to the initial juvenile densities, but rather were strongly influenced by the presence of adult conspecifics. Both results could relate to competition for food. Both Forrester (1990) and Jones (Fig. 5) have found that supplemental feeding can advance the onset of maturation in reef fishes. In *P. amboinensis*, adult females given supplemental food produced a significantly greater number of clutches during the breeding season (Fig. 6).

Competitive interactions can have a negative influence on the growth, maturation, and fecundity of inferior competitors, particularly when they are displaced

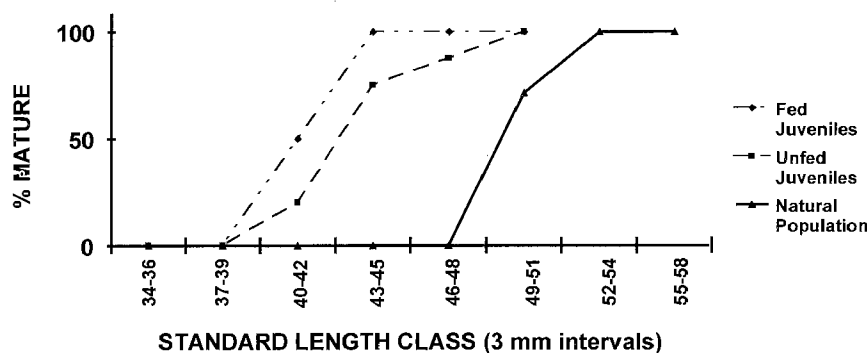


FIGURE 5 Influence of supplemental feeding on the onset of maturation in juveniles of *Pomacentrus amboinensis* in the absence of adults. Size at maturation for the fed group is compared with unfed juveniles on control experimental patch reefs and with juveniles collected from undisturbed populations.

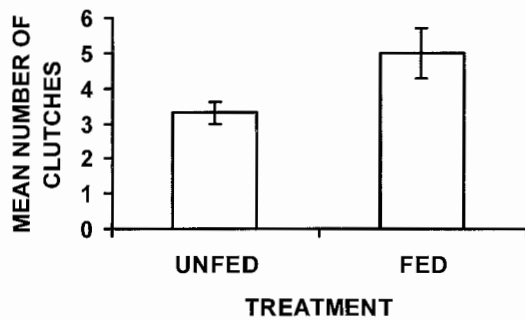


FIGURE 6 Influence of supplemental feeding on the frequency of spawning by marked female *Pomacentrus amboinensis* on experimental patch reefs. Frequency of spawning is compared to that for females exposed to natural food levels.

into lower quality habitats. For example, Munday *et al.* (2001) found that among coral-dwelling gobies at Lizard Island, a superior competitor (*Gobiodon histrio*) limited access of an inferior competitor (*Gobiodon brochus*) to a high-quality coral habitat (*Acropora nasuta*). Both goby species prefer *A. nasuta*, where they exhibit their highest growth rates (Munday, 2001) (Fig. 7). *Gobiodon brochus* grew at approximately half the rate in the low-quality coral habitat (*Acropora loripes*) it is normally found in compared to the high-quality habitat it is competitively excluded from (Munday, 2001). Reproductive success is closely linked to body size in coral-dwelling gobies (Kuwamura *et al.*, 1993). Therefore, habitat-related differences in growth rate are predicted to have substantial effects on lifetime reproductive success. Similarly, Clarke (1989, 1992)

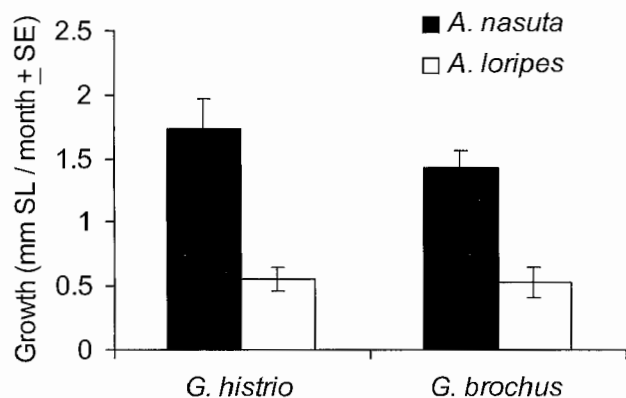


FIGURE 7 The coral-dwelling gobies, *Gobiodon histrio* and *Gobiodon brochus*, both grow faster in colonies of *Acropora nasuta* than in colonies of *Acropora loripes* at Lizard Island (P. L. Munday, unpublished data). However, *G. brochus* is excluded from colonies of *A. nasuta* and is forced to use the inferior habitat as a result of competition with *G. histrio* (see Munday, 2001).

found that interspecific competition resulted in habitat partitioning in two planktivorous blennies of the genus *Acanthemblemaria* living on dead corals. The dominant species (*Acanthemblemaria spinosa*) occupies the tips of the coral and displaces *Acanthemblemaria aspera* downward. Both prefer to be higher, where they exhibit higher feeding rates, faster growth, and higher fecundity. This seems to be a case of competition for food, with the dominant species having a major effect on the energetic parameters of a subordinate species, but having no direct influence on survival. Clarke argued that the subordinate species could tolerate less food because it has a lower metabolic rate.

Thresher (1983b) produced a conceptual model of the factors that influence reproductive success in the only damselfish that broods its larvae, *Acanthochromis polyacanthus* (Fig. 8). He found reduced reproductive output correlated with increased numbers of other planktivorous species who were apparent food competitors. Selective removal of these competitors supported this idea. Moreover, he showed that juvenile growth rate was related to the strength of the current in the vicinity of the brood of juveniles, the date that the juveniles were spawned, and the size of the initial brood. Together these three variables explained 73% of the variability in juvenile growth. Juvenile mortality was positively related to the initial size of the brood and the mean number of fishes of all species present within the area.

