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Coral Reef Fish Ecology

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INTRODUCTION

Since the mid 1970's, there has been an ongoing controversy regarding the mechanisms responsible for maintaining the high species diversity of fishes on coral reefs. Some investigators contend that the assemblages are in equilibrium, with interspecific competition causing the species to occupy well-defined unique roles in the community. Others maintain that the fish assemblages have a very large random component to their species composition and relative abundances, either because (1) many guilds are composed of species that are actively competing but are essentially interchangeable (lottery hypothesis: [Russel et al., 1974](#); [Sale, 1974, 1977, 1980](#); [Talbot et al., 1978](#)), or (2) populations are maintained below the carrying capacity, thus relaxing competition (recruitment-limitation hypothesis: [Williams, 1980](#); [Robertson et al., 1981](#); [Victor, 1983, 1986](#); [Wellington & Victor, 1985](#)). Recent investigations have considered the effects of predation on the structure of coral reef fish populations ([Hixon and Beets, 1991](#)).

The primary question between these views centers around pre-recruitment or post-recruitment processes, is the primary controlling influence on the larvae or the adults? As almost all coral reef fish have a pelagic larval stage in which the larvae face wide dispersion and heavy predation, resulting in high larval mortality, most coral reef fish larvae do not survive long enough to find suitable habitat to settle onto. If larval supply was sufficiently limited, competition among new recruits and adults would not occur as there would never be sufficient numbers of species similar in needs for space and food to be limiting.

Coral reefs are unique ocean ecosystems in that they have extremely high productivity and diversity, yet they occur in a virtual desert of organic nutrients. Coral reefs are composed of species that are highly evolved and specialized. This specialization has traditionally been explained by niche diversification as a result of past competition among previous species requiring similar resources. Clearly, the coral reef environment must have an affect upon its inhabitants, but the question remains as to the strength of these effects in shaping the evolution of coral reef fish species.

To what degree might we expect niche diversification to have taken place, how limiting are resources on a coral reef, and how much interspecific competition is actually taking place for these resources? As it takes adults to produce the prodigious quantities of larvae, and the adults live on coral reefs, there exists the possibility that even though recruitment may be very low, the reef environment can still play a role in the evolution and local assemblage makeup of coral reef fishes.

The interactions of new recruits to a reef with the current inhabitants of the reef does probably play a very significant role on the survival of the new recruits, and their ultimate reproduction. As piscivorous fish are common among coral reefs, it is evident that they probably play a significant role in shaping the assemblages of fishes found on coral reefs. To avoid predation, coral reef fishes require refuge

from predation. This refuge may be provided by the physical makeup of the reef itself, or through behavioral adaptations of coral reef fishes to reduce their individual threat of being consumed (schooling). The specific requirements of individual species for refuge space on the reef has been shown to be highly variable among species, with few species requiring the same resources. The difficulty in using this as evidence of niche diversification lies in the fact that it is not known if there is simply an insufficient number of fishes on the reef, due to either limited recruitment and/or predation, to cause a saturation of the reefs shelter resources, or if in fact the reason there is little overlap among species shelter requirements is due to past competition resulting in such a high degree of specialization that interspecific competition is now low.

Recently, researchers have begun to consider the possibility that low recruitment, predation, and competition all play major roles in structuring the assemblages of fishes on coral reefs, and these different effects take precedent at different times in the lives of individual coral reef fishes. Evidence for and against each effect has been accumulating among studies, with a trend that the significance of each effect is dependent upon the physical and temporal scale to which the effect was investigated.

In this paper, I review the challenges faced by, and the ecology of fishes during the three main stages of their life history, larval, settlement-juvenile, and adult. The different theories of how coral reef fish communities are structured are discussed, and interjections on how these theories relate to my favorite coral reef fish genus, *Acanthemblemaria*, are included.

Larval Ecology

The larval ecology of reef fishes may be the key the elusive understanding of what is controlling the abundance and distribution of reef fish populations. Settlement patterns of larval fishes may reflect processes occurring within the reef population or processes taking place in the oceanic plankton. Consensus has not been reached among researchers as to the significance of oceanic processes, but if oceanic processes can account for the observed patterns of both juvenile and adult abundances, one would not expect traditional equilibrial or other resource-limitation-based ecological theories to apply in coral reef fish ecology ([Victor, 1986](#)).

