COMPETITIVE INTERACTIONS BETWEEN CALIFORNIA REEF FISHES OF THE GENUS *EMBIOTOCA*[1]

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Abstract. *Embiotoca lateralis* and *E. jacksoni* are very similar morphologically and exhibit the greatest dietary overlap within a guild of microcarnivorous subtidal reef fishes off Santa Barbara, California. Within this zone of sympatry, they segregate by depth: *E. lateralis* numerically dominates shallow reef areas covered by various algae, from which it picks its prey; *E. jacksoni* dominates and forages over deeper areas covered by a relatively food-poor "turf" of sessile invertebrates and small algae.

E. lateralis rarely fed from turf-covered substrates experimentally translocated from deep water, while *E. jacksoni* frequently fed from translocated shallow algae. In allopatry, however, each species occupies all reef depths and commonly forages over both food substrates. When *E. lateralis* was experimentally removed from a reef inhabited by both species, *E. jacksoni* entered shallow areas and foraged over algae. However, removing *E. jacksoni* from another reef did not affect the distribution of *E. lateralis*. *E. lateralis* aggressively dominated *E. jacksoni*, and *E. jacksoni* avoided foraging near *E. lateralis*. *E. lateralis* eventually entered and foraged over deep reef areas only when all shallow algae and *E. jacksoni* were removed.

Sympatric population densities of *E. lateralis*, here at the southern margin of its geographical range, are much lower than those of allopatric populations elsewhere. Hence, shallow food sources may be sufficiently abundant that marginal *E. lateralis* populations occupy only this richest end of the bathymetric reef food gradient. This situation may provide a competitive refuge for *E. jacksoni* in less productive deep reef areas, thus maintaining the coexistence of these species within the same habitat.

Key words: aggression; avoidance behavior; coexistence; competition; Embiotoca; *field experiments; habitat gradient; niche overlap; resource partitioning; Santa Barbara Channel.*

INTRODUCTION

Competition occurs when animals inhibit each others' access to common resources that are actually or potentially limiting (Birch 1957). During the past decade, much theoretical literature has dealt with the role of interspecific competition as a determinant of animal community structure (e.g., MacArthur 1972, May 1973). Unfortunately, field evidence for competition has remained largely circumstantial, mostly in the form of uncontrolled "natural experiments" or analyses of "resource partitioning" (Connell 1975). In spite of arguments to the contrary (e.g., Diamond 1978), the controlled manipulation of natural populations constitutes the most unequivocal test for competitive interactions (Miller 1967, Connell 1975). Such analyses of the spatial distribution of animals and their resources can additionally provide realistic means of defining and discussing the concept of "niche overlap" (Colwell and Fuentes 1975).

Although interspecific competition has been experimentally investigated for a number of invertebrates, relatively few such studies of vertebrate populations have been reported (recent reviews by Colwell and Fuentes 1975, Connell 1975, Pianka 1976). This is especially true for fishes. While competition has been demonstrated among certain tropical reef species by removing territorial individuals (Low 1971, Sale 1975, Robertson et al. 1976, Williams 1978), detailed experimental investigations of fish competition have been limited thus far to one temperate marine (Larson 1977) and one freshwater system (Werner and Hall 1976, 1977, 1979).

This paper reports observational and experimental field evidence that competition is a major determinant of the within-habitat distributions of a sympatric pair of California reef fishes: *Embiotoca lateralis* (striped surfperch) and *E. jacksoni* (black surfperch). Data on the behavioral mechanisms of competitive exclusion and the ecological mechanisms of sympatric coexistence, as well as a discussion of the niche relations of these species, will also be presented.