Competition influences not only the growth, but also other aspects of performance such as body condition, which in turn can have direct effects on maturation and reproductive output. Condition has been shown to influence maturation and fecundity of females in a variety of fish species (Hislop *et al.*, 1978; Kjesbu *et al.*, 1991, 1998; DeMartini, 1991; Koslow *et al.*, 1995). Lipid storage appears to be particularly important for gonad development (Ballantyne *et al.*, 1996). Duston and Saunders (1999) showed that seasonal food deprivation led to reduced growth and condition, which reduced maturation in Atlantic salmon. They showed that, regardless of body size, a high condition factor was necessary in late winter for maturation to occur. The physiological decision to mature in these fishes may be dependent on some measure of either the rate of storage or the turnover of surplus energy (Thorpe, 1986; Thorpe *et al.*, 1990). A reduction in food intake prior to the spawning season or during oocyte development can reduce fecundity and egg size (Kjesbu *et al.*, 1991). These potentially important processes have received little attention in the coral reef fish literature.

Factors that influence growth trajectories during the juvenile phase are likely to have major lifetime

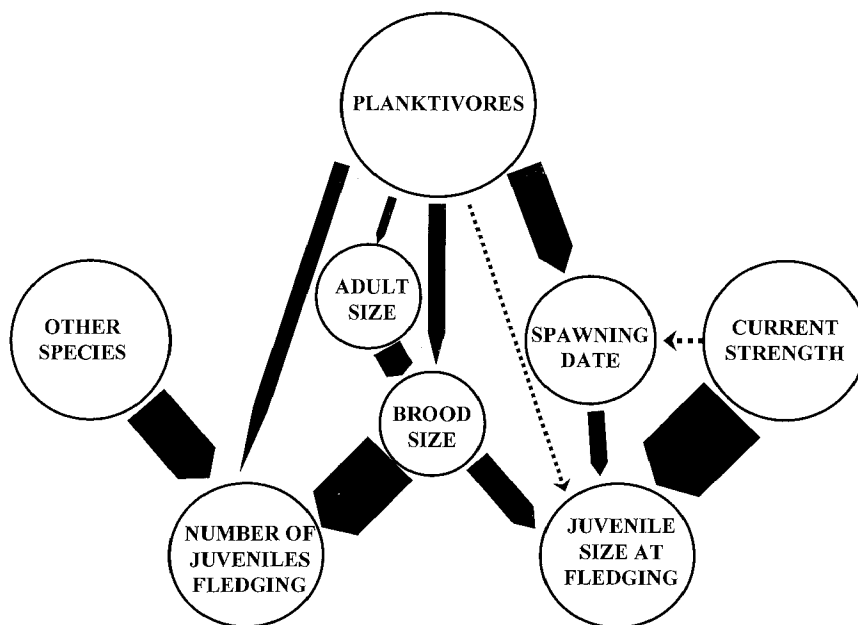


FIGURE 8 Summary of the determinants of reproductive success in a brooding damselfish *Acanthochromis polyacanthus* at One Tree Reef, Great Barrier Reef. Width of the arrows is proportional to the amount of variance accounted for by the variable; direction of the arrow indicates the direction of the causal relationship. Solid arrows indicate statistically significant relationships; dashed arrows indicate trends in data (with permission from Thresher, 1983b).

fitness implications for individuals in size-structured populations. There is some evidence to suggest that size and growth advantages that are present at or shortly after settlement are maintained and reinforced in later life. Tupper and Boutlier (1995a) monitored the growth of recently settled Atlantic cod *Gadus morhua* and found that size differences that were present at settlement were accentuated through time. Likewise, for a reef fish, Forrester (1990) monitored the sizes of groups of juvenile humbug damselfishes (*Dascyllus aruanus*) and found that initial differences in size were maintained and the variance increased over an 8-month period. The formation of social hierarchies within species magnifies variability in growth-related traits, as dominant individuals garner a disproportionate amount of the food resource (Forrester, 1991). Also, when there are size-related changes in diet, larger individuals may be able to access higher energy food sources, which will contribute to faster growth. For example, large piscivorous juveniles rapidly outgrow nonpiscivorous members of the same cohort (e.g., Buijse and Houthuijzen, 1992; Juanes and Conover, 1994).

So does this mean that a fish's fate is predestined by its growth history? Well, possibly not. Fishes do appear to undergo rapid physiological responses when conditions improve (e.g., Cowen, 1991; McCormick and Molony, 1992), which suggests that they have the ability to compensate for poor growth history (McCormick, 1998a). Growth compensation after settlement has been shown to occur in the laboratory for the winter flounder *Pleuronectes americanus* (Bertram

et al., 1993), although there are presently no examples of it occurring in tropical reef fishes. Given the differences in the ecological and physiological environment between the larval and benthic life phases, it is unlikely that traits promoting high growth in the larval phase will be the same as those promoting growth after settlement.

B. Behavioral Interactions and Stress

There are three ways that behavioral interactions can exert a negative influence on energetic parameters. First, dominant individuals may limit access to food by subordinates, especially if food is in short supply. However, behavioral interactions may limit growth though limiting access to an important resource even if there is a plentiful supply. For example, Adams and Huntingford (1996) found that at high stocking densities dominant Atlantic salmon, *Salmo salar*, monopolize food and cause social growth suppression even when food is abundant. Clifton (1990) found that dominant members of territorial groups of the Caribbean parrot fish, *Scarus iserti*, reduced the amount of time subordinates spent feeding and limited a subordinate's access to high-quality resources.

