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## Competition Between California Reef Fishes Niche Inclusion or Co-Extension?

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"Competition" occurs when animals inhibit each other's access to common resources that are actually or potentially limiting (see Birch, 1957). The ecological "niche", on the other hand, is an abstraction that has been variously defined (e.g., Elton, 1927; Hutchinson, 1957; MacArthur, 1968; Vandermeer, 1972). Unfortunately, operational definitions of the term have been conspicuously difficult to formulate, so relating niche theory to real biological systems has posed an important problem for ecologists. This is especially true when dealing with niche overlap between actively or potentially competing species. By discussing niches solely in terms of the primary dimensions of food and space, one can compute various overlap indices based on different measurements of what animals eat and where they occur (e.g., Cody, 1968; Schoener, 1968). Although such indices are useful in determining whether or not species are potential competitors, however, the most unequivocal test for interspecific competition involves experimental manipulations of the spatial distribution of animals and their resources (Connell, 1975).

Therefore, any practical definition of the niche must involve a spatial component subject to experimental investigation. This paper reports part of an experimental study of competitive interactions between the California reef fishes *Embiotoca jacksoni* and *E. lateralis* (Hixon, 1979). The "niche" of these fishes is thus operationally defined as the depth range each species occupies along a food density gradient extending from a relatively food-rich shallow zone to less productive deep reef microhabitats. Using this limited, but practical definition, an attempt will be made to relate current niche theory to experimental field data on this two-species system. Altering Hutchinson's (1957) original concepts, then, the "realized niche" will represent each species' bathymetric distribution in the presence of its competitor, while the "fundamental niche" will constitute each species' distribution after its competitor has been experimentally removed.

### The Theory

In their review of experimental evidence for competition, Colwell and Fuentes (1975) distinguished and exemplified three types of fundamental niche relations among competing species: niche inclusion, reciprocal niche overlap, and coextensive niches. These model niche relations are depicted in figure 1. Since niche dimensions have lately been visualized as bell-shaped curves ("utilization functions") representing a species' resource utilization along some resource gradient (e.g., May, 1974), figure 1 has been similarly constructed. Relating these concepts to the above definition of the niche, this paper will discuss "resource utilization" in terms of numbers of individuals and the "resource gradient" in terms of depth of occurrence, parenthetically labelled in figure 1.

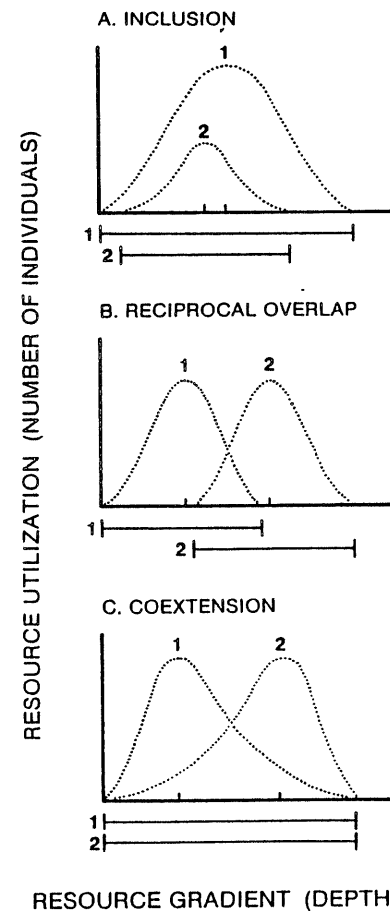


Figure 1. Model fundamental niche relations between two competing species. See text for further explanation.

"Niche inclusion", then, occurs when the fundamental niche of one species (a specialist) is a sub-region of the niche of another (a generalist), as depicted in figure 1a (see also Miller, 1967). "Reciprocal niche overlap" occurs when the fundamental niches of two species overlap, but each contains an exclusive region in which the other cannot exist (fig. 1b). "Coextensive fundamental niches" overlap completely, although they may differ qualitatively, i.e., each species may be the dominant competitor in a different subregion of the same niche (fig. 1c). Where competition occurs in nature, of course, we observe realized niches, so an important problem in community ecology is to determine which of the three fundamental niche models prevails in any given system.