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 (Fig. 1), a marine ecotone off California separating cold-temperate biota north of Point Conception from warm-temperate communities to the south (Hubbs 1948, Hedgpeth 1957, Briggs 1974, Horn and Allen
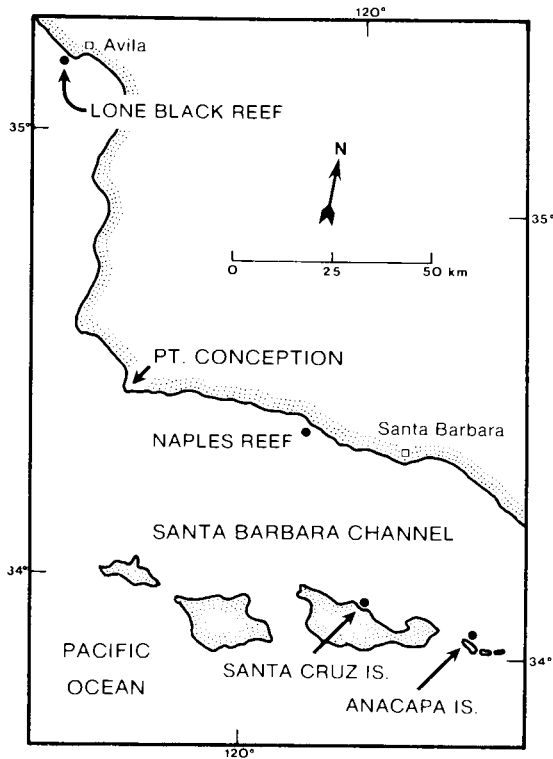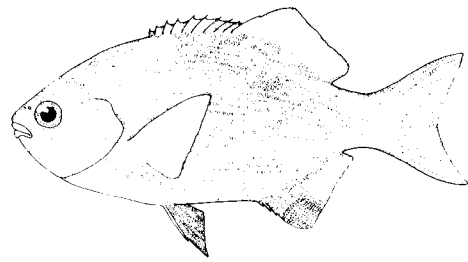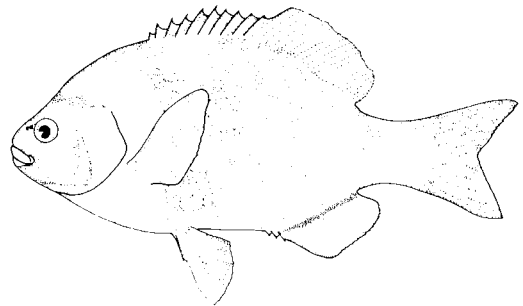
FIG. 1. Map of the south-central California coast showing the locations of the four primary study areas. The Santa Cruz Island study area includes the three experimental reefs (sites A, B, and C).

Embiotoca lateralis

Embiotoca jacksoni

FIG. 2. The *Embiotoca* congeners. Drawings of adult specimens by D. J. Miller, California Department of Fish and Game.

1978). *E. lateralis* rarely occurs south of this area, while *E. jacksoni* seldom occupies reefs north of Point Conception (D. J. Miller and L. J. Haldorson, *personal communication*). Morphologically, these fishes are very similar (Fig. 2). Each attains a maximum total length of ≈35 cm (Miller and Lea 1972). They are sexually monomorphic, except for a small copulatory organ located on the anal fin of males, and are nearly identical in mouth size and dentition (Tarp 1952, DeMartini 1969).

Within subtidal rock reef communities off Santa Barbara, the *Embiotoca* congeners are numerically dominant members of a foraging guild of four year-round resident embiotocids (A. W. Ebeling, *personal communication*). Along with *Rhacochilus toxotes* and *Damalichthys vacca*, these fishes are generally observed swimming within a metre of the reef substrate and feeding on small benthic animals (Limbaugh 1955, Quast 1968, Feder et al. 1974, Alevizon 1975b, Ebeling and Bray 1976, Ellison et al. 1979, Ebeling et al., *in press*). Tagging studies indicate that most of these fishes exhibit home ranges ≈50 m in diameter, although considerable wandering between adjacent reefs is apparent (Hixon 1979).