The second way that behavioral interactions can influence fitness is by causing or elevating physiological stress (Billard *et al.*, 1981). The aquaculture literature is replete with studies demonstrating that high densities cause stress and lead to greater variance in life history characteristics. Elevation of stress, whether

from behavioral interactions or environmental stress, inhibits growth by exerting effects on metabolic and endocrine pathways that regulate growth (Pankhurst and Van der Kraak, 1997). In fishes, stress leads to elevations of the hormone cortisol, which plays an important role in glucose production (Vijayan *et al.*, 1996). It also interacts with other hormones that are responsible for growth and development. Elevated levels of cortisol have been shown to have diverse and consistent effects, including reduced somatic growth, reduced reproductive output, and, in extreme cases, reproductive senescence (Pankhurst and Van der Kraak, 1997). Stress has inhibitory effects on all stages in the reproductive process, including gamete development and quality (Carragher and Pankhurst, 1991), egg and larval quality (McCormick, 1998b, 1999a; Morgan *et al.*, 1999), and survival (Campbell *et al.*, 1992, 1994).

Physiological stress can also influence food intake directly. An individual's foraging success can be influenced by its appetite, visual and chemosensory abilities and ability to capture, handle, and ingest prey. Any stress that impacts on this sequence will adversely affect an individual's energy intake and growth. For instance, handling stress has been found to result in the loss of feeding behavior for a length of time that correlates with the reestablishment of normal physiological status (Schreck *et al.*, 1997). The interactions between behavioral and physiological processes that lead to stress-related effects on foraging efficiency are poorly understood.

A third way in which density-related behavioral interactions can influence fitness is by changing the energy budget of individuals. Elevated population densities force individuals of all levels of a social hierarchy to put more energy into aggression and social interactions, and less into growth, storage, and reproduction. For example, Marchand and Boisclair (1998) found that increasing the stocking density of juvenile brook trout (*Salvelinus fontinalis*) caused a reduction in growth rate, but did not reduce food consumption. At high densities fish were more aggressive and mobile, leaving less energy available for growth.

Few studies have attempted to weigh the relative importance of these three mechanisms (differential access to food, physiological stress, and changes in activity) by which behavioral interactions can influence energetic of individuals. In the freshwater fish *Tilapia zillii*, Koebele (1985) ran a series of five experiments to determine their relative importance in influencing the growth of juveniles. He found that disproportional food acquisition, driven by established dominance hierarchies, was the primary mechanism responsible for the high variance in growth within social

groups. Dominant fish ingested more food, either by acquiring a limited ration first and preventing access to food by subordinates, or by inhibiting a subordinate's feeding behavior. These mechanisms have not been investigated in coral reef fishes.

Whatever the mechanism, social interactions appear to regulate reproductive function in many vertebrates. Dominant individuals can regulate access to mates, reproductive condition, timing of maturation, and the determination of gender in subordinates. Such effects are widespread in site-attached reef fishes living in small social groups. Interactions appear to occur most frequently between individuals of near similar size or social status. Jones (1987b) found that adults did not affect the growth of 0+ juveniles up until just prior to maturity, at which time adults began to suppress juvenile growth. This effect on growth was particularly marked in the larger, dominant juveniles. In species with polygynous mating systems, dominant males often suppress the growth of females, which also inhibits sex change from female to male (Warner, 1988c). The reverse occurs in clown fishes; the breeding pair of this species consists of a large female that represses growth of and sex change by the smaller, subordinate male (Fricke, 1983).

Lifetime fitness can be highly dependent on a juvenile's initial position in a social hierarchy. For many fishes that have seasonal cycles of recruitment and growth, the exact timing of settlement can affect social status, which will in turn influence rate of growth and maturation. For example, in salmonids Metcalfe *et al.* (1990) found that juveniles high in social status are more likely to smolt (i.e., metamorphose into the migratory marine phase) in their second year, whereas those of low status are subject to growth suppression by dominant fish and smolted in their third year. Similarly, juveniles of the reef fish *P. amboinensis* settling early in the recruitment season exhibit a growth advantage over late settlers, which is accentuated over time (Jones, 1987a). Early settlers may mature in their first year, but slow-growing late settlers must wait another year before reaching the critical size (Jones, 1987a).

V. Predation: Indirect Effects on Competition and Energetic Processes

The intensity of stress or competitive interactions over food will initially be set by recruitment levels, and will be reduced in proportion to subsequent losses. However, predation can indirectly result in a number of nonlethal effects on prey fish populations. This can include an increase in competition for food when fishes

are concentrated in areas serving as refuges from predators (Mittelbach and Chesson, 1987). Predation pressure and crowding effects may be strongly correlated, if increasing predation pressure forces individuals into smaller areas of safe habitat. There is evidence for strong density-dependent growth of juveniles in species occupying specialized shelter sites, which results in delayed maturation (e.g., Jones, 1987b; Forrester, 1990; Booth, 1995; Steele, 1998). Hence, predator-mediated habitat use can exact a cost in terms of growth and reproduction, but this appears to be a trade-off against improved survivorship in shelter sites and in schools. Habitat structure appears to influence the growth of some species that use the habitat primarily for shelter (e.g., Jones, 1988b). Because this cannot be explained by food availability, the differences are likely to be related to differences in the threat of predation on different substrata. For example, gobies of the genus *Gobiodon* appear to grow much more slowly in less preferred coral shelter sites, in which coral branches are closely spaced (Munday, 2001). This may relate to an increase in the time spent on predator avoidance on some corals or to a mechanical restriction on their ability to forage successfully.