### The System

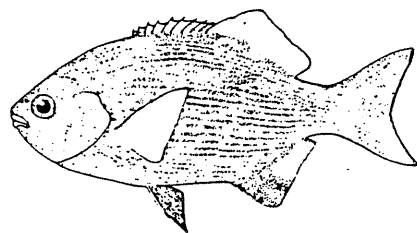
The *Embiotoca* congeners are coastal fishes of the viviparous family Embiotocidae. The major zone of sympatry for these species is the Santa Barbara Channel, a marine ecotone off California separating a relatively cold-water biota north of Point Conception from warm-water communities to the south (Hedgpeth, 1957). *E. lateralis* rarely occurs south of this area, while *E. jacksoni* seldom occupies reefs north of Pt. Conception (D. J. Miller, pers. comm.; pers. obs.). Morphologically, these fishes are very similar (fig. 2). Each attains a maximum total length of

about 35 cm (Miller and Lea, 1972). They are sexually monomorphic, and are nearly identical in mouth size and dentition (Tarp, 1952; DeMartini, 1969).

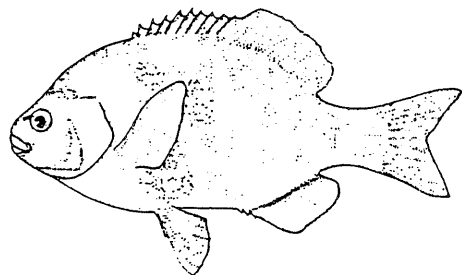
Within areas of reef and kelp off Santa Barbara, the *Embiotoca* congeners are numerically dominant members of a foraging guild of four year-round resident embiotocids (A. W. Ebeling and D. R. Laur, in prep.). Along with *Rhacochilus toxotes* and *Damalichthys vacca*, these fishes are generally observed swimming within a meter of the reef substrate and feeding on small benthic animals (Quast, 1968; Feder et al., 1974; Ebeling and Bray, 1976). Quantitative analyses of dietary overlaps within this guild have been completed by Ebeling (unpub. data), who sampled 30 individuals of each species. Fourteen categories of prey were distinguished on the basis of both taxonomic separation and relative size. The major categories included various small crustacea, polychaete worms, and ophiuroid brittle stars. An indication of proportional dietary overlap between each species pair was calculated using the similarity index of Colwell and Futuyma (1971), the value of which ranges from 0, when species share no prey types, to a maximum of 1, when species utilize common prey in identical proportions. With an index value exceeding 0.6, the *Embiotoca* congeners exhibit by far the greatest dietary overlap within their guild.

Ongoing investigations of the forage base of these fishes by D. Laur (U. C. Santa Barbara) indicate that the primary prey of the *Embiotoca* congeners, gammarid and caprellid amphipods, occur on basically two substrates. These prey are most densely distributed on medium-sized algae (especially *Gelidium robustum*) that dominate shallow reef areas, while in deeper areas they are found on benthic "turf", a low-laying matrix of small colonial animals and algae covering much of the reef bottom. Field observations indicate that *E. lateralis* picks its prey almost exclusively from shallow "algae", while *E. jacksoni* normally forages over deeper "turf" (Hixon, 1979; Ebeling and Laur, in prep.).

In summary, then, the *Embiotoca* congeners are very similar morphologically, overlap extensively in diet, yet forage over different substrates where they are sympatric. An experimental study of food substrate utilization and spatial relations between these fishes was thus undertaken to determine whether or not these species compete with each other and what relationship exists between their fundamental niches.



*Embiotoca lateralis*



*Embiotoca jacksoni*

Figure 2. The *Embiotoca* congeners. (Drawings by D. J. Miller, California Dept. Fish & Game.)

## Methods

The competitive and niche relations of the *Embiotoca* congeners were studied in three ways: (1) a "natural experiment", comparing within-habitat distributions between areas of sympatry and near allopatry; (2) food substrate translocation experiments, comparing the utilization of shallow "algae" moved to deep reef areas and deep "turf" moved to shallow areas with normal foraging patterns; and (3) population removal experiments, comparing the within-habitat distributions of each species before and after its congener had been removed.

The within-habitat distributions of the fishes were documented at various locations by laying 30 m transect lines horizontally along 3 m depth contours from the shallowest to the deepest parts of a reef. As a SCUBA diver swam along each line at a constant pace, the number of individuals of each species occurring within 2 m of the line were tallied. As a "natural experiment", counts were made at similar reefs off Avila, north of Pt. Conception (where *E. lateralis* occurs nearly alone), Santa Cruz Island (within the major area of sympatry), and Anacapa Island (where *E. jacksoni* occurs nearly alone). (See Hixon, 1979, for exact locations and descriptions of these sites.)