Quantitative analyses of dietary overlaps within this guild have been completed by A. W. Ebeling (*personal*

communication), who sampled 30 individuals of each species. Fourteen categories of prey were distinguished on the basis of taxonomy, relative size, and hardness. The major categories included various small crustaceans, 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. The results of this analysis revealed an index value of .61 for the *Embiotoca* congeners, while overlaps for all other species combinations within the guild ranged between .11 and .44. Thus, the *Embiotoca* congeners clearly exhibit the greatest dietary overlap within their guild.

Ongoing investigations of the forage base of these fishes by D. R. Laur (*personal communication*) indicate that the primary prey of the *Embiotoca* congeners, gammarid and caprellid amphipods and various bryozoans, 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 in lower densities on benthic "turf," a diverse aggregate matrix of small benthic invertebrates and

algae covering much of the reef bottom. Larson (1977) documented a similar bathymetric density gradient for larger benthic crustaceans occurring in the same habitat.

These data pose a number of questions concerning interspecific competition and community structure. Do the *Embiotoca* congeners, which overlap broadly in diet, exhibit spatial segregation where they are sympatric, as predicted by the theory of resource partitioning (see Schoener 1974)? If so, what are the environmental bases of this separation? Do these species exhibit different within-habitat distributions in areas of allopatry, as suggested by previous "natural experiments" (see Cody 1974)? Do the *Embiotoca* congeners, in fact, compete with each other? If so, what are the behavioral mechanisms effecting competitive exclusion within this sytem? What factors allow these species to coexist within the same habitat? Finally, how does this system relate to existing niche theory? The present study was undertaken in an effort to answer these questions.

STUDY SITES

This work took place in and about the Santa Barbara Channel off southern California; this area constitutes the major zone of sympatry for the *Embiotoca* congeners (Fig. 1). The primary study sites were located in the vicinity of Frys Harbor, on the north shore of Santa Cruz Island, and Naples Reef, located 32 km across the channel near Santa Barbara. Ebeling and Bray (1976) and Ebeling et al. (*in press*) detail the general community structure of fishes that inhabit these reefs.

The typical island habitat consists of a high-relief rocky bottom, descending steeply from shoreline cliffs and meeting sand flats at depths ranging from 15 to 24 m, at 10–50 m from shore. The mainland reef is located ≈1.6 km offshore and measures ≈2.2 ha. Depths across the reef flat average 6–9 m, although some ridges project to within 5 m of the surface. The bottom surrounding the rock reef is ≈15 m deep and is variously comprised of sand and rock cobble. Both sites support perennial stands of giant kelp (*Macrocystis pyrifera*), which generally become most dense in the summer and fall. The dominant understory perennial alga is *Gelidium robustum*, which covers most rocky areas <≈6 m deep. A diverse "turf" of small benthic organisms covers most reef areas at depths below this shallow algal zone.

Study sites north and south of the main zone of sympatry were located at Lone Black Reef and Anacapa Island, respectively (Fig. 1). Lone Black Reef is located ≈0.5 km offshore near Avila, and measures ≈0.2 hectares. The rocky reef flat averages ≈5 m in depth, although a central ridge projects to a depth of ≈3 m. The bottom surrounding the rock reef consists of sand and rock cobble, and is ≈12 m deep. The dominant perennial algae include *Gelidium, Laminar-*

ia dentigera, and *Dictyoneurum californicum.* The Anacapa Island site closely resembles those at Santa Cruz Island, although the abundance of algae (primarily *Macrocystis, Gelidium,* and *Eisenia arborea*) is noticeably greater.

METHODS

Activity patterns

Since very little was known of the daily and seasonal behavioral patterns of the *Embiotoca* congeners, I gathered detailed time budget data by means of a specially designed activity-event recorder used in conjunction with SCUBA. Observations were made on an approximately weekly basis between March 1977 and August 1978. To distribute observations evenly through time, each year was arbitrarily divided into the four solar seasons. Similarly, each day was divided into 2-h intervals covering the 10–14 h between sunrise and sunset, since these fishes are inactive at night (Ebeling and Bray 1976). Within each time interval, I observed each of six (occasionally four) adult individuals of each sex of each species for 5 min in areas where the two species co-occurred. Thus, a total of 2460 min (41 h) of quantitative observation time was evenly distributed over all seasons and daylight hours for each sex of each species. To control for variations in environmental factors between sample periods, I observed both sexes of both species during each dive.