Few studies have directly investigated the effects of predation risk and the costs of predator avoidance on energetic processes in coral reef fishes. However, Connell (1998a) found that the growth of juvenile *Acanthochromis polyacanthus* was higher when predators were experimentally excluded (Fig. 9). A similar result was obtained for the temperate reef fish *Lythrypnus dalli*, which reduced its foraging rate and grew more slowly in the presence of predators (Steele, 1998). *Pomacentrus amboinensis* appears to grow more slowly

in shallow water, where this species appears to spend more time sheltering from predators (Jones, 1997). If predators aggregate at sites of greater abundance, a density-dependent reduction in growth rates may occur because individuals must devote more time to predator avoidance.

Predation risk is known to affect energetic processes in a variety of animals (Prejs, 1987; Magnhagen, 1993; Lima 1998). For example, the presence of the largemouth bass, *Micropterus salmoides*, causes small bluegill sunfish, *Lepomis macrochirus*, to spend longer periods in dense cover where there were fewer planktonic prey, leading to slower growth rates (Werner *et al.*, 1983). In the freshwater guppies, intimidation by predators reduces the growth of adults and causes a 50% reduction in egg production (Fraser and Gilliam, 1992). A decline in growth and reproductive output associated with an increase in predation pressure is likely to be due to the higher level of harassment, which may interrupt feeding activity (Prejs, 1987). Holbrook and Schmitt (1988) experimentally varied predation pressure on juvenile black surfperch *Embiotoca jacksoni* and showed that they are more closely associated with shelter and feed on less preferred algae at higher predation pressure. However, the opposite effect has been reported for juvenile coho salmon (*Oncorhynchus kisutch*). In the presence of predators, the social hierarchy in groups of juveniles breaks down, allowing smaller fishes to grow faster than they do in the absence of predators (Reinhardt, 1999).

Predation can also influence the use of space by fishes. Individuals of a prey species may avoid areas without actually encountering the predator by the detection of chemicals released by predators or injured

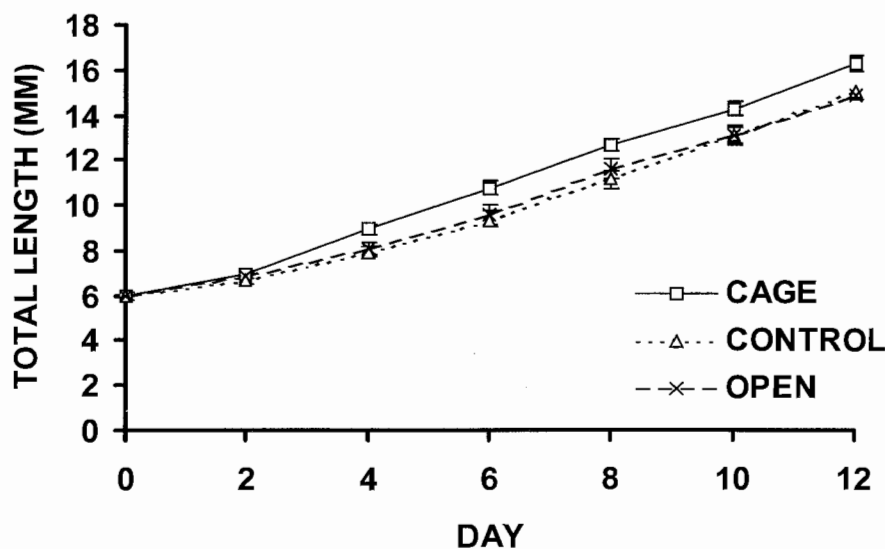


FIGURE 9 Effects of piscivore exclusion on the growth of juvenile *Acanthochromis polyacanthus* at One Tree Reef, Great Barrier Reef (with permission from Connell, 1998a).

prey. The fathead minnow, *Pimephales promelas* (Mathis and Smith, 1992), and the European minnow, *Phoxinus phoxinus* (von Frisch, 1941, cited in R. J. F. Smith, 1997), have been shown to avoid regions where alarm pheromones are present. These alarm pheromones are released only by mechanical injury (Smith, 1992) and are therefore a reliable indicator of the action of a predator for other potential prey. Alarm pheromones in the feces of predators may also indicate high-risk habitats (G. E. Brown *et al.*, 1995a) and the predatory pike counter this by defecating away from their foraging areas when eating minnows (G. E. Brown *et al.*, 1995b). It is currently unknown whether chemicals released by predators influences the distribution of small fishes on coral reefs. It would be of particular interest to know whether the presence of pheromones from predators influences the choices made at the time of settlement, when prey species are naïve and most vulnerable.

VI. Competition and Stress: Indirect Effects on Predation and Numerical Processes

Competition for food directly affects energetic parameters via the acquisition of energy, but in itself is not an agent that directly causes mortality (Section IV). Food availability and crowding can reduce the average (compensation) and increase the variance (depen-sation) in important energetic parameters. At the population level, reductions in growth or condition can lead indirectly to greater mortality rates under selective predation regimes. In addition, enhanced variability in growth rates, body size, and nutritional condition means that some individuals are more susceptible than others to the actions of selective predators.

