

INTEGR. COMP. BIOL., 44:390–399 (2004)

Connectivity, Recruitment Variation, and the Structure of Reef Fish Communities¹

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SYNOPSIS. Coral reefs contain the most speciose communities of fishes on this planet, so it is appropriate to use these to explore how fish species are organized into communities. While descriptive data suggest that the diverse communities of fish on coral reefs are equilibrium assemblages of species, all finely adapted to specific and unique ecological roles, these are highly dynamic, non-equilibrium assemblages with structure driven more by patterns of recruitment and loss of individual fishes, than by patterns of resource allocation among differently adapted phenotypes. As a consequence, local assemblages differ in structure, and structure wanders through time. Individual fish are confronted by different mixes of species in different times and places. The recruitment process that drives these dynamics is complex, being governed by several mechanisms, and local populations receive some portion of their recruitment from distant sources. Information on this connectivity among local populations is critically important for management which is based increasingly on use of marine protected areas (no-take zones) both to conserve, and to provide sustainable fisheries. At present, however, we do not know the spatial scale or the extent of this connectivity, and this critical knowledge gap impedes both management, and fundamental understanding.

INTRODUCTION

Coral reefs can support the most highly diverse fish communities on this planet. “Can” because not all reefs support highly diverse fish faunas (Fig. 1). Indeed the geographical patterns in diversity are an interesting subject in their own right (Bellwood and Hughes, 2001; Connolly *et al.*, 2003; Mora *et al.*, 2003). “The most highly diverse” because the high diversity extends to families, orders, and higher divisions among the fishes. This is in contrast to those other centers of high species richness, such as the rivers of Amazonia and the great lakes of Africa, where the high species diversity is primarily centered in one or a few families (Sale, 1980a). As well as being potentially very diverse, reef fish communities are primarily communities of advanced Perciformes, although with a good representation of other groups of fishes. They are the result of a pronounced radiation of advanced species that evolved during the Tertiary, along with the Scleractinian reefs they occupy (Choat and Bellwood, 1991; Bellwood and Wainwright, 2002).

Early ecological study of reef fish communities began with assumptions carried over from terrestrial ecology (Ehrlich, 1975; Sale, 1980a). There was an expectation of equilibrium, and of stable patterns of coexistence of co-evolved species based on fine-scale niche diversification within closed communities. Early reports upheld these expectations. Indeed, there is ample evidence in the highly evolved trophic structures of reef fishes, or in their sometimes precise habitat requirements, to support explanations of high diversity based on fine niche partitioning along the trophic and

habitat axes (Findlay and Findlay, 1985, 1989; Westneat, 1995). However, maintenance of community structure through niche partitioning and related processes requires strong compensatory interactions among species that will ensure their patterns of relative abundance track patterns of resource availability, and despite the congruent morphological and ecological patterns of differentiation among species, the dynamics of reef fish communities reveal a very different, and considerably more interesting picture than the static equilibrium such processes would generate (Sale, 1991). My goal is to summarize current understanding of these systems, while noting that many colleagues hold different views, and to review the implications for the sustainable management of reef fishes both for conservation and for fishery resources.

REEF FISH COMMUNITIES ARE OPEN SYSTEMS

The change in ecological understanding that occurred during the 1970s and 80s has been reviewed previously (Sale, 1980a, 1988, 1991). Suffice that it came about when ecologists were able to spend more time on coral reefs, to make repeated visits, and to do manipulative field experiments. Nothing reveals the workings of a system better than the good kick a manipulation represents, although careful study of the system over an extended period of time can also be revealing. The short visit to collect fish that are then examined in the lab for clues about the ecology is only a snapshot of the community being studied. And snapshots are necessarily static.

To fully appreciate the dynamics of reef fish populations and communities one must recognize that these are fundamentally open ecological systems comprised of local populations that are replenished by the settlement of larvae following a sometimes lengthy pelagic phase (Mora and Sale, 2002). A handful of exceptional species, worldwide, lack any pelagic phase. Otherwise reef fish species either spawn demersal eggs that hatch

¹ From the Symposium *Patterns and Processes in the Evolution of Fishes* presented at the Annual Meeting of the Society for Integrative and Comparative Biology, 4–8 January 2003, at Toronto, Canada.