Most coral reef fishes have a pelagic, usually larval, stage resulting in a life history with two distinct and very different phases. These stages differ in almost all characteristics, from morphology to size, habitat, food, and behavior. The duration of the pelagic stage is species dependent, flexible, and ranges from 9 to well over 100 days ([Victor, 1986](#); [Thresher et al, 1989](#)). Size at settlement ranges from 8 to 200 mm, and from 2% to 80 % of the size at sexual maturity ([Lies, 1991](#)). The

pelagic stage probably determines the geographical size of population units, with the pelagic stage of most species broader than the demersal, adult stage ([Leis, 1986](#))

Coral reef fishes are very fecund, with egg production from 10,000 to over 1,000,000 per female ([Sale, 1980](#)), but mortality approaches 100%, with the majority of the mortality taking place during the pelagic stage. This high mortality of larval may have a major influence on adult population sizes of coral reef fishes ([Doherty, 1983](#)) as it may limit the supply of new recruits to a reef. The pelagic stages of reef fishes are very different morphologically from benthic adults as reef fish larvae do not hatch fully developed, reef fish eggs are small and larvae are small, and larvae need different morphological features for their pelagic existence than demersal adults.

Compared to other zooplanktors, reef fish larvae are rare, with concentrations of all taxa combined seldom exceeding 5 per cubic meter ([Leis, 1991](#)) and their distributions are ephemeral and highly structured. The distributions are controlled by physical oceanographic processes including circulation patterns, currents, and topography ([Leis, 1991](#)). Reef fish larvae eat a wide variety of microzooplankton taxa, with dietary overlap between species, fair to extreme feeding specialization in some, and ontogenetic shifts in diets in most species ([Leis, 1991](#)). No studies have shown that starvation is a major cause of mortality of reef fish larvae in tropical, supposedly food-sparse, waters ([Doherty et al., 1985](#)). On the contrary, the high incidence of feeding reported by most studies indicates that the fish larvae are finding adequate food. However, starving larvae may disappear quickly from the water column as a result of increased predation. ([Leis, 1991](#)).

The mortality of coral reef fish larvae in the pelagic stage is high and predation plays the dominant role in larval mortality ([Hunter, 1984](#)). During their pelagic stages, reef fishes may be consumed by a wide variety of predators, including corals, pelagic cnidarians and ctenophores, other larval fishes, and both reef and coastal pelagic adult fishes. The majority of coral reef fish larvae move away from the immediate vicinity of their natal reef some distance into more open water. This dispersal during the pelagic stage of reef fishes may be adaptive because reef fishes live in a patchy, uncertain environment ([Barlow, 1981](#)); however, this does not explain why so many taxa spend the pelagic stage far offshore.

An offshore pelagic stage may be an energy saving mechanisms because drifting in a rather slow ocean current demands less energy than position maintenance swimming in the reefs where tidal currents are strong ([Bourret et al., 1979](#)). The low abundance of reef fish larvae nearshore may also be due to very high predation pressure in the immediate vicinity of reefs ([Johannes 1978](#)). As coral reef fish larvae are very difficult to experiment with, there is very little evidence on which to draw conclusions as to why coral reef fish larvae have a pelagic stage. During the larval planktonic stage of coral reef fishes, a great deal of dispersal occurs and

may play a major role in determining the range of a species. Although, the planktonic larval duration has not been found to have a major effect on the geographic range of coral reef fishes. Little of the observed variation in species range seems to be accounted for by planktonic larval duration ([Victor 1986](#); [Wellington and Victor, 1989](#)).

Our current understanding of the larval ecology of coral reef fishes is that these larvae clearly face major challenges, and that most larval individuals succumb to these challenges. Aspects of the larval stage of coral reef fishes are definitely an important period of the life history of coral reef fishes, but the jury is still out as to whether this stage is the dominant, or, as has been suggested, the only stage that has a significant influence on the assemblages of fishes occurring on coral reefs. Although, even with the high larval mortality, it is possible that enough do survive long enough to recruit onto coral reefs and face post-larval influences and selection pressures.