A. Body Size and Growth: Susceptibility to Predators

If either competition for food or behavioral interactions lead to a reduction in body size or growth, a greater mortality rate can result from the greater susceptibility to size-selective predation. Being larger than average seems to be a distinct advantage if you are a fish trying to avoid being eaten. Sogard (1997), in a review of the importance of body size to the survival of juvenile fishes, found general support for the "bigger is better" hypothesis. Among reef fishes, Jones (1997) found that small *Pomacentrus amboinensis* exhibited a higher mortality as compared to large juveniles over

the first year of life. Likewise, Carr and Hixon (1995) compared the sizes of recruits exposed to predators for a month to those of recruits living on isolated patch reefs without benthic predators. For one species of wrasse, *Halichoeres pictus*, there was no selective mortality. However, for the damselfish, *Chromis cyanea*, mean size was larger where predators were absent. This was either due to density-dependent growth or to size-selective mortality removing the smallest individuals. Manipulations of adult density of the temperate wrasse *Tautoglabrus adspersus* were found to affect growth and survival of newly settled conspecifics (Tupper and Boutilier, 1995a). An elevation in adult densities reduced juvenile growth and survival, whereas a reduction in densities led to an increase in growth and enhanced survival. A relationship between body size and survival suggests that the mechanism causing variation in survival is related to growth. However, mortality in fishes is not always size selective (McCormick and Kerrigan, 1996; Sogard, 1997). Whether faster growth in prey fishes is an advantage may depend on the characteristics of the predator(s).

The situation in which juveniles suffer intense competition that affects growth, and as a consequence extends the period that they are susceptible to predators or starvation, has been referred to as "competitive bottleneck" (Bystrom *et al.*, 1998). This situation is most well known in freshwater fish, particularly those that have a limited growing season (Post and Evans, 1989; Olson *et al.*, 1995; Bystrom *et al.*, 1998). For example, interspecific competition between the perch (*Perca fluviatilis*) and the roach (*Rutilus rutilus*) increases the mortality of the roach by increasing the time during which it is subject to gape-limited predation and reduces the numbers reaching a size and condition capable of overwintering (Bystrom *et al.*, 1998). In the same way, competition among juvenile reef fishes represents a bottleneck that limits entry into the adult population (Jones, 1987b, 1990). As competition intensifies, this increases both the period over which competition occurs and the period over which juveniles are exposed to size-selective predators.

The size distribution of the main predators will also have a marked influence on the nature of any selective removal of prey that occurs. Predators are usually gape limited, and the size distribution of prey they target is a function of their size. Where recruitment of prey and predators is seasonal, such as along the Great Barrier Reef and in temperate waters, the selectivity of loss may be a function of the timing of recruitment in relation to their key predators. The optimal growth rate of prey will depend on their position relative to the prey selection curves of the predators (Rice *et al.*, 1997).

For instance, newly recruited snappers (*Lutjanus quinquelineatus*) are known to be voracious predators of newly settled fishes around patch reefs at Lizard Island on the Great Barrier Reef (Sweatman, 1993). Fishes that recruit early in the season would increase their survival probabilities by growing rapidly, thereby remaining ahead of the optimal size targeted by the predators.

B. Condition and Susceptibility to Predation

Fish do not enter the demersal phase of their life cycle at settlement in the same condition, with an equal probability of survival. At settlement individuals exhibit subtle differences that may affect their ability to survive (McCormick, 1998a). These differences are in part due to genotype, but in the main are due to the myriad of other biological and environmental factors that impact on the larval phase (see Chapter 8 for details). Kerrigan (1994) found that temporal differences among settlement pulses (between and within years) explained 38% of the variability in size and only 23% of the variability in larval duration for the common damselfish, *Pomacentrus amboinensis*, from the Great Barrier Reef. The rest of the variability in these attributes was explained by differences among individuals within a pulse. In virtually all physical and biochemical facets measured there have been ecologically relevant levels of variability. This includes growth rates (McCormick, 1994), proximate body composition [total lipids, proteins, carbohydrates (e.g., McCormick and Molony, 1992, 1993; Kerrigan, 1996)], sensory development (McCormick, 1993), burst swimming speed (McCormick and Molony, 1993), and sustained swimming capacity (Stobutzki, 1998). It has been suggested that much of the variation in life history traits, both within and between cohorts, is driven by density-dependent processes acting during the larval phase (McCormick and Molony, 1992). Interestingly, there is little relationship between different measures of condition, with the exception of morphological measures that usually correlate well with fish length (McCormick and Molony, 1993; Kerrigan, 1996). This lack of correlation between measures suggests that the action of selective predation directed toward one trait, such as fish length will have little influence on the levels of variability in other traits (McCormick, 1998a).

These energetic or qualitative differences among individuals can have a marked influence on the fate of individuals. Mesa *et al.* (1994) reviewed 37 experimental papers since 1960 on the effects of "substandard" prey condition in predator-prey interactions.

Categories of "substandard" prey included fishes subjected to disease, physical stressors, thermal shock, or chemical pollutants. Overall, 73% of the experiments showed that prey of lower condition were captured in higher than expected proportions. Mesa and colleagues noted, however, that "most were simplistic, empirical laboratory studies."

Two studies have examined the influence of variable body condition at settlement on the survival of two coral reef fishes. Booth and Hixon (1999) collected juveniles of a Caribbean damselfish *Stegastes partitus*, brought them back to the laboratory, and fed them either high or low rations. After 7 days fishes were placed in pairs on coral heads, one fish from each feeding regime. Survivorship of the high-ration fishes was double that of low-ration fishes over the next 10 days. Laboratory experiments suggested that selective predation by fishes on low-ration prey was the mechanism for the survival differences. Similar results were found in a field study of the damselfish *Pomacentrus amboinensis* from the Great Barrier Reef. Hoey and McCormick (unpublished) collected naive newly metamorphosed fishes from light traps, tagged them using a fluorescent elastomer, and then assigned them randomly to groups on different patch reefs on a shallow sand flat, which is part of their natural habitat (Jones, 1990). Fishes were left for 2 days and then collected. Whilst migration was negligible, fishes on some patch reefs sustained very high mortality but others had minimal losses. Physical and biochemical measures of condition of the survivors of four patch reefs that sustained high mortality (50%) were compared to those of fishes from four patch reefs that sustained low mortality (<5%). Results clearly showed that it was the juveniles with low growth rates and lipid levels that were being selectively removed by predators on the high-mortality reefs (Fig. 10).