During each sample period, I gathered data primarily on the foraging and aggressive activities of the fishes. Foraging data consisted of the tallied number of feeding bites a fish made on each of two different food substrates: (1) "turf," consisting of the diverse aggregate matrix of small benthic animals and plants that covers both rock substrates and interstitial cobble depressions; and (2) "algae," consisting mainly of algal species ranging between ≈0.2 and 0.5 m in length (primarily the red algà *Gelidium robustum*), but also including larger laminarian algae (primarily the giant kelp *Macrocystis pyrifera*). Aggression data consisted of the number and species of fishes toward which the subject made overt agonistic movements (usually outright chases).

Avoidance behavior

Preliminary field observations suggested the existence of avoidance behavior between the *Embiotoca* congeners. Unfortunately, one-on-one avoidance is very difficult to demonstrate among such highly mobile animals as fishes. The fact that one individual moves away when approached by another does not necessarily indicate that such movement is motivated by avoidance. Thus, by their very nature, field studies of avoidance behavior must rely on indirect evidence.

For reasons discussed below, I attempted to determine whether or not individual *E. jacksoni* tend to avoid *E. lateralis* when they enter areas numerically

dominated by *E. lateralis*. My approach to this problem was statistical. If the mean distance between an intruding *E. jacksoni* and the nearest *E. lateralis* was significantly greater than that between a random point and the nearest *E. lateralis*, then I would conclude that some behavioral interaction (or "avoidance") was occurring between the fishes, i.e., that the mean distance between the fishes was significantly greater than expected at random.

I accomplished this comparative nearest neighbor analysis within a fairly uniform, nearly vertical reef face that was numerically dominated by *E. lateralis* throughout the study. This area extended from the surface to a depth of ≈6 m, measured 30 m in width, and was part of the control reef during the fish removal experiments (see below). First, I would find an *E. jacksoni* individual that had entered the observation area. While hovering several metres above the fish, I would scan the surrounding area until I located the nearest *E. lateralis* individual. Immediately, I would mark the approximate positions the fish had occupied at that instant with surveying tape, then measure the distance between the two points to the nearest 0.5 m. I would then repeat the procedure, except that I would hover over another randomly located marker and measure the distance between it and the nearest *E. lateralis* individual. The fish did not appear to be attracted to such markers. Thus, within an area dominated by *E. lateralis*, I was able to compare the distance between an intruding *E. jacksoni* and the nearest *E. lateralis* with that between a random point and the nearest *E. lateralis*. On eight dates between December 1977 and December 1978, I completed 50 pairs of these observations. The means of these data were compared by an approximate *t* test, which compensates for unequal variances (Sokal and Rohlf 1969).

Spatial patterns

I documented within-habitat distributions of the *Embiotoca* congeners by laying a 30-m transect line along each 3-m depth contour from the shallowest to the deepest parts of a reef. Utilizing SCUBA, I swam along each line at a constant pace, and tallied the number of both adult and subadult individuals of each species occurring within 2 m of either side of the line. The distributions of the relatively rare young-of-the-year juveniles (<≈7 cm total length), which occur on the reefs during the summer, were too patchy to document using this method. Instead, I made visual surveys of the reefs and noted the depth of occurrence of such individuals.

To compare the bathymetric distributions of the fishes with those of their food substrates, I estimated the relative cover of algae and turf by randomly placing 10-m lines along the same depth contours. The length of each line overlaying algae, turf, and bare rock or sand was measured to the nearest 10 cm, and used to estimate proportional cover.