To determine if each species would utilize the other's primary food substrate if that substrate was made readily available, shallow "algae" was translocated to deep water and deep "turf" was moved to shallow water at Santa Cruz Island. To control for this manipulation, both substrates were translocated simultaneously and placed side-by-side on meter-square plastic trays anchored to the bottom. Thus, algae and turf were offered together in both shallow and deep reef areas. Test substrates were selected from those over which fishes had been observed actively foraging. Each pair of trays was then observed on four separate occasions between October, 1977, and August, 1978, for a total of three hours. During these periods, the number of individuals of each species foraging over (i.e., vertically oriented toward) each tray, as well as the number of actual feeding bites, were tallied.

The most unequivocal evidence for competitive exclusion comes from controlled population removal experiments (Connell, 1975). The experimental design is straightforward. If one species expands its distribution into contiguous areas formerly occupied by an experimentally removed species, without expanding its range at a control site, then it is most likely that competition produced the original distributions. Such an experiment was run at Santa Cruz Island. Two permanent transect lines were established at each of three similar yet spatially isolated reefs. One line of each pair was set at a depth of 4 m, the apparent center of the bathymetric distribution of *E. lateralis*, and the other at a depth of 10 m, the approximate distributional center of *E. jacksoni*. Between March and July of 1977, ten sets of baseline population counts (described above) were made at each site. To control for any general variations in environmental factors, counts were made on the same days at all sites. Then, over a two day period in July, four SCUBA divers speared 130 *E. jacksoni* at one site and 56 *E. lateralis* at another, which constituted all the fish that could be found. The third site served as a control.

Following this manipulation, ten additional sets of population counts were made at each site, with the experiment ending in October of 1977. After each set of experimental counts, any new or remaining individuals of the "removed" species were speared. Eventually, 63 additional

*E. jacksoni* and 45 additional *E. lateralis* were removed. Within six months of the completion of these experiments, the population density of each removed species had returned to baseline levels, presumably due to immigration from nearby reefs.

For reasons discussed below, a similar removal experiment was run during the summer of 1978. This time, however, algal food substrates were removed from the shallow zone of one reef, as well as all *E. jacksoni*. Some 20 diver-hours were required to effectively defoliate a reef area measuring approximately 70 m by 9 m using knives and hedge shears. A total of 118 *E. jacksoni* were removed during this experiment.

## Results

This section qualitatively summarizes the results of the above experiments. Hixon (1979) details these results with numerical data and analyses.

The "natural experiment" compared bathymetric distributions of the *Embiotoca* congeners between areas of sympatry and near allopatry. Where either species occurred nearly alone, it occupied all reef microhabitats, extending from shallow water to the reef base at depths of about 18 m. In sympatry, however, *E. lateralis* numerically dominated only shallow areas to a depth of about 6 m; *E. jacksoni* dominated all deeper areas. Moreover, the two species exhibited surprisingly little overlap in their bathymetric distributions. The species' sympatric distributions are apparently not influenced by physical factors such as water temperature, nor by biological factors such as differential predation (Hixon, 1979). Also, their allopatric distributions resemble those reported from other such areas off northern and southern California (Miller and Geibel, 1973; Haldorson, 1978; E. S. Hobson, pers. comm.).

The food substrate translocation experiments compared the two species' forage "preferences". When algae and turf were offered side-by-side in shallow water, *E. lateralis* still foraged almost exclusively over the tray containing algae, a result consistent with previous field observations. When presented both food substrates in deep water, on the other hand, *E. jacksoni* readily fed from both. There was, in fact, no significant difference between the number of bites taken from the two substrates. This experimental result contrasts sharply with previous observational data, which indicate that *E. jacksoni* normally forages over turf, and only rarely enters shallow water and feeds off algae. In areas where either species occurred nearly alone, individuals were commonly observed feeding from both substrates.

The population removal experiments constituted direct tests for interspecific competition. During the initial experiment, there were no significant changes in the bathymetric distribution of either species at the control site. Also, where *E. jacksoni* was removed, the distribution of *E. lateralis* remained unchanged; *E. lateralis* did not move into deep areas formerly occupied by *E. jacksoni*. Where *E. lateralis* was removed, on the other hand, the distribution of *E. jacksoni* changed rather dramatically. The density of *E. jacksoni* not only increased significantly in shallow water, but also decreased significantly in deep water, indicating a net movement of resident fish into areas formerly dominated by *E. lateralis*.

The second removal experiment was run to determine why the bathymetric

distribution of *E. lateralis* did not change after its competitor had been removed. This experiment was designed to test the idea that food is not limiting for *E. lateralis* in the area of sympatry. This seemed reasonable because the density of this species is relatively low here at the southern margin of its range. Algal food substrates were thus removed from reef areas dominated by *E. lateralis* to increase the "economic density" (sensu Elton, 1958) of that species, thus "forcing" it to utilize deeper microhabitats formerly occupied by *E. jacksoni*. However, while population densities did not change significantly at the control site, almost all *E. lateralis* left the test site rather than forage over deeper reef areas. These fish presumably crossed some 100 m of open water swimming to the nearest neighboring reef.