C. Social Hierarchy and Predation

The social hierarchies that form in small social groups can lead to differential probabilities of mortality for group members. Often mortality rates of subordinates are higher than they are for dominant individuals. Post *et al.* (1997) monitored the fate of high- and low-density cohorts of yellow perch (*Perca flavescens*) in a Canadian lake. They found that at high density, recruit cohorts split into a fast-growing group that inhabits the normal littoral area of the lake, and a slow-growing component that remains pelagic. It appears that interference competition by dominant (littoral) individuals at high densities forces the subordinate group into suboptimal habitats, where they sustain twice the mortality of the faster growing group. There are examples

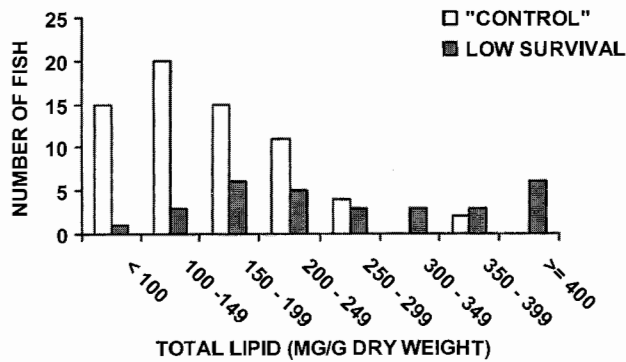


FIGURE 10 Selective predation on low-fat fish. Results of an experiment illustrating the selective nature of predation on newly settled *Pomacentrus amboinensis* at the reef edge. Fishes that were placed on patch reefs and that sustained low mortality levels over a 2-day period (control) have lower levels of total lipids, compared to those fishes from patch reefs that sustained high mortality levels (from Hoey and McCormick, unpublished).

of juvenile coral reef fishes occupying marginal habitats during years of extremely high recruitment [e.g., siganids (Tsuda and Bryan, 1973), surgeonfish (Pillai *et al.*, 1983), and cod (Dufour *et al.*, 1996)], but it is not known whether subordinate individuals are forced into marginal habitats.

The impact of behavioral interactions tends to be most accentuated when there are large size differences, at which time mortality can increase. A number of studies have shown that the growth and subsequent survival of juveniles are reduced in the presence of adults (e.g., Jones, 1987b; Tupper and Boutilier, 1995a). For example, Tupper and Boutilier found that growth and mortality of juvenile cunner *Tautoglabrus adspersus* were influenced by elevated densities of adults; removal of adults resulted in enhanced growth and recruitment success. Heightened levels of mortality may occur because adults force juveniles into lower quality habitats, where the predators are more effective.

In some circumstances it may be the dominant individuals that suffer higher mortality rates. For example, dominant males can be exposed to risk of higher mortality during spawning, by the nature of their higher activity level and gaudy color patterns. This appears to be the case in the Caribbean scarid, *Sparisoma radians*, in which the terminal males, who are much more active during courtship than are other members of the social group, are exposed to higher levels of predation by yellow jacks, *Caranx bartholomaei* (Clifton and Robertson, 1993).

Interestingly, changes in foraging behavior associated with a change in the availability of a food resource

can lead to density-dependent loss. Experiments with anuran tadpoles have shown that activity patterns associated with foraging increase with the depletion of an important food resource (reviewed by Werner and Anholt, 1993). Food depletion may be due to density or environmental changes. As searching activity increases in response to reduced food availability, encounter rates with predators and therefore per-capita mortality rates increase (Anholt and Werner, 1995). This model suggests that food availability, behavior, and predation risk are inextricably linked and the effect of one on survival cannot be understood without the others. Given the generality of the trade-off between growth and mortality rate, this mechanism may also be of importance for reef fishes.

In some instances, behavioral interactions lead to positive density effects on energetic and population processes [so-called Allee effects (Stephens *et al.*, 1999)]. Many of these effects appear to relate to the advantages of living in groups. Individuals in large broods of *Acanthochromis polyacanthus* grow faster compared to those in small broods (Connell, 1998a). Either this is because larger broods are more effective at finding patches of prey or because individuals can afford to spend less time on vigilance or more time on foraging in larger broods. Similar explanations may apply to species in which juveniles preferentially settle into coral heads containing conspecifics (Sweatman, 1985b; Jones, 1987a), and survival is better in larger social groups (Jones, 1987a; Booth, 1995).

VII. Role of Habitat Structure and Habitat Selection

There is increasing evidence that the structure of coral reef habitats can have a major influence on the abundance of reef fish populations and the structure of reef fish communities (e.g., Ormond *et al.*, 1996; Munday *et al.*, 1997; Munday, 2000; Jones and Syms, 1998; Syms and Jones, 2000). Correlations between fish abundance and habitat availability suggest that some resource provided by the habitat must play a role in limiting populations. Habitat structure can affect the magnitude of recruitment in space and time, particularly in species that exhibit strong habitat selection at the time of settlement onto the reef (Tolimieri, 1998a; Srinivasan *et al.*, 1999; Schmitt and Holbrook, 1999b; Syms and Jones, 2000).

Habitat structure can also modify patterns of juvenile growth (Jones, 1988b, 1997) or mortality (Jones, 1988b; Beukers and Jones, 1997). However, at the

population level there appear to be no generalizations emerging as to which parameters—numerical or energetic—will be affected. To extend the work on the significance of habitat structure, we need to be able to identify the actual ecological processes that are responsible for interactions between habitat structure and demography. This requires that we isolate the critical resources that are provided by the habitat and whether these include shelter from predators, food resources, living space, or a combination of these factors.

