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American Naturalist, Volume 120, Issue 1 (Jul., 1982), 121-127.

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American Naturalist
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Wed Oct 31 11:26:29 2001

COMMUNITY STRUCTURE OF CORAL REEF FISHES: ARE THE PATTERNS MORE THAN THOSE EXPECTED BY CHANCE?

Anderson et al. (1981) present data on distribution of chaetodontid fishes in an attempt to discriminate between two alternative hypotheses on community structure. These are (1) conventional niche theory in which "local coexistence of species is facilitated by the resource partitioning among them" (Anderson et al., p. 492) because of present-day or past competition, and (2) a nonequilibrial view espoused by Sale (1977, 1978, 1980*b*; Sale and Dybdahl 1975, 1978), and Talbot et al. (1978), which emphasizes the role of stochastic elements in larval recruitment and in mortality in determining local coexistence of species like reef fishes. Although Anderson et al. begin by noting that their data do not falsify either hypothesis, they conclude very strongly that there is no need for "alternative hypotheses" (p. 494) to conventional niche theory. We submit, instead, that when available data do not falsify either of two or more alternative hypotheses, it is the most parsimonious one which should be favored until such time as new data prove it inadequate. Niche theory contains a number of implicit assumptions concerning the equilibrial status of communities, and biotic interactions among component species which are responsible for maintaining this structure. In our view, these make it the less parsimonious alternative.

Here we avoid the thorny problems of the testability or otherwise of niche theory (Peters 1976), and attend instead to the data Anderson et al. put forward. We extend the analysis of some of their data, present new data on distribution of the species they examined, and show that their data do not provide the degree of support for conventional niche theory that they claim. We reference several predominantly experimental studies not cited by Anderson et al. which we believe provide further reason to doubt the adequacy of niche theory for reef fish communities. In doing this, we do not claim that the nonequilibrial model, as presently realized, is completely adequate either, and we point to specific patterns for which it cannot account.

Central to the paper by Anderson et al. are data on the relative abundance of each of the 14 most common species of butterfly fish at sites in each of five regions along a 50-km transect stretching from the outer Great Barrier Reef to coastal reefs within 6 km of the coast of Queensland, Australia (their table 4, fig. 2). Anderson et al. describe several features of the pattern of distribution of these 14 species on the transect. Here, we examine three particularly important ones. First, they note that there is a conspicuous geographical replacement of species along the transect, with no more than eight of the 14 being other than rare or absent at any site. They then distribute the 14 species among four feeding guilds (containing 2, 3, 4, and 5 of the species, respectively) and observe, second, that there are substantial trophic differences among species which coexist locally (i.e., in the same region of the transect). Third, they note that there is segregation

Am. Nat. 1982. Vol. 120, pp. 121–127.
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within feeding guilds along the length of the transect, with different guild members common from region to region. These latter two features are precisely what would be predicted by conventional niche theory, but are they also unlikely under alternative hypotheses?

The simplest hypothesis that might be proposed concerning the distribution of fish on this transect is that it is completely random, with each species equally likely to occur at any site. This is clearly shown by figure 2 of Anderson et al. to be incorrect. The geographical replacement they note is pronounced, with several species being substantially more abundant on some parts of the transect than on others. Additional support for the reality of this geographical replacement comes from a recent visual census and explosive sampling program carried out (by D. McB. W.) on reefs near Townsville, Queensland, about 4° south of the transect sampled by Anderson et al. This survey sampled three outer shelf reefs, about 100 km offshore, three midshelf reefs (50 km out), and two inshore reefs (about 10 km from the coast). All the reefs were apparently typical in appearance and fauna. Most of the chaetodontids present were also recorded by Anderson et al. and, for the most part, species were of comparable abundance on the two transects. A tendency for species to replace each other along the transect was also apparent off Townsville (table 1), and the pattern of replacement was similar to that described by Anderson et al. (Williams 1982). Similar geographical segregation was evident in other families of fishes.

That such segregation of species occurs on such long transects does not surprise us. It has been widely recognized, as least since the study of Hiatt and Strasburg (1960), that reef fishes are habitat specialists on a broad spatial scale (see especially, Goldman and Talbot 1976; also Ehrlich 1975; Sale 1980*b*), and these transects went from open oceanic regions to coastal, sediment-rich waters. However, while the observation of geographical replacement of species is compatible with niche theory, it is not required by that theory. Furthermore, as Anderson et al. note, the nonequilibrial view of reef fish systems has been concerned with local coexistence, not broad-scale segregation of species, so observation of broad-scale segregation is not relevant to evaluating this hypothesis either.