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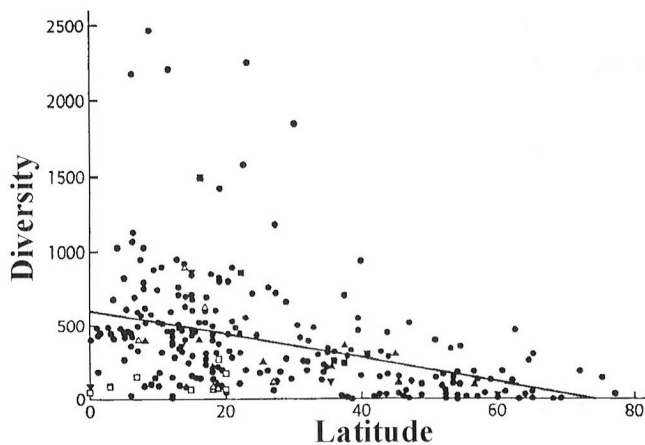


FIG. 1. Numbers of fish species recorded in a number of coastal locations throughout the world. There is a tendency for shore fish communities to be speciose, particularly in equatorial regions, however, even here some, even on reefs, can be relatively depauperate, supporting no more species than a typical temperate rocky shore. (taken from Jones *et al.*, 2002).

within days into larvae that move immediately up into the water column, or they spawn in midwater, producing buoyant eggs that hatch in hours or days (Leis 1991). In either case, otolith microstructure reveals that the ensuing pelagic phase lasts from 7 to 10 days in a few species like members of the genus *Amphiprion*, to several months in some Acanthuridae and Monacanthidae. A typical pelagic duration is 28 to 35 days—offering substantial time for travel between natal and settlement site. While the duration of this pelagic journey should guarantee that fish travel at least hundreds of meters, it is an open question whether they typically travel a little, or a lot further than this. The spatial scale above which reef fish populations become closed (because the scale is large enough to contain larval dispersal) remains unknown, but could be very extensive for fish of average (1 month) larval duration. It could also be considerably smaller if fish use their sensory and locomotory capabilities to minimize their transport away from natal reefs (Cowen *et al.*, 2000).

The patchy distribution of coral reef habitats also serves to subdivide populations on many spatial scales, and most fishes seldom move among patches of suitable habitat once the larval stage is completed. Exceptions are those species that show ontogenetic habitat shifts, typically from mangrove and seagrass habitats to coral reefs (Eggleston, 1995; Nagelkerken *et al.*, 2000), and those that engage in spawning migrations to distant aggregation sites (Colin and Clavijo, 1988; Colin, 1992; Sadovy, 1994). As a consequence, local populations of most reef fish species, sometimes occupying patches of suitable reef habitat that may be only tens or hundreds of square meters in extent, exist as small breeding groups that receive an unknown but likely considerable proportion of their settling larvae from other nearby or more distant populations. This openness interrupts the expected link between local competitive success of individuals and their relative

contribution to future generations at that local site, thus precluding simple selective mechanisms for the evolution of adaptations to local conditions or local mixes of species (Sale, 1991). The adaptation and specialization of reef fishes must be looked for on a regional scale where, as shown below, the individual faces a highly variable mix of potential competitors, predators and mutualistic partners. Local reef fish communities are not co-evolved systems.

While it is appropriate that studies of the evolution and phylogeny of fishes emphasize the differences among species, their particular specializations, and the competitive interactions among sibling species that likely drove their evolution, modern ecological study of fish on coral reefs reminds us that in these open ecological systems, life need not be a continuous struggle among narrowly and precisely specialized species. The adaptability of reef fishes, and their ability to persist despite the close proximity of other, ecologically very similar species, are correlates of their open communities with the flexible population dynamics these allow.

Critical studies in the 1970s that showed the dynamics of reef fish communities included studies of the colonization of artificial reefs (*e.g.*, Talbot *et al.*, 1978), and of the recovery of experimentally denuded natural reefs (*e.g.*, Sale and Dybdahl, 1975; Sale, 1980b). These studies were done at quite small spatial scales on single coral heads, or on natural or artificial reefs seldom more than 1 m³ in size. At these small scales, reef habitat did not support a narrowly prescribed number of stipulated species adapted to live there. Instead, a broad range of species were able to occupy any given site, usually far more species than would ever be found there at one time, and the particular mix of fishes present at any one time was heavily influenced by the particular prior history of colonization. Long-term non-manipulative studies of the fish communities present at particular small sites showed very considerable variation through time in species composition—an apparent consequence of variable patterns of colonization by newly settled recruits, and of mortality of prior residents (Sale *et al.*, 1994).

This early work on community dynamics was dismissed by some because of the small scale at which it was done (at a time when virtually all reef ecology was done on “the reef” out in front of the field station). Lower resolution, non-manipulative studies, done at larger spatial scales, continued to sustain a view of ecological equilibrium and orderliness (*e.g.*, Anderson *et al.*, 1981), prolonging the paradigm shift that was inevitably occurring (Sale, 1988). However, there were also some larger scale studies of recruitment dynamics that showed a surprisingly profound variability in this process over a broad range of spatial and temporal scales (Doherty and Williams, 1988; Fowler *et al.*, 1992). These provided a ready mechanism to generate the differing histories that could explain the patterns in community composition across sites or through time, and could reconcile the small-

scale manipulative, and the broader-scale descriptive studies.