Settlement and Recruitment Ecology

Since coral reefs are patchy habitats and reef fishes are generally sedentary, the only significant recruitment to local reef fish populations comes from the settlement of planktonic larvae. The extent to which reef fish populations are affected by patterns of settlement of larvae is an unresolved question. In contrast to the general assumption that animal populations are close to the carrying capacity of their environment ([MacArthur 1972](#)), recent studies of coral reef fish populations have shown that the supply of resources on the reef does not limit populations. A shortage of competent larvae may be keeping reef fish populations below the level at which the supply of food and space limits population sizes ([Williams 1980](#); [Doherty 1982](#)). Local factors determining the settlement characteristics of a limited supply of larval fishes could therefore play an important role in structuring the assemblages of coral reef fishes. An understanding of the settlement and recruitment ecology of coral reef fishes is therefore necessary.

The intensity of settlement of coral reef fish is variable both during and between seasons. In more temperate areas, such as One Tree Island on the Great Barrier Reef, this variability is intense, with virtually all settlement occurring during the summer ([Russel et al. 1974, 1977](#), [Talbot et al. 1978](#), [Williams 1983](#)). In the tropical Caribbean, settlement variability is less intense, being highest in the spring and fall and lower in the winter ([Luckhurst and Luckhurst, 1977](#); [McFarland et al., 1985](#)).

An explanation for seasonal cycles of settlement in tropical reef fishes is that settlement cycles simply reflect the varying breeding capabilities of adults, where seasonal energy surpluses could lead to higher fecundities ([Victor, 1986](#)). Although, it is usually assumed that the observed seasonality of settlement reflects

seasonal variation in larval survival rates ([Luckhurst and Luckhurst, 1977](#)), and adult spawning cycles are tailored to these predictable variations ([Doherty, 1983](#)).

Daily fluctuation in numbers of new recruits have been reported to occur both on lunar cycles ([Randall, 1961](#); [McFarland et al., 1985](#)) as well as independent of lunar cycles ([Williams, 1983](#)), and are generally ascribed to similar patterns of spawning by adults. The daily settlement pattern probably reflects the fluctuating survival rates of larvae, rather than the variable production of zygotes ([Victor, 1986](#)). Most settlement of reef fish larvae probably occurs at night ([Robertson et al., 1988](#)).

Movement of larvae inshore around the time of the new moon may help larval survival as the larvae would be passing over reefs on the darkest nights of the month, and tidal cycles occurring at the new moon may assist inshore migration. The tendency to settle near the time of the new moon may be an adaptation to reduce visual predation on incoming fish larvae by nocturnal planktivores. The magnitude of settlement is extremely variable over time ([Luckhurst and Luckhurst, 1977](#); [Russell et al., 1977](#); [Talbot et al., 1978](#); [Williams and Sale, 1981](#)).

What factors determine the magnitude of settlement is unclear, but theories accounting for differences in magnitude are abundant. Coral reef fish larvae settle over a broad range of sizes, with a trend in similarity in size at settlement within families. There is no apparent order on the variety of settlement sizes, but there is some pattern of small and transparent species settling in the back reef habitats where predation pressure may be lower ([Shulman, 1985](#)). Fishes that settle larger have a higher survivorship than those that settle small ([Doherty, 1982, 1983](#); [Victor, 1986](#)). An advantage must exist for settling small to outweigh the huge losses from early mortality. It may be that species that settle small are settling after only a short period of time in the plankton ([Victor, 1991](#)) thus reducing planktonic dispersal and their threat to predation while in the plankton column. Within species, the size at settlement does not appear to vary much ([Victor, 1991](#)).

The age of coral reef fishes at settlement is much more variable than the size at settlement, ranging from having had no planktonic phase to having spent many months as pelagic plankton ([Victor, 1991](#)). Little information is available on the relationship between size and age at settlement as few studies documented both size and age for the same species.