There is increasing evidence that habitat selection at settlement may be a trade-off between the numerical and energetic consequences of particular choices. Growth and life expectancy will both contribute to differences in fitness associated with different habitat choices. Shelter-site selection may be critical, because an individual may immediately pay the ultimate price for a bad choice. Not surprisingly, many species are exceedingly selective when it comes to recruiting into shelter sites (e.g., Ohman *et al.*, 1998a), particularly where predation pressure is high (Steele, 1999). Species such as *Pomacentrus amboinensis* appear to settle preferentially into habitats that improve chances for both growth and survival (Jones, 1997). In other instances there will be a trade-off between growth and mortality. For example, in *Dascyllus albisella*, juveniles appear to settle preferentially into larger groups because the improved survivorship rate offsets the cost of slower growth and delayed maturation (Booth, 1995). Conversely, pinfish (*Lagodon rhomboides*) seem to choose seagrass beds over open sandy areas because higher growth rates allow them to achieve more quickly a size that protects them from predation (Levin *et al.*, 1997b). The relative contributions of population and energetic parameters to the fitness and survival require further investigation.

VIII. Secondary Population Characteristics: Interaction between Numerical and Energetic Processes

Generally, the factors affecting spatial and temporal patterns in the structure of reef fish populations are poorly understood. Patterns of recruitment and mortality will be the proximate determinants of the age structure of populations (e.g., Doherty and Fowler, 1994a), whereas patterns of growth and size-specific mortality will determine the size structure (e.g., Jones, 1984). To explain the dynamics of fish populations it is necessary to understand the processes that explain both age and size structures, and the consequences of having differ-

ent age or size structures (Jones, 1991; Trippel *et al.*, 1997; Robertson, 1998a). In animals for which key life history transitions are more closely related to size than age, recruitment to these life history stages must be a function of both mortality, and growth. Hence, recruitment, mortality, and growth will determine the size of the breeding population (Jones, 1984). The overall biomass of the population and its reproductive potential will also be determined by both numerical and energetic processes (Fig. 1), but their relative importance has not been evaluated. The longer an animal lives, the greater the potential stability in the face of fluctuations in recruitment or intercohort variation in survival [i.e., the storage effect (Warner and Chesson, 1985)]. In addition, the larger an animal grows and the more flexible the growth rate, that greater the stability in breeding population size.

IX. Numerical and Energetic Links between Stock and Recruitment

A. Interactions between Growth and Mortality in Larvae

Decades of research on temperate fish larvae have emphasized that recruitment is the product of both numerical and energetic processes occurring during the larval phase. Both the importance of food availability and the way this interacts with density have been shown to be key factors influencing the growth and survival of larvae through to recruitment. The availability of planktonic prey of the correct size, at key life stages such as first feeding, appears to drive cohort success (Hjort, 1914; Cushing, 1972; Leggett and Deblois, 1994). At this stage, food availability acts not only directly on mortality levels through starvation, but also indirectly through growth rate effects. Food abundance has been shown to elevate larval growth and development rates, thereby reducing larval-stage duration. In this way, fast-growing larvae, in contrast to slow-growing larvae, are exposed for a shorter period of time to the high levels of predation characteristic of the early larval phase (the "stage-duration" hypothesis). Bigger fish have been shown to be more successful at capturing prey (creating a positive feedback, elevating growth further), and better at evading predators (the "bigger is better" hypothesis). It is generally regarded that larvae that grow slowly or are in poor physical condition will be more susceptible to predation. Predation therefore works in concert with processes that influence growth and body condition. Predation may be the proximate factor that removes juveniles from the population, but the ultimate

cause may be related to energetic processes (Hunter, 1981; Bailey and Houde, 1989). Although most of this scenario is based on temperate nonperciform species, it has been assumed that larval mortality in tropical species is governed by a similar suite of numerical and energetic processes (Houde and Zastrow, 1993).

Because of the almost absolute levels of mortality during the larval phase, small changes in larval mortality rates can lead to order-of-magnitude differences in recruitment (Houde, 1987, 1989; Fogarty, 1993). Any biological or physical factor that reduces larval growth will influence mortality by increasing the period that a larva is exposed to the high predation pressure characteristic of the larval environment. This relatively simple view is supported by a large volume of empirical evidence and simulations (see reviews of Cowen and Sponaugle, 1997; Houde, 1997). The little evidence that is available for tropical reef species is reviewed in Chapter 8 (this volume) and generally supports the importance of factors that influence larval growth and the interactive nature of energetic and numerical processes in determining recruitment success.

B. Is Recruitment Related to Parent Stock?

The relationship between the abundance of a spawning population and recruitment of juveniles is one of the fundamental questions of fisheries biology. Despite this, there is still wide opinion as to the importance of the size of the breeding population in determining recruitment (Myers, 1997). Myers and colleagues have examined this question with a compilation of data encompassing over 300 temperate fisheries stocks (Myers and Barrowman, 1996). Using a meta-analysis they found that when there was a large range in spawning biomass in the data set, the largest recruitment tended to occur when spawner abundance was large, and the lowest recruitment tended to occur when the spawner abundance was low (Myers, 1997). If the range of the spawner abundance was low in the data set then there was no clear relationship between spawner abundance and recruitment. Both spawning stock size and condition have been implicated. For example, Marshall and Frank (1999a,b) found that recruitment in haddock (*Melanogrammus aeglefinus*) correlated with indices of growth, condition, and adult body size (a proxy for egg production). Stock-recruitment relationships may also be influenced by direct links between female condition and offspring quality/survival (Kerrigan, 1997; Laine and Rajasilta, 1999).