VARIABLE PATTERNS OF SETTLEMENT AND RECRUITMENT

The difficulty and cost of working directly with larval reef fishes has been one reason for the focus of studies on settlement and recruitment, and we know far more about the ecology of reef fish in the two weeks following settlement than in the two weeks prior to that event. While settlement tends to occur at night and is difficult to quantify directly, ecologists have tended to sample recruitment (animals which settle and survive) quite soon after settlement, rather than later in life as is typical in fisheries biology. As a result, a lot of the spatio-temporal variation in settlement can be captured in the recruitment data. In addition, since a substantial portion of post-settlement mortality occurs within the first week or two following arrival, recruitment data recorded within a few weeks of settlement can be a good proxy for the additions to breeding populations that will subsequently occur (Williams *et al.*, 1994).

Studies of recruitment have demonstrated substantial variation both spatially and temporally, and at a number of scales, commencing with Williams and Sale (1981), who collected recruits the day after settlement and demonstrated order of magnitude variation in recruitment to patches of the same coral species in a single coral reef lagoon. Substantial variation existed between patches 1 km apart, and among species. Patterns in this variation differed significantly between years. The latter was particularly surprising because it meant that spatial patterns in recruitment could not be explained by orderly differences among species in habitat preferences. Subsequent studies validated and extended this work (reviewed in Doherty and Williams, 1988; Caley *et al.*, 1996), and we learned that reef fishes were no different to other fish species in exhibiting wildly fluctuating recruitment success. Today, if one reports that recruitment is highly variable in space and time, one is greeted by polite yawns—this is one well-documented fact, although, in my view, its implications are not widely appreciated, particularly when we recognize that most recruitment studies have examined numbers remaining after early post-settlement mortality has occurred. The supply of fish to breeding populations is markedly variable in space and time. Implications of this will be considered later.

Causes of recruitment variation remain elusive. Some studies find that subtle habitat preferences make it possible to predict distribution of recruitment of particular species, and some temporal variation has been tied to patterns of spawning activity (Tolimieri, 1995; Holbrook *et al.*, 2000; Schmitt and Holbrook, 2000; Munday, 2002; Sponaugle *et al.*, 2002). Differences in habitat are usually confounded with differences in spatial location among sites, but Sale *et al.* (2004), in a regional-scale study using an extensive set of data

from 15 species at sites on seven reefs over three years, showed that habitat differences among sampling sites were responsible for only a minor portion of spatial variation in recruitment. While habitat varied among their sites, and even changed through time as corals grew, principal components extracted from habitat variables accounted for little of the variation in fish recruitment at scales of site (1 km) or reef (10 km). Redundancy analysis of the fish assemblage revealed that of the 51.6% of variation in recruitment that could be explained, 18.6% was unique to spatio-temporal scales, 26.3% was shared by spatio-temporal and microhabitat variables, and only 6.7% of total variation in recruitment could be attributed exclusively to variation in habitat. Their interpretation was that while differences in microhabitat undoubtedly play a role in determining the small-scale distribution of fish, these effects do not scale up to play a major role in determining patterns of distribution on larger scales.

Modeling studies (*e.g.*, Limouzy-Paris *et al.*, 1997; Cowen, 2002) reveal significant variability in the current stream in coral reef regions, and this can distribute larvae to many different down-stream locations. In addition, larval mortality is so high (close to 100%) that this factor alone introduces significant stochasticity into patterns of settlement to reefs. The consensus appears to be that settlement is driven by a multiplicity of variable factors that determine where fish are transported and how well they survive during larval life, and that post-settlement survival similarly depends on a variable availability of habitat, food and predators. Under such circumstances, and especially given the often heavy mortality in the hours or days immediately following settlement, considerable spatio-temporal variation in recruitment is expected, but far from easily understood.

LARVAL ECOLOGY, CONNECTIVITY, AND COMMUNITY STRUCTURE

To be fair, the non-equilibrium paradigm emphasized here would not be unanimously endorsed by all reef fish ecologists. We vary in the extent to which we tolerate departures from the orderliness in ecological structure imparted by interspecific biotic interactions and natural selection in closed ecosystems, and the many examples of highly specialized adaptations in reef fish habitat requirements and trophic apparatus are good evidence that selection and competition have been very important in determining their evolution. But processes driving evolution do not necessarily determine current ecological relationships among species (remember the 'ghost' of competition past), and while there are examples of local species abundances being set by biotic interactions after settlement, there are equally good examples of abundances being set by patterns of arrival of new recruits (*e.g.*, compare reviews by Doherty [2002] and Hixon and Webster [2002]).