Substrate translocation experiments

I tested the food substrate "preferences" of the fishes by translocating reef rock supporting shallow algae to deep water (12 m) and deep turf-covered rocks to shallow water (3 m) at Santa Cruz Island. To control for this manipulation, both substrates were translocated simultaneously and placed side by side on 1-m² plastic trays anchored to the bottom. Thus, algae and turf were offered together in both shallow and deep reef areas. I selected the test substrates from those over which fishes had been observed actively foraging. I then observed each pair of trays on four separate occasions between October 1977 and August 1978, for a total of 3 h. During these periods, I tallied the number of times individuals of each species completed "foraging passes" over (i.e., vertically oriented toward) each tray, as well as the number of actual feeding bites.

Algae removal experiments

To determine the effect of altering food substrate abundance on the distributions of the fishes, shallow algae were removed at a small reef off Santa Cruz Island by divers using knives and hedge shears. Some 20 diver-hours were required over a 2-d period to defoliate effectively the reef from the surface to a depth of ≈6 m, an area measuring ≈70 m × 9 m. Within several months of each defoliation, most of the algae had regrown. This manipulation was run twice. The first test, run during May and June 1978, involved only the removal of algae. The second, run from August to December 1978, included the removal of *E. jacksoni* as well as algae (see below).

Fish removal experiments

Tests for competitive exclusion involved controlled population removal experiments (sensu Connell 1975). I placed two permanent transect lines at each of three similar yet spatially isolated reefs at Santa Cruz Island (sites A, B, and C). I set one line of each pair 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 1977, I made 10 sets of baseline fish counts (described above) 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 2-d period in July, four SCUBA divers speared 130 *E. jacksoni* at site A and 56 *E. lateralis* at site B, which were all the fish that could be found. The third site (C) served as a control.

Following this manipulation, I made 10 additional sets of counts at each site, with the experiment ending in October 1977. After each set of experimental counts, I speared any new or remaining individuals of the "removed" species. Eventually, I removed 63 additional *E. jacksoni* and 45 additional *E. lateralis*.

TABLE 1. Seasonal foraging effort of the *Embiotoca* congeners over different food substrates. Data, expressed as number (*n*) and proportion (*p*) of foraging bites, were gathered between March 1977 and August 1978.

Season (total observation time)	Food substrate	*E. lateralis*		*E. jacksoni*	
		n	*p*	*n*	*p*
Fall (540 min)	Algae	508	0.97	37	0.13
	Turf	14	0.03	246	0.87
Winter (600 min)	Algae	450	0.98	46	0.12
	Turf	9	0.02	322	0.88
Spring (600 min)	Algae	583	0.93	97	0.17
	Turf	42	0.07	487	0.83
Summer (720 min)	Algae	664	0.96	96	0.16
	Turf	26	0.04	517	0.84
Total (2460 min)	Algae	2205	0.96	276	0.15
	Turf	91	0.04	1572	0.85

Within 6 mo 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.

I ran replicates of these experiments from August to December 1978, and compared the results with the original baseline data. Replication involved switching treatments between the removal sites, and additionally removing algae from the shallow zone of site B (see above). A total of 163 *E. jacksoni* and 101 *E. lateralis* was removed during the replicates.

RESULTS

Distributional and foraging patterns

Fig. 3B depicts the bathymetric distributions of adults and subadults of the *Embiotoca* congeners at control site C off Santa Cruz Island. As at other island sites (Hixon 1979), *E. lateralis* numerically dominated only shallow water areas to a depth of ≈6 m; *E. jacksoni* dominated all deeper areas. Moreover, the two species exhibited surprisingly little overlap in their bathymetric distributions. Both species were rarely found over deep sand flats below the base of the reefs.