It is generally considered that coral reef fishes have a highly dispersive larval stage. Consequently, most

studies on reef fishes have been carried out at too small a scale to examine the potential for the size of the breeding stock to determine subsequent recruitment onto the reef. However, there is increasing evidence that not all larvae disperse long distances and some may not disperse at all. Ecologically significant amounts of self-recruitment may occur on individual reefs at scales of kilometers to tens of kilometers (Jones *et al.*, 1999; Swearer *et al.*, 1999; Cowen *et al.*, 2000; Palumbi, 2001). This raises the possibility that local processes affecting the size of the breeding population may exert some influence on subsequent recruitment to the reef. However, only one attempt to link spawning output to recruitment has been undertaken for a tropical reef fish. Meekan *et al.* (1993) measured the spawning output and recruitment of the common damselfish, *Pomacentrus amboinensis*, at Lizard Island on the northern Great Barrier Reef. Using time-series analysis, they found that although the temporal sequence of spawning output matched that of recruitment, the fluctuations in the magnitude of spawning did not account for fluctuations in the abundance of recruits. This is despite the fact that a significant number of larvae spawned at Lizard Island do not disperse away from this reef (Jones *et al.*, 1999). This suggests that lack of a relationship between spawning output and the magnitude of recruitment may have been due to variation in larval mortality.

X. Conclusions

A pitfall of the multifactorial view of population limitation in populations of coral reef fishes has been its tendency to reduce the field to a series of case studies, each with their own interesting peculiarities. If the only generalization is that there are no generalizations, how far have we progressed? If it is really true that nothing is important all the time and everything is important some of the time, will we ever have the foundation for models that explain population limitation for more than one or two well-studied species? You cannot escape the conclusion that any attempt to formulate general models, even today, will be premature. Such a small proportion of known reef fish species have been studied and only a small proportion of those have been studied to the necessary depth. Model species such as *Pomacentrus amboinensis* have the characteristics necessary to test hypotheses using manipulative experiments, but we are only too aware that model species may not be representative of reef fishes as a whole. The processes limiting the vast majority of species that are relatively rare have not been examined at all (see Chapter 4, this volume).

On the other hand, the realization that many factors may be important has opened up what was once a very narrow field. Studies on nearly every life history stage and every process are now potentially worthwhile. At the very least, we now have some information on nearly everything that "might" be important. Up until 10 years ago reviews of the subject were dominated by studies on damselfishes (see Doherty, 1991; Hixon, 1991; Jones, 1991). Although damselfishes are still the most popular choice for testing new hypotheses, in recent years there has been a dramatic increase in the taxonomic breadth of the field. We have a greater understanding, not only of some of the larger, more mobile reef fish families, but also the even more numerous smaller, specialized reef fish families that were once considered an anomaly (Munday and Jones, 1998). So even though generalizations may be premature, there has never been a better time to formulate them.

We suggest that the new breadth of information supports the view that different ecological processes (competition, predation, etc.) act in fundamentally different ways, and each one has an indirect influence on the other. Different processes cannot be directly compared in terms of relative importance in the short term, because to detect them in the short term we have to measure different variables. Thus, at this stage we cannot test models that predict the circumstances under which resource limitation might be more important than predator limitation or vice versa (cf. Osenberg and Mittelbach, 1996). Our prediction is that in the long term, energetic processes associated with resource limitation will play an important role in explaining population patterns. However, almost no studies have been carried out long enough for the lagged effects of density-dependent energetic processes to be evaluated.

The different processes that ultimately govern population trends operate on and can only be detected on different time scales. Factors affecting the survival of new settlers may be detected in a matter of days. The effects of processes directly affecting juvenile growth and mortality can often be detected in a matter of weeks to months. Patterns of recruitment and predation can set both the short-term and the long-term dynamics of populations. The indirect effects of competition and stress on growth-mediated predation rates could take years to observe. Robertson's (1996) removal experiment, which detected the competitive dominance of *Stegates planifrons*, was carried out over 10 years, with the full

effect of competition taking 4 years to observe. This experiment is one of the few adequate demonstrations of interspecific competition among reef fishes. The effects of competition on reproductive output and its role in determining recruitment patterns could take decades to observe (Gurney and Nisbet, 1985; Nisbet and Onyiah, 1994). To measure the relative effects of any two processes requires that both are measured over time scales commensurate with the slowest acting process. Otherwise the importance of slow-acting processes will be underestimated.

At this stage, our greatest understanding of the dynamics of reef fish populations concerns variation in recruitment, the influence of predation on mortality, and the influence of competition on growth. Our understanding of the interdependence of numerical and energetic processes has lagged behind other disciplines. To define the kinds of indirect processes that may be potentially important we frequently have had to draw from the literature on freshwater and other marine fishes. Much greater attention must be given to additional factors, such as the energetic consequences of the risk of predation and the long-term numerical consequences of competition, behavioral interactions, and stress. Population structure and the size of the breeding population will reflect ontogenetic changes in the suite of processes affecting the quantity and quality of individuals in successive cohorts.

Whether generalizations ultimately turn out to be right or wrong they all have one thing in common. They encourage research by both supporters and detractors, which inevitably directs attention to where it is needed most. In our model we have highlighted the lack of information on the lagged effects of energetic processes on population dynamics, and we hope this stimulates research in that area. However, unless the average time span of population studies on reef fish increases substantially, the importance of these processes will not be recognized. Our lack of information on the quantitative and qualitative link between stock and recruitment is a major impediment to a complete understanding of population regulation in reef fishes.

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