At present there is hot debate concerning the extent to which reef fish larvae are retained to recruit back to their natal populations rather than being dispersed

to other sites. That a larval life is nearly universal despite widespread existence of parental care of the eggs argues strongly that pelagic life is biologically important for reef fishes, but we do not know the spatial scales on which the larvae spend their lives. The debate, which is unfortunately being couched as “retention” vs. “dispersal” (Warner and Cowen [2002] and accompanying papers, Mora and Sale [2002]), exists because we have sufficient evidence to know that larval reef fish are well-adapted, behaviorally complex, pelagic organisms that do not disperse passively on water currents, but inadequate information concerning the extent of their abilities to control their larval dispersal, and whether these abilities are used to stay close to home or to travel widely (Stobutzki, 2000; Mora and Sale, 2002). The argument is about the spatial scale of connectivity, and its resolution will be important for management of coral reefs and their fisheries. Its resolution also has important implications for our fundamental understanding of the structure and dynamics of these communities. If larvae are predominantly retained at local (kilometer) spatial scales, selective processes can operate at similarly local scales, and local reef fish communities may be fundamentally equilibrational systems, structured primarily by the biotic interactions among local residents. If, as I suspect, there is considerable exchange of larvae among local populations, even at 10 kilometer (100 km²) scales, history and settlement dynamics are more likely to be the primary factors determining dynamics of local populations, and community structure will be less orderly.

Recent studies of the swimming abilities of larval reef fishes have demonstrated considerable variation among taxa, while confirming that most are conspicuously more capable swimmers than are the temperate species, such as plaice, that were the initial focus of studies of larval fish biology (Stobutzki and Bellwood, 1997; Stobutzki, 1998). Studies of their sensory capabilities are similarly demonstrating previously unsuspected competencies (Myrberg and Fuiman, 2002), and simple behavioral experiments are suggesting they may use these sensory and swimming capabilities to swim towards reefs they can hear, or smell (Stobutzki and Bellwood, 1998; Tolimieri *et al.*, 2000, 2002; Leis and Carson-Ewart, 2001; Montgomery *et al.*, 2001; reviewed in Leis and McCormick, 2002), or to remain in the near vicinity of, rather than being advected away from reefs (Doherty *et al.*, 1996). Advances in these areas are limited by the technical difficulties inherent in studying the behavior of pelagic organisms that are undergoing rapid ontogenetic changes in morphology, physiology and behavior, and by the relative paucity of sensory physiologists interested in studying these creatures.

More conventional oceanographic studies of the distribution of reef fish larvae are hampered by the scarcity, relative to other plankton, of reef fish larvae, and by their considerable abilities to avoid collecting gear. Efforts to solve these technical difficulties have re-

sulted in the use of larger nets, and the development of plankton purse seines, light traps, channel nets and crest nets—all new collecting gear designed specifically to sample these elusive organisms. No existing method samples without bias, and all are limited to use in particular habitats (Choat *et al.*, 1993). Most yield modest numbers with their inherent stochasticity, and results of studies of larval distribution tend to be suggestive rather than definitive. Nevertheless, data reveal that reef fish larvae have definite depth preferences that are specific to a species and may change ontogenetically, and that their horizontal distribution is frequently strongly patterned relative to the locations of reefs, islands, and coastlines (Sponaugle and Cowen, 1996, 1997; Cowen, 2002). These are capable organisms, although we have a long way to go to learn how they use their capabilities.

Additional work, and the use of innovative methods (Thorrold *et al.*, 2002), is going to be necessary before we will be able to estimate the extent of connectivity among local populations of coral reef fishes with any certainty. There is some urgency to undertake this work, and the importance of connectivity will be discussed in the final section. First, however, it is worthwhile to evaluate the consequences of recruitment variation—whether that variation is due purely to natural stochasticity in a process (larval ontogeny) in which close to 100% of each cohort die, or to the coupling of that variation with the variable delivery of additional larvae from other populations in an inter-connected metapopulation.

ECOLOGICAL CONSEQUENCES OF RECRUITMENT VARIATION

Consider a set of nearby local patches of the same general type of reef environment, such as a series of windward fore-reefs that might be expected to support very similar species of fish, assembled into very similar communities. When recruitment rates can vary by an order of magnitude among locations and among successive seasons, and when these variations are not closely correlated among species (as is predominantly the case—Doherty and Williams, 1988; Tolimieri *et al.*, 1998), the delivery of new cohorts to local populations must differ, and the local communities thus formed will differ also. Such levels of spatial and temporal variation in recruitment are common among reef fish species (Doherty and Williams, 1988; Sale *et al.*, 2004), as they are among other coastal marine species with pelagic larvae (Caley *et al.*, 1996). These spatio-temporal differences in replenishment of populations may lead to the formation of substantially different local communities, or they may be ameliorated in either or both of two ways, so that community structure remains apparently more constant (Fig. 2).