We believe that the possible reasons for broad-scale habitat segregation in reef fishes are many, that species do differ in their ecological requirements, but that these differences need not be the result of competition, or dependent on continued competition for their maintenance. For example, the geographical replacement demonstrated in these transects might result passively under certain regimes of water movement, or actively, if larvae of each species independently chose to settle in those (different) habitats to which they were best adapted. Explicit experimental studies are needed on this question. In conjunction, explicit extensions to the nonequilibrial view may be warranted.

The other two features of distribution discussed above concern apparent patterns of niche partitioning. These are patterns predicted by conventional niche theory, but not by the nonequilibrial model, and can be tested against null models assuming independent distribution of species. For example, the trophic differences observed among the chaetodontid species which coexist locally add significant weight to the conventional niche argument only if these differences are

TABLE 1

CENSUS DATA FOR CHAETODONTIDS ON TOWNSVILLE TRANSECT

Abundance	Offshore (15 sites)	Midshelf (15 sites)	Inshore (10 sites)
3.0–3.9 ...		*C. rainfordi* (HC) *C. aureo-fasciatus* (HC) *C. baronessa* (HC)	*C. aureofasciatus* (HC)
2.0–2.9 ...	*C. trifasciatus* (HC) *C. ornatissimus* (HC) *Forcipiger flavissimus* (NC) *C. trifascialis* (HC)	*C. trifasciatus* (HC) *C. plebius* (HC) *C. trifascialis* (HC) *C. vagabundus* (G)	
1.0–1.9 ...	*C. citrinellus* (G) *C. plebius* (HC) *C. pelewensis* (HC) *C. unimaculatus* (SC) *C. ulietensis* (G)	*C. citrinellus* (G)	*C. rainfordi* (HC) *C. lineolatus* (SC)
< 1.0	14 species	11 species	9 species

NOTE.—Fish were recorded while swimming a zigzag path from 0 to 12 m for 45 min in each site. Abundance classes of 1, 2–5, 6–25, and 26–125 fish/site were assigned values of 1, 2, 3, and 4, respectively, and the abundance of each averaged over all sites in each of three regions. Trophic categories (in parentheses) are those of Anderson et al. (1981) with the inclusion of one additional species, *Chaetodon pelewensis*. HC = hard coral, NC = noncoralline, SC = soft coral, G = generalist.

greater than expected in similar-sized subsets of species randomly selected from all those regionally available (cf. Schoener 1974). Anderson et al. (p. 484) make no such claim, only stating that "all groups of sites contain members from three of the four trophic categories" (p. 484). One of us (D. McB. W.), using data from their table 4, calculated back to the number of fish seen per 100 m in each region of their transect (assigning abundances to each species at each site as the means of the given class ranges), and summed across sites to estimate the relative abundance of each species on the transect. Under the null hypothesis of random distribution of species across sites, transect results were synthesized by allocating individuals randomly, without replacement, from this total pool, until each region held the requisite number of fish. This procedure was repeated 300 times, and the chance was assessed of obtaining fewer than three guilds in each region. The probability of fewer than three guilds is .10, .04, .04, .01, and .00 for the outer barrier, inner barrier, far central, near central, and near-shore regions, respectively. The result obtained by Anderson et al. is not particularly unusual under this null hypothesis, and cannot therefore be used as evidence supporting the conventional niche model.

The results of the Townsville transect (Williams 1982) are also pertinent here. On the midshelf sites of this transect, although there were a similar number of species, and somewhat greater densities of fish than on the far and near central sites censused by Anderson et al., only two trophic categories were represented among the common species, and the six most abundant species (comprising over 95% of chaetodontids present) all belonged to a single trophic group, the hard coral

feeders (table 1). Trophic diversification is not a necessary condition for coexistence of chaetodontid fishes, even though it is likely to occur through chance alone, given the number of species, and the range of trophic specializations available in the region.

Turning to the third feature noted by Anderson et al., if the habitat segregation observed within guilds is, as they presume , the result of the effects of competition among these trophically similar species, it follows that habitat partitioning within guilds should be greater than that among randomly chosen, but similar-sized, subsets of the 14 species. (Members of these randomly formed groups would tend to be drawn from several or all of the four guilds.) One of us (P. F. S.) using the data in their figure 2, tested this proposition. Randomly chosen groups of species were formed subject to the two requirements that all 14 species would be assigned to groups, and four groups, containing 2, 3, 4, and 5 species, respectively, would be formed. The distribution of each species across the five habitats (transect regions) was assumed to be fixed as in figure 2 of Anderson et al. (using the midpoints of ranges in their table 4 as numerical values for the abundance classes in this figure). By using a simple percentage overlap formula and these numerical abundances, mean overlap in distribution across the five habitats was computed for the species in each group formed. Twenty-five sets of such "pseudoguilds" were measured, to generate mean expected degree of overlap, and associated variance for each size of guild. These are compared in table 2 to actual values of overlap among members of the real guilds. The data show no tendency for there to be greater partitioning of habitat within the actual feeding guilds than among similarly sized groups of randomly chosen species.