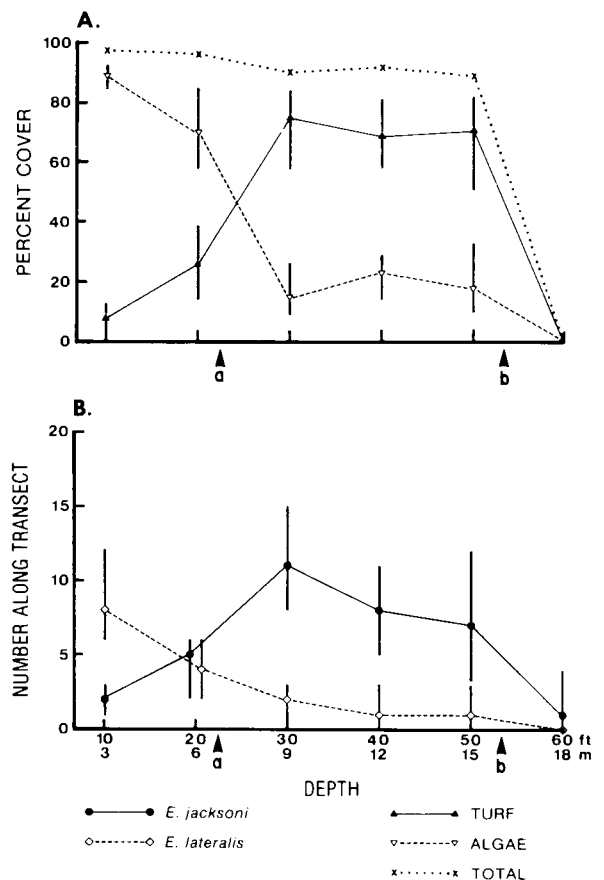Spatial separation of the species did not appear to

FIG. 3. Bathymetric distributions of food substrates (A.) in relation to those of the *Embiotoca* congeners (B.) at site C off Santa Cruz Island. Graph A: Each symbol depicts the mean and range of three transect measurements made during July 1978. Graph B: Each symbol depicts the mean and range of 10 transect counts made between August 1977 and September 1978. Point a indicates the depth below which dense algal stands terminate. Point b indicates the depth at the base of the reef, below which lay sand flats.

have been causally influenced by physical factors. Species distributions were not correlated with water temperature or visibility, since these parameters varied little over the observed depth range. When pres-

TABLE 2. Distributions of the *Embiotoca* congeners and their food substrates over the two primary microhabitats at Naples Reef. Since fish transect data were gathered biweekly between June 1977 and December 1978, while food substrate coverage data were gathered only in July 1978, fish transect data for July 1978 are given parenthetically for a comparison during this period (*n* = 4 per microhabitat).*

Microhabitat (depth)	Number per transect†		Proportional cover‡	
	E. lateralis	*E. jacksoni*	Algae	Turf
Reef crest (6 m)	5.4 ± 0.7 (5.6 ± 2.4)*	4.5 ± 0.7 (3.0 ± 2.6)	0.83 ± 0.06	0.16 ± 0.07
Reef flat (8 m)	0.7 ± 0.3 (0.8 ± 1.5)	10.9 ± 2.1 (6.3 ± 0.8)	0.23 ± 0.07	0.69 ± 0.04

† Mean ± 95% confidence interval (*n* = 30 per microhabitat).
‡ Mean ± 95% confidence interval (*n* = 6 per microhabitat).

TABLE 3. Bathymetric distributions of young-of-the-year juveniles of the *Embiotoca* congeners at Naples Reef and Santa Cruz Island. These data were gathered from late May to early September 1978.

Depth (m)	Total number observed	
	E. jacksoni	*E. lateralis*
Naples Reef		
3–6	21	5
6–9	11	1
9–12	3	0
12–15	4	0
Santa Cruz Island		
0–3	17	21
3–6	13	4
6–9	9	0
9–12	12	0

ent, thermoclines occurred below the transition zone separating the species. Moreover, although wave surge and light intensity are known to decrease with depth (Sverdrup et al. 1942, Jerlov 1968), wide variations in these factors did not overtly influence the bathymetric distributions of these fishes.