If mortality schedules subsequent to recruitment are strongly density-dependent, pulses of high recruitment will be followed by enhanced mortality and the standing population will remain at or close to an equilibrational size. Hixon and Webster (2002) have reviewed ex-

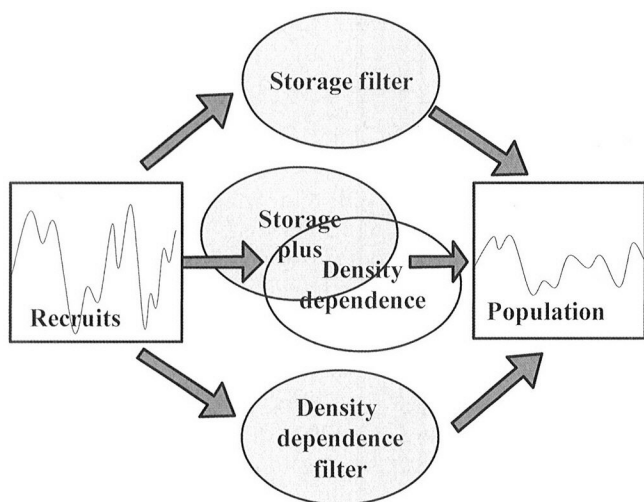


FIG. 2. The two ways of ameliorating fluctuations in population size caused by highly variable rates of recruitment. Variation in recruitment might be dampened by subsequent density-dependent mortality, by the storage over many recruitment seasons characteristic of long-lived, slowly-recruiting species, and by both these processes together. Despite these possibilities for amelioration, there is evidence that considerable variation in population size usually remains.

amples of such density-dependence and emphasized its importance in regulating population size. However, I believe the prevalence and importance of such mechanisms tends to be overstated. There are many examples where mortality has been found to be density-independent over a broad range of densities of fishes. See also Doherty (2002).

If the species concerned are long-lived, so that successive cohorts of recruits represent only a small proportion of the total population present, then quite large fluctuations in rate of recruitment will generate only small ripples in population size, even in the absence of any density-dependent compensation. Only if rate of recruitment is higher than the long-term average for a series of successive cohorts will overall population size change measurably—as well as protecting against recruitment failure, the storage effect (Warner and Chesson, 1985) is an efficient dampener of fluctuations in recruitment regardless of whether they are to higher or lower than long-term average levels.

Density-dependence and storage can act together or separately or not at all. The effect of both is to minimize the effects of temporally variable recruitment on total population size. If populations are sufficiently acted on by one or both mechanism, the strongly varying patterns of recruitment will not change the overall species composition, or overall density of a reef fish community. However, there will still exist variation in age structures and schedules of mortality for the component species. These variations can have significant impacts on the social organization of each local population, and on its reproductive potential.

Studies of the behavior of reef fishes have inadvertently demonstrated the extent of variation in com-

munity structure. Aldenhoven (1986a) reported substantially different social structures among local populations of *Centropyge bicolor* a few kilometers apart at Lizard Island, Great Barrier Reef. She suggested these different social structures developed because the demography of these local populations was substantially different despite their proximity, and generally similar environments (Aldenhoven, 1986b). Differences among populations occurred in rates of recruitment, rates/ages of maturation, and rates of mortality. Other authors, studying particular species in different geographic locations, have reported conflicting patterns of social organization and reproductive ecology—these differences appear to be real, and due to differences in density, age structure, or mortality schedules at the various locations (Shapiro, 1991; Warner, 1991, 1997). Some of the best data concern the reproductive ecology of the Bluehead wrasse, *Thalassoma bifasciatum*. In this species, as in many wrasses, there are terminal phase males that are larger, older, and colorful, and initial phase males that are smaller and drab in color. The terminal phase males, which are predominantly derived through protogyny, tend to have high reproductive success, pair spawning with numerous females per day, while the initial phase males are usually less successful, participating in group spawning and sneaking occasional fertilizations with terminal phase males and their females. In a series of elegant, largely manipulative, studies (reviewed in Warner, 1991, 1997), Warner and his students have been able to demonstrate that the relative abundance of initial phase males varies among populations, and that it is related to local population size, which itself depends on extent of suitable habitat—large patch reefs support large populations. Initial phase males are proportionally more abundant in larger populations that become denser when they aggregate at the patch reef edge to spawn each day. Sexual strategies of initial phase males are more successful in more crowded groups. Given that *T. bifasciatum* has pelagic larvae like virtually all reef fishes, this very local variation in expression of male sexual strategies is almost certainly a phenotypic response to local population size or to density at spawning sites (or to some strongly correlated factor). Its result is to vary demography among locations. Should recruitment variation or altered mortality schedules set up differences in density of this species, we can anticipate a modification of male sexual patterns as a result.