## Discussion

The results clearly suggest that the *Embiotoca* congeners actively compete with each other. The "natural experiment" and field observations indicate that where these species cooccur, they segregate spatially and utilize different food substrates. Where either species occurs nearly alone, however, it utilizes the full range of reef microhabitats and forages over both food substrates. These data suggest that the two species have coextensive fundamental niches (fig. 1c).

However, translocation and removal experiments in the area of sympatry suggest different niche relations. *E. jacksoni* can utilize all microhabitats and both food substrates. Yet *E. lateralis* will not descend to deeper reef areas nor forage over turf, even if forced to abandon its "preferred" shallow zone by removing its algal food substrates. Thus, the fundamental niche of *E. lateralis* appears to be included within that of the more generalized *E. jacksoni* (fig. 1a).

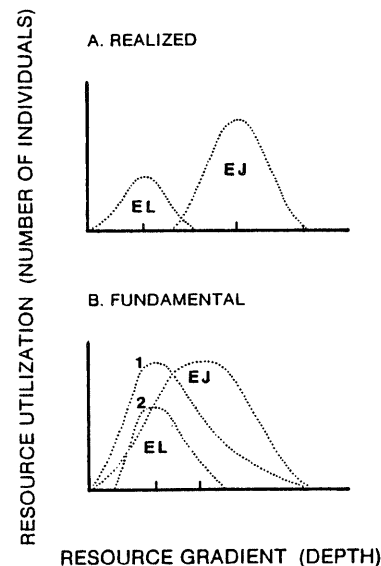


Figure 3. Hypothetical niche relations between *Embiotoca jacksoni* (EJ) and *Embiotoca lateralis* (EL). See text for further explanation.

How can these alternative conclusions be reconciled? I suggest that the relatively low population density of *E. lateralis* in the area of sympatry may account for apparent niche inclusion. The density of *E. lateralis* north of Pt. Conception, where this species occurs nearly alone, is considerably greater at all reef depths than at the southern margin of its range, where it cooccurs with *E. jacksoni* (Hixon, 1979). Individuals in these relatively dense populations also forage over both food substrates, which may account for increased dietary breadth in this species north of Pt. Conception (Haldorson, 1978). Hence, while *E. lateralis* populations may be at or near carrying capacity north of Pt. Conception, marginal populations in the area of sympatry with *E. jacksoni* may be well below

carrying capacity. What limits the marginal population densities of *E. lateralis* is unknown, but warmer water may be a factor. This would explain why *E. lateralis* feeds almost exclusively from algae and does not competitively exclude *E. jacksoni* from all reef microhabitats where the two species cooccur; *E. lateralis* is simply occupying the richest part of the reef--the relatively productive shallow zone--and is under no intra-specific competitive pressure to exploit deeper areas. Thus, even if forced to abandon the shallow zone when its algal food substrates are removed, *E. lateralis* "prefers" to find another shallow reef rather than forage over less productive deeper areas at the defoliated reef.

This population density hypothesis is illustrated in figure 3. The realized niche relations (fig. 3a) represent the observed bathymetric distributions of the *Embiotoca* congeners in the area of sympatry. The fundamental niche relations (fig. 3b) show *E. jacksoni* occupying all reef microhabitats, as it does in the absence of its competitor. The fundamental niche of *E. lateralis*, however, is represented by two curves. The upper curve (1) represents the niche of this species at relatively high population densities, where *E. lateralis* occupies most reef areas yet is most abundant in the food-rich shallow zone. This resembles the situation where this species occurs nearly alone north of Pt. Conception. Combining this curve with that representing *E. jacksoni*, we observe niche coextension (cf. fig. 1c). The lower curve (2) in figure 3b represents the niche of *E. lateralis* at relatively low population densities, where this species occupies only its "preferred" shallow zone. This resembles the situation south of Pt. Conception, in the area of sympatry with *E. jacksoni*, where the fundamental niche of *E. lateralis* appears to be included within that of its congener (cf. fig. 1a). In this situation, *E. jacksoni* occupies a competitive refuge in deeper microhabitats that *E. lateralis* will not utilize. This condition apparently maintains the continued coexistence of these species within the same California reef habitat.

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Note added in proof:

Subsequent to the writing of this paper, E. lateralis not only returned to the reef where shallow algal food substrates and all E. jacksoni had been removed, but also occupied deep microhabitats exclusively, thus providing more positive support for the population density hypothesis.