Anderson et al. (1981) draw particular attention to the problem of deciding on the spatial scale most appropriate to an ecological study. They suggest that differences in scales used may be responsible for the single most crucial difference in view of reef fish community structure between advocates of conventional niche theory, and of nonequilibrial models. This difference concerns the relation between stock size and recruitment to populations. We have elsewhere documented a lack of relationship between rates of recruitment to sites, and sizes of resident populations of reef fishes (Sale 1979, 1980*a*; Williams 1980; Williams and Sale 1981). These studies have been done at small spatial scales appropriate to the range of movement of adult fish. One of us (P. F. S. in cooperation with P. J. Doherty) is currently collecting similar data on a substantially larger scale. Based on these and other (e.g., Talbot et al. 1978) local scale studies, as well as on the extensive fisheries literature concerning stock and recruitment in commercially fished populations at a much larger spatial scale, Sale (1977, 1978, 1980*b*) has argued for the essential lack of relationship between recruitment and stock size to be expected (at all scales) in populations of fish (and similar organisms) characterized by high fecundity, early dispersal, and high early mortality. Collecting evidence on the degree to which rates of recruitment depend on sizes of stocks is necessarily slow, particularly when working at large spatial scales. It is wrong to assume, as advocates of conventional niche theory must, that recruitment and stock size are strongly related, when no evidence explicitly supports, and some contradicts this belief.

TABLE 2

MEAN OVERLAP IN HABITAT (transect region) USE OBSERVED AMONG PAIRS OF SPECIES OF CHAETODONTID FISHES BELONGING TO EACH OF FOUR FEEDING GUILDS, AND AMONG SPECIES IN RANDOMLY CREATED "PSEUDO-GUILDS" OF THE SAME SIZE

	FEEDING GUILD			
	Hard Coral	Soft Coral	Noncoralline	Generalist
No. of species	5	2	3	4
Overlap				
Mean observed	.470	.562	.197	.482
Mean random	.483	.478	.517	.449
Variance	.251	.281	.299	.226
Significance:				
t (25 df)	.026	−.155	.574	−.069

NOTE.—Observed overlap (measured as percent similarity, Sale 1980*a*) does not differ significantly from that in "pseudo-guilds" for any size of guild. Original data from fig. 2 in Anderson et al. 1981.

The scale at which studies are done will also influence other of the results obtained. Elsewhere, Sale (1980*b*, in press) has specifically addressed this problem with particular reference to the temporal constancy of community structure (e.g., Ogden and Ebersole 1981), or the predictable recovery of structure following disturbance (e.g., Brock et al. 1979) reported from larger scale studies. Both results are directly predicted from nonequilibrial hypotheses and the results of smaller scale studies. Importantly, this constancy and predictable recovery cannot be taken as evidence for existence among reef fishes of the equilibrium community structure of conventional niche theory, if results from smaller scale studies are also to be accommodated.

If the approach of Anderson et al. is in some degree typical of that used in the study of terrestrial vertebrate systems, perhaps the adequacy of conventional niche theory for these studies needs rigorous examination also. Certainly the data presented by Anderson et al. do not confirm this hypothesis for chaetodontid fishes. Furthermore, some elements in their data (such as evidence of modest change in species composition at one site over 2 yr [their table 1]), or in the data we present here are at least as compatible with a nonequilibrial view as with conventional niche theory.

In finding habitat partitioning, and then inferring competitive exclusion, within feeding guilds, Anderson et al. used the approach of hunting for patterns expected under a favored hypothesis. This approach never confirms an hypothesis, yet continues to be widely used despite pleas for an hypothesis-testing approach instead (Connell 1974; Peters 1976; Connor and Simberloff 1979; Lawlor 1980; Sale, in press). Their discussion (Anderson et al. 1981, tables 6, 7) of still broader-scale patterns across the Pacific, which appears to advocate niche shifts by whole communities through evolutionary time, is a further example of such pattern-seeking behavior. Perhaps Polar bears and penguins have competitively excluded one another also?

ACKNOWLEDGMENTS

Field work near Townsville was supported by the Australian Institute of Marine Science. We thank Tony Underwood, from whom we took the polar bear and penguin example, and Gordon Anderson, Anne and Paul Ehrlich, Jon Roughgarden, Barry Russell, and Frank Talbot—colleagues and friends with whom we have to disagree.

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Submitted October 26, 1981; Accepted December 23, 1981