These studies of behavioral ecology sum to indicate that spatial and temporal variation in the demographic properties of reef fish populations exist, including dramatically different patterns of social organization, and that some at least of these are responses to variation in density set by variable recruitment. Variability in density of reef fish populations has been long documented (Sale, 1980a), but largely ignored until recently, probably because we do not notice what we do not expect to see. In addition, new demographic studies are revealing considerable spatial variation in rates of growth, maturation, and survivorship. While these

mostly focus on geographic-scale comparisons (Choat and Axe, 1996; Choat and Robertson, 2002), some are done at smaller scales (Kritzer, 2004), and on species (damselfishes, Meekan *et al.*, 2001) for which we can reliably discount any effects of differential fishing pressure. I anticipate that much more evidence of local variation in population age structure, demographic rates, and social organization will be forthcoming, and that recruitment variation will be found to drive some of this variation, just as it drove variation in age structure in *Pomacentrus molluccensis* and *P. wardi* (Doherty and Fowler, 1994a, b). We must anticipate that different local populations of reef fish species may differ substantially in a number of demographic properties, and that these differences will modify their social behavior, their reproductive potential, and perhaps, their interactions with other species.

What about evidence of effects of recruitment variation on community structure and dynamics? Studies that rigorously compare structure of local communities at several replicate sites, and monitor structure through time to detect any changes have been rare. Many early studies used less precise census methods, sampled only a few times, and used relatively crude indices of community similarity (*e.g.*, the Jaccard index that uses only presence/absence data) to conclude that temporal change was slight (reviewed in Sale, 1991). Ault and Johnson (1998) used replicate reef-slope contiguous and patch reef sites, and followed sites for two years. They found temporal changes at each site to not differ from a random walk, although the extent of change tended to be somewhat less than expected, particularly on contiguous reef sites. This suggested to Ault and Johnson that the drift of community structure might be constrained in some way. Patterns of change were unique to specific sites.

Chittaro and Sale (2003) used an extensive database on small patch reefs to compare the communities that assembled in this reef habitat at One Tree Reef, Great Barrier Reef and at Tague Bay, St. Croix, U.S. Virgin Islands. The patch reefs used were quite similar in size and structure, and were in very similar lagoonal/back-reef environments. One might anticipate that they would be occupied by very similar communities of fishes, despite existing in totally separate biogeographic provinces. Twenty patch reefs had been monitored over 10 years in Australia, and 20 comparable patch reefs had been monitored over 5 years at St. Croix.

In order to compare community structure at sites that shared no species, it was necessary for Chittaro and Sale to assign all species to one of 12 trophic guilds (based on diet, time and habitat of foraging). Further, the small size of these patch reefs was such that pronounced variation in species composition was known to occur through time at the level of single reefs (Sale *et al.*, 1994). Thus meaningful comparison between regions required pooling of data across patch reefs, to create a single sample of the 'patch reef community' typically numbering 2,000–3,000 individuals at each location. The results obtained when they ana-

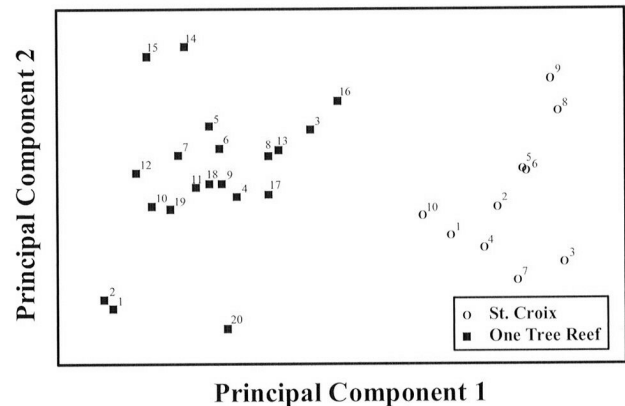


FIG. 3. Structure of reef fish communities assembled at comparable sets of 20 replicate patch reefs in lagoonal/back-reef habitats at One Tree Reef, Great Barrier Reef, and Tague Bay, St. Croix, U.S. Virgin Islands. All species have been assigned to one of 12 trophic guilds in order to permit the biogeographic comparison. Numbers on graph represent successive censuses of the communities over 10 (One Tree Island) or 5 (Tague Bay) years. At each census the community is located in a phase space defined by the first two Principal Components extracted from a database listing numbers of fish present belonging to each trophic guild. The communities are trophically different in the two locations, and both have wandered in structure during the years of monitoring (modified from Chittaro and Sale, 2003).

lyzed these pooled patch reef communities (Fig. 3) are relevant here in two ways. First, they demonstrate that the reef fish communities that develop in one particular kind of habitat (patch reefs) are structurally (trophically) different in the Virgin Islands and on the southern Great Barrier Reef. The patch reef fish fauna at the St. Croix site was more dependent on plankton, while that at One Tree Reef was more dependent upon algae. Whether this is a general feature of patch reef communities in these two regions is not known. If it is general, it suggests that despite sharing most taxonomic types (at family or even genus level), the reef fish faunas of these biogeographic provinces have evolved patch reef communities that play different trophic roles—another example of a lack of determinism in how these systems are assembled.