Processes determining if and where coral reef fish larvae settle out of the plankton are not well understood. What exactly influences a larvae to choose a specific location for settlement has not been determined. The ability of larval individuals to determine the local characteristics, including the availability of shelter, number of predators, and supply of food probably varies with species, as some are settling very immature while other are settling as fully developed juveniles. Many reef fishes settle while still clearly larval, while others remain in the pelagic

environment after transition to a juvenile stage ([Leis and Rennis, 1983](#); [Leis 1978](#)). Some reef fishes may settle into habitats other than coral reefs, such as tide pools ([Randall, 1961](#)), estuaries ([Keener et al., 1988](#)), seagrasses ([Bell et al., 1987](#)), algal beds ([Bellwood and Choat, 1989](#)), or mangroves ([Lindeman, 1989](#)). Leis describes the transition from pelagic environments to reef environments as seemingly dangerous "First, the prospective settler must pass through the wall of mouths that surrounds many reefs. Second, an animal well adapted both morphologically and behaviorally to the pelagic environment must quickly become well adapted to the reef environment. The animal must be extremely vulnerable during this transition...How most species cope with this seemingly vulnerable period between settlement and recruitment is unknown." ([Leis, 1991](#)).

Post Recruitment Ecology

In 1975, Paul Ehrlich stated "No ecologist studying coral reef fishes would doubt that there is life after recruitment" ([Ehrlich, 1975](#)), but the importance of that life stage on the population assemblages of coral reef fishes has been under considerable debate among coral reef fish ecologists. Post recruitment processes include interspecific interactions, such as interspecific competition, lottery competition for territories, predation, and intraspecific interactions, such as intraspecific competition and nonrandom recruitment.

Interspecific Interactions In the early evolution of our understanding of coral reef fish ecology, interspecific interactions among resident fishes was used to explain observed patterns in assemblage structure, with emphasis placed on competitive interactions.

Competition: Studies done in the Great Barrier Reef, the Caribbean, and other locations at a wide range of spatial scales, from microhabitat to much broader geographic scales, invoked competitive interactions as an explanation of the observed processes, but simply invoking them did not establish that that competitive interactions were actually occurring ([Sale, 1991](#)). Few experimental studies investigating interspecific competition have been undertaken, but manipulative experiments designed to test for effects of one species on another are increasing. In the majority of these experimental studies, pairs of species are selected that are most likely to interact, given basic data on their diets and use of space. Most of these studies have not detected important effects of interspecific competition on demographic parameters. Interactions between *Pomacentrus flavicauda* and *P. wardi* ([Doherty, 1982, 1983](#)), between *Pomacentrus ambionensis* and *Dascyllus aruanus* ([Jones, 1987, 1988](#)), and between *Pomacentrus flavicauda* and *Salarias fasciata* ([Roberts, 1987](#)) were not shown to influence basic parameters such as abundance, growth, or mortality. However, some demographic effects have been detected, suggesting that interspecific

competition may alter distributional patterns among habitats, but not overall abundances of species populations. [Clarke \(1989\)](#) demonstrated in both non-manipulative and manipulative studies that two closely related species of blennys, *Acanthemblemaria spinosa* and *A. asperi*, compete for the suitable shelter sites, (vacant tube worm holes). *A. spinosa*, which was shown to have a higher metabolism, is competitively superior in securing the sites which have the greatest access to planktonic food drifting by, relegating *A. asperi*, which has a slower metabolism and lower feeding requirements, to lower sites with less food availability. This study, which has been mostly ignored by coral reef fish ecologists, provides pretty convincing evidence for niche partitioning. As *Acanthemblemaria* sp. are quite different from most coral reef fish species in that they have very specific shelter resource needs, the applicability of this study to coral reef fishes as a whole may seem suspect. When it is considered that this is a very small coral reef fish, obviously not capable of producing larvae to the same degree as larger coral reef fishes, yet adult competition is taking place, questions as to the validity of the recruitment limitation hypothesis are raised, and no studies have shown that *A. sp.* larvae have a significantly different ecology than other coral reef fishes.

Lottery Competition for Territories: Evidence suggests that availability of living sites limits the populations of coral reef fishes, with similar species of fish competing for limited space on the reef ([Sale, 1978](#)). This competition is continuous, yet unlikely to lead to either niche diversification or competitive exclusion ([Sale, 1991](#)). Sale demonstrated that for three species of permanently territorial pomacentrids, territory was defended throughout the year, although not necessarily against other adults, but rather against newly arriving recruits. The lottery hypothesis is an attempt to explain how limited shelter sites can lead to competitive interactions faced by recruits, yet not by adults. In this theory, the priority of arrival of recruits, rather than subtle differences in requirements or competitive abilities of adults, determines which species holds a territory. Once a fish is in a territory, its optimal strategy for reproductive success would be to stay put, breed often, and disperse the resulting offspring widely ([Sale, 1982](#)). This strategy would allow an individual to maximize its chances of getting offspring into suitable living sites as such sites appear. The 'lottery' is among newly arriving recruits with similar space requirements, which enter a lottery for occupying available sites. Once a larvae arrives, it secures its position within the community and should be able to defend the site against latecomers. Adults produce prodigious quantities of gametes so that some of their offspring may win the 'lottery' and be the first to arrive at a newly vacant site. As long as some sites are won by each species, the lottery continues. This hypothesis may explain why there is such high within-site diversity, as many species could be winning the lottery to a sufficient degree

to continue playing. This hypothesis can be compared to a recent trend in human communications. When the idea of using radiowaves for private mobile telephone conversations became technologically feasible, a huge auctioning of a limited bandwidth of airspace was undertaken. The auctioning occurred not on a national basis but rather at a local level, with individual towns and municipalities selling the right to use the airwaves. There were many companies with the potential of setting up a cellular phone network, but airspace was awarded to only those companies which were present when the airspace was being sold in a specific region. There was an initial competition between the companies (bidding), but once a company was awarded the airspace, the competition ceased as it was impossible for another company to take their airspace away from them unless the original company went out of business. In this case, there was an initial competition among new companies for space, but this competition had little ability to cause cellular phone technology to change or to exclude other companies from the cellular phone communications business as there are many localities wishing for this service. As each company which successfully purchased airspace was given a local monopoly on the market, selection pressure for the best company by the cellular phone customers was not present. (Personal conjecture)

Predation: The predation hypothesis, which states that postsettlement mortality due to piscivory determines adult patterns of abundance, received little attention until the late eighties, yet predation may have an important role in structuring the assemblages of coral reef fishes. The predation hypothesis asserts that predation on new recruits, juveniles, and adults results in such low population sizes that severe resource limitation and competition are precluded. The risk of predation on coral reefs is great and reef fishes have evolved a variety of mechanisms to minimize the risk ([Hixon, 1991](#)). Predation structures a prey assemblage by altering the absolute and relative abundances of species, thus affecting the distributions and perhaps the local diversity of the prey. Piscivorous reef fishes are diverse in behavior as well as taxonomy, and can be divided into five major categories: (1) open-water species that pursue their prey, such as jacks; (2) cryptic species that ambush their prey, such as lizardfishes; (3) species that apparently habituate prey to an illusion that they are nonpredatory, such as groupers and snappers; (4) species that slowly stalk their prey, such as trumpetfishes; and (5) species that attack prey within crevices, such as moray eels. ([Hixon, 1991](#)). The abundance as well as the diversity of piscivorous fishes is high, accounting for up to 54% of the total fish biomass (at One Tree Island on the Great Barrier Reef)([Gordon and Talbot, 1976](#)). In addition, a considerable host of invertebrate and tetrapod piscivores also occur on coral reefs, including anemones, cone snails, mantis shrimps, seastars, seasnakes, and seabirds. Prey minimize their risk of predation in a