More directly relevant to the present discussion is the clear demonstration that the trophic composition of each of these pooled patch reef communities has wandered from census to census, and that the extent of this wandering is broadly comparable at the two locations. Assignment of each species to one of 12 trophic guilds must reduce the apparent extent of change observed (there were 90 species recorded in St. Croix and 141 at One Tree Reef). Over the years monitored there have been substantial changes in the composition of the fish communities that occupied these sets of small patch reefs. Numbers of fish, and numbers of species present varied among censuses, ranging at St. Croix from 1,520 to 2,944 fish, and from 34 to 51 species of the 90 recorded at least once. At One Tree Reef numbers ranged from 1,786 to 3,628 fish, of from 54 to 86 of the 141 species. The true extent of variation

TABLE 1. Aspects of the structure of the patch reef community sampled at One Tree Reef.*

Species	Census			
	2	14	16	20
Total fish	2,375	3,196	2,050	1,905
Total species	63	76	65	54
<i>Apogon doederleini</i>	828	775	187	442
<i>Asteropteryx semipunctatus</i>	217	386	429	291
<i>Acanthochromis polyacanthus</i>	222	410	169	114
<i>Cheilodipterus quinquelineata</i>	84	147	101	78
<i>Amblygobius phalaena</i>	24	67	125	145
<i>Apogon gracilis</i>	0	326	0	0
<i>Chromis nitida</i>	113	57	20	11
<i>Ecsenius mandibularis</i>	34	69	0	88
<i>Pomacentrus melanochir</i>	84	41	45	61
<i>Pomacentrus molluccensis</i>	65	59	60	48

* Shown are numbers of fish, of species, and of each of the 10 species that were most common overall at this site (in order of overall abundance), for each of censuses 2, 14, 16, and 20. These censuses are the ones most far apart on Figure 3, and the variation among them provides a scale to the wandering evident in that figure.

in species abundances can be gained from inspecting the species composition at censuses 2, 14, 16 and 20 of the One Tree Reef patch reefs (the four most different in Fig. 3). Table 1 lists the total number of fish and species, and the numbers of each of the 10 most abundant species overall for each of these censuses. All but one of these species (*P. molluccensis*) show at least a 2-fold change in numbers, most show a 5-fold variation, and three exhibit at least a 10-fold variation. These are substantial changes in abundance among the most common species. Coupled with the changes in species composition, they confirm that community structure has measurably changed. The pattern is similar at St. Croix. The simplest explanation of these changes, given the non-directional pattern evident in Figure 3, is that they result from the varying patterns of replenishment and loss of individual fishes.

A profound conclusion can be drawn from these considerations of effects of recruitment variation on community structure. This is that the mixes of species that we call communities of coral reef fishes are flexible mixes, and the consequences for any particular recruit can vary substantially depending on the particular mix it confronts at a site. If recruits are variably distributed, so that species' relative abundances in communities differ from place to place, and if these patterns of relative abundance also differ through time at any one place, the things we call communities are changeable things, with a structure that can only be defined probabilistically. Notions about the role of interspecific interactions in determining coexistence must accommodate a much less deterministic view of community organization that has been usual in the past.

CONNECTIVITY AND THE MANAGEMENT OF REEF FISH COMMUNITIES AND REEF FISHERIES

Highly variable patterns of recruitment are not necessary for high degrees of connectivity among local populations. However, both seem likely given the duration of larval lives, the sensory and behavioral ca-

pabilities of larvae, their high levels of average mortality, and the variability of physical processes of the water mass around reefs. Connectivity is literally measured as the flux of successful propagules from one local population to another, because movement among sites by older fish does not occur in the great majority of species. (I use the word "successful" to stress that for effective connectivity, the propagule must survive to become a functional part of the breeding population it has joined.)

The levels of connectivity among local populations will determine whether they function as essentially isolated, "almost closed" populations, or as a metapopulation, with the separate dynamics of individual populations being buffered by subsidy of recruitment from other populations. Thus, knowing the levels of connectivity among a set of nearby populations is important for our fundamental understanding of their demographies. A small beginning has been made to developing the theory of metapopulations of demersal fishes (e.g., Man *et al.*, 1995; Crowder, *et al.*, 2000; Armsworth, 2002), frequently in the context of reef fish management.