number of ways. Various morphological deterrents include tough skins, fin spines, exceptionally deep bodies, the ability to inflate, swimming abilities, mucous envelopes, cryptic coloration, eyespots, conspicuous "warning" coloration, toxic tetrodotoxin, ostracitoxin and venomous bites. Prey fish also avoid predation through various behavioral patterns including schooling, spawning, and daily activity patterns. Testable predictions of the predation hypothesis are both indirect and direct. Two indirect predictions are that cohorts of reef fishes under intense predation should suffer disproportionately high mortality early in life, and that comparing different reef systems should result in a positive relationship between refuge availability and prey fish densities. For prey survivorship, a general pattern that small, young, or otherwise naive animals are more susceptible to predation than larger, older, experienced adults, therefore, if predation affects prey abundance, then mortality is likely to be more severe for early-aged individuals than for adults. Concerning prey refuge availability, the possibility exists that predators cause prey to compete for refuge space ([Holt, 1984, 1987](#)). Two direct predictions are that in the absence of piscivores, the density of prey fish occupying a particular reef would reach a limit imposed by other processes, such as recruitment limitation or competition, thus a comparison of otherwise similar reef systems with broadly different piscivore densities should result in a negative relationship between piscivore and prey-fish densities, and that local prey species richness and/or evenness should shift in predictable ways as predation intensity increases over a broad range ([Hixon, 1991](#)). Both correlative and experimental evidence support these predation hypothesis predictions, but insufficient evidence exists to conclude unequivocally that piscivores strongly affect the absolute and relative abundances and, by extension, the community structure of reef fishes ([Hixon, 1991](#)). Hixon puts the role of predation in context as a part of a continuum of processes, "It is easy to envision a combination of low larval abundance (recruitment limitation) and high postsettlement predation precluding competition for food, yet forcing prey fishes to compete for refuge space." ([Hixon, 1991](#)). Predation would be limiting the role of competitive interactions when recruitment was low, but if predation was not intense when recruitment is high, competitive interactions could manifest. In the case that predation was intense, competition for nonrefuge resources would be precluded, yet refuges from predation may be limiting so that competition for shelter occurs ([Holt, 1984, 1987](#)). Even in cases of recruitment limitation, if predation was high, competition for refuge space would still exist. Intraspecific Interactions Little attention has been paid to the role of intraspecific interactions in reef fishes, yet conspecifics are likely to be the neighbors most similar ecologically to a reef fish, and the reef fish life history appears to make it unlikely that neighbors will be close relatives ([Awise and Shapiro, 1986](#)). Without altruism derived through kin selection, intraspecific competition

should be especially prevalent. Studies investigating intraspecific competition in newly recruited fishes to experimental reefs with and without adults have demonstrated that intraspecific competitive effects do occur, but that they are usually effects on growth and maturation rather than on survivorship ([Doherty 1983](#); [Jones 1987](#)). Competition has been implicated in explaining differences in the growth rates of early and late settlers. [Ochi \(1986\)](#) suggested that the growth of late-settling Amphiprion was limited by competitive interactions with early settlers. Experimental evidence for *Pomacentrus ambionensis* ([Jones, 1987](#)) shows that late settlers grow considerably faster on reefs that do not also harbor individuals that settled earlier. Experimenting with variations in the numbers of available shelter holes and the numbers of fishes on small artificial reefs, [Buchheim \(1992\)](#) demonstrated in a very resource specific coral reef fish, the spiny head blenny, *Acanthemblemaria spinosa*, that intraspecific competition for shelter sites does occur among adults, and fishes without suitable shelter sites quickly fall to predation, in this case, by lizardfish, (*Synodus* sp.) ([Buchheim and Hixon, 1992](#)).

Discussion

The understanding of the processes involved in maintaining high species diversity of fishes on coral reefs has evolved considerably in the past twenty years. A complete cycle has occurred in which competition was originally viewed as the primary controlling influence on coral reef fish evolution and diversity, then was refuted, and is now shown to have possible impact, but not to the degree as was attributed to competition originally.

Competition fell out of popularity among coral reef fish ecologists as a viable theory with the larval and recruitment ecology of coral reef fishes was considered; it was suggested that competition could not take place as the levels of fishes successfully recruiting to reefs was too low for competitive interactions to occur. This recruitment limitation hypothesis created a large controversy among coral reef fish ecologists, as it does not provide any means for post recruitment processes to have an influence on the assemblages of coral reef fishes. Peter Sales 'Lottery Hypothesis' was another hypothesis, taking a different route, that refuted adult coral reef fish competition, although larval supply was assumed to be abundant.

The influence of predation was ignored until the late Eighties, but the ramifications of the effects of predation again created controversy. Predation theory allows for competitive interactions to take place even when recruitment is low, and the effects of piscivores has been shown to have a significant influence on the composition of coral reef fish communities.



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