Throughout the tropics, management of coastal resources is increasingly being done by spatially-explicit means—by managing our impacts on particular pieces of coastal ocean, usually in a patchwork of contiguous more- and less-managed sites (reviewed in Bohnsack and Ault, 1996; Sale, 2002). This trend has developed for three reasons. Firstly, traditional management of fisheries by setting restrictions on size/age of harvested individuals, on fishing gear, or on level of effort (including seasonal closure of the fishery) is data-intensive, and exceedingly difficult to implement in a multi-gear, multi-target, mixed-species fishery of the kind typical in tropical coastal waters. In most countries, resources are totally inadequate for such an approach. Secondly, spatially-explicit management, by the creation and policing of no-take reserves, or other kinds of reserve where activities are regulated to control catch, is technically easier to implement, and usually

generates quick, positive responses from the targeted species in the form of greater abundances and larger sizes (older animals) within the protected area. Thirdly, protected areas can serve a conservation function as well as a fishery management function, and thus garner support from components of society outside the fishery management group.

Unfortunately, protected areas or no-take reserves do not necessarily serve the fishery management or conservation functions that justified their establishment, even if fish are larger and more numerous within their borders (Russ, 2002). In many cases, they fail because they are simply paper parks, legally defined, legislated, staffed perhaps, but not really managed—human impacts on resources inside their borders remain as high as they are outside the borders. Even when the protected area is adequately managed it may not serve its planned function adequately. A single protected area established for conservation should be sized appropriately for the demography of the species it is designed to protect. It should be large enough that a reasonable proportion of larval propagules will complete their pelagic lives and settle within its borders. (By “reasonable proportion” I mean a proportion sufficient to sustain that population indefinitely in the absence of subsidy from populations outside the borders—only in this way can an isolated protected area truly protect the biota within its borders.) It may be possible to use protected areas of smaller size for conservation if there are several of them, located in sufficient proximity to one another that their propagules can subsidize the recruitment within each. That fish within the borders of protected areas live longer and therefore become larger and more numerous than outside does not, of itself, demonstrate that these requirements for sustainability have been met. Will these populations continue to exist in a future where serious further degradation of populations outside the protected area take place?

A protected area that is intended to support a sustainable fishery also has size and siting requirements. The presence of denser populations of larger animals within its borders will enhance the reproductive output of a no-take reserve. This production of propagules may further increase density within the reserve, leading to net outward migration of animals across the borders, and may provide a significant subsidy of recruitment to areas outside the borders. These two processes of spill-over and subsidy have been used to justify to fishing communities the need to remove fishing grounds from use in order to create no-take reserves, yet there is as yet scant evidence that most no-take reserves significantly improve fishery sustainability in the surrounding region (Russ, 2002). To be effective, the no-take zone must be of a size sufficient to support a breeding population that will yield sufficient propagules for subsidy and eventual spill-over of residents, and must be sited so that the dispersed propagules will arrive in the fished regions outside its borders.

Clearly, to do it properly, the establishment of pro-

tected areas whether for conservation or for fishery management purposes must be done in a context of detailed knowledge about the existing connectivities among sites in the region. This information does not currently exist, and there is a critical need to develop the methodologies that will be necessary, and to collect it. Given the evidence that reef fish populations and the communities they form appear to be relatively indeterminate in structure, lacking strong internal compensatory mechanisms to recover when perturbed by impacts such as fishing, I believe it is vital that we “get the management right.” Nature will not easily “restore” reef fish communities once we have changed them through our over-fishing.

ACKNOWLEDGMENTS

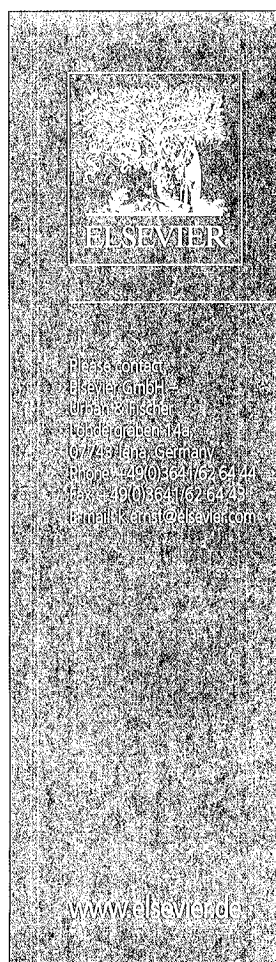
I thank Francesco Santini and Gustavo Bazeta for inviting me to participate in the symposium. Original work reported in this paper was supported over many years by various Australian, U.S., and Canadian funding agencies. The manuscript benefited from review by Jake Kritzer, Bob Warner and two anonymous referees. These individuals will not all agree even with the revised text, but I thank them for helping me write more clearly.

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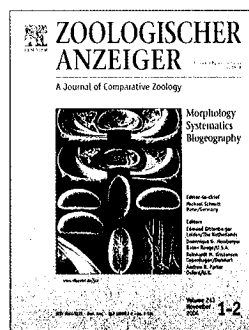
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Zoologischer Anzeiger



2005
Volume 244 with 4 issues
ISSN 0044-5231

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