Considering biological factors, all potential predators of the *Embiotoca* congeners, including electric rays (Bray and Hixon 1978), sharks, large serranid basses, and pinneped marine mammals, occur at all depths throughout the study area. It seems unlikely, therefore, that the spatial separation of these species resulted from differential predation.

The bathymetric distribution of *E. lateralis* was, however, positively correlated with the percent cover of algae (Fig. 3, $r = .95$, df $= 4$, $P < .01$). Moreover, activity budget data revealed that *E. lateralis* took an annual average of 96% of its foraging bites from algae (Table 1). The distribution of *E. jacksoni*, on the other hand, was positively correlated with the percent cover of benthic turf (Fig. 3, $r = .94$, df $= 4$, $P < .01$), from which this species took an average of 85% of its foraging bites (Table 1).

Further evidence that the distributions of these fishes are correlated with those of their respective primary food substrates was collected at Naples Reef off the mainland (Fig. 1). Here, dense algal stands were re-
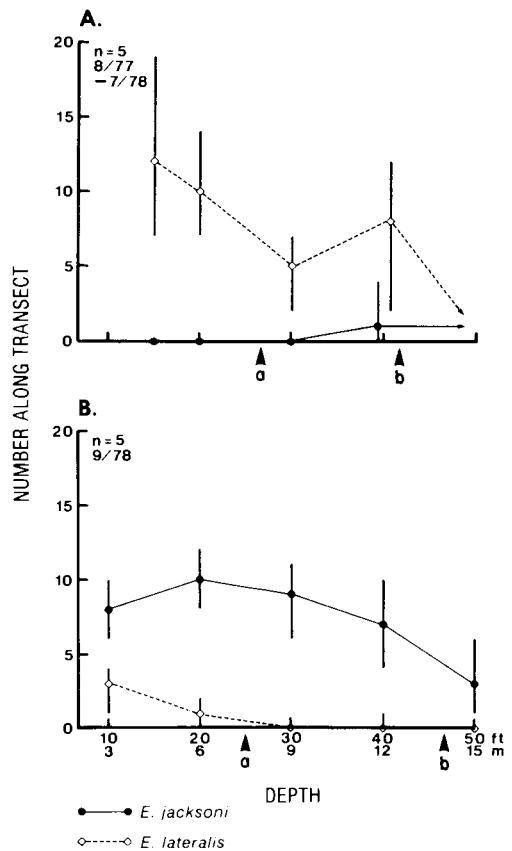

FIG. 4. Bathymetric distributions of the *Embiotoca* congeners at Lone Black Reef (A.) and Anacapa Island (B.). Each symbol depicts the mean and range of five transect counts made during the periods indicated. Depth points a and b are the same as described in Fig. 3. Data were not collected over sand flats below the base (depth point b) of Lone Black Reef due to consistently poor water clarity. However, both species were rarely observed over such areas at other locations, so a similar pattern is probable here.

stricted to the reef crest at a depth of ≈6 m. Therefore, fish counts and food substrate coverages were measured on only two sets of transect lines, one along the reef crest, and the other along the main reef flat at a depth of ≈8 m. These data exhibit a pattern similar to that found at the island site: the distribution of *E.*

TABLE 4. Foraging effort of the *Embiotoca* congeners over paired trays containing translocated food substrates. *E. lateralis* normally forages over shallow algae, while *E. jacksoni* normally forages over deep turf. Data based on 3-h observation of each tray pair between October 1977 and August 1978.

Species	Depth of tray pair	Contents of tray					
		Shallow algae			Deep turf		
		Passes	Bites	Ratio*	Passes	Bites	Ratio*
E. lateralis	Shallow (3 m)	10	26	2.6***	8	2	0.3***
E. jacksoni	Deep (12 m)	18	25	1.4	20	31	1.6

* Mean number of bites per foraging pass.
*** Significantly different ratios ($P < .001$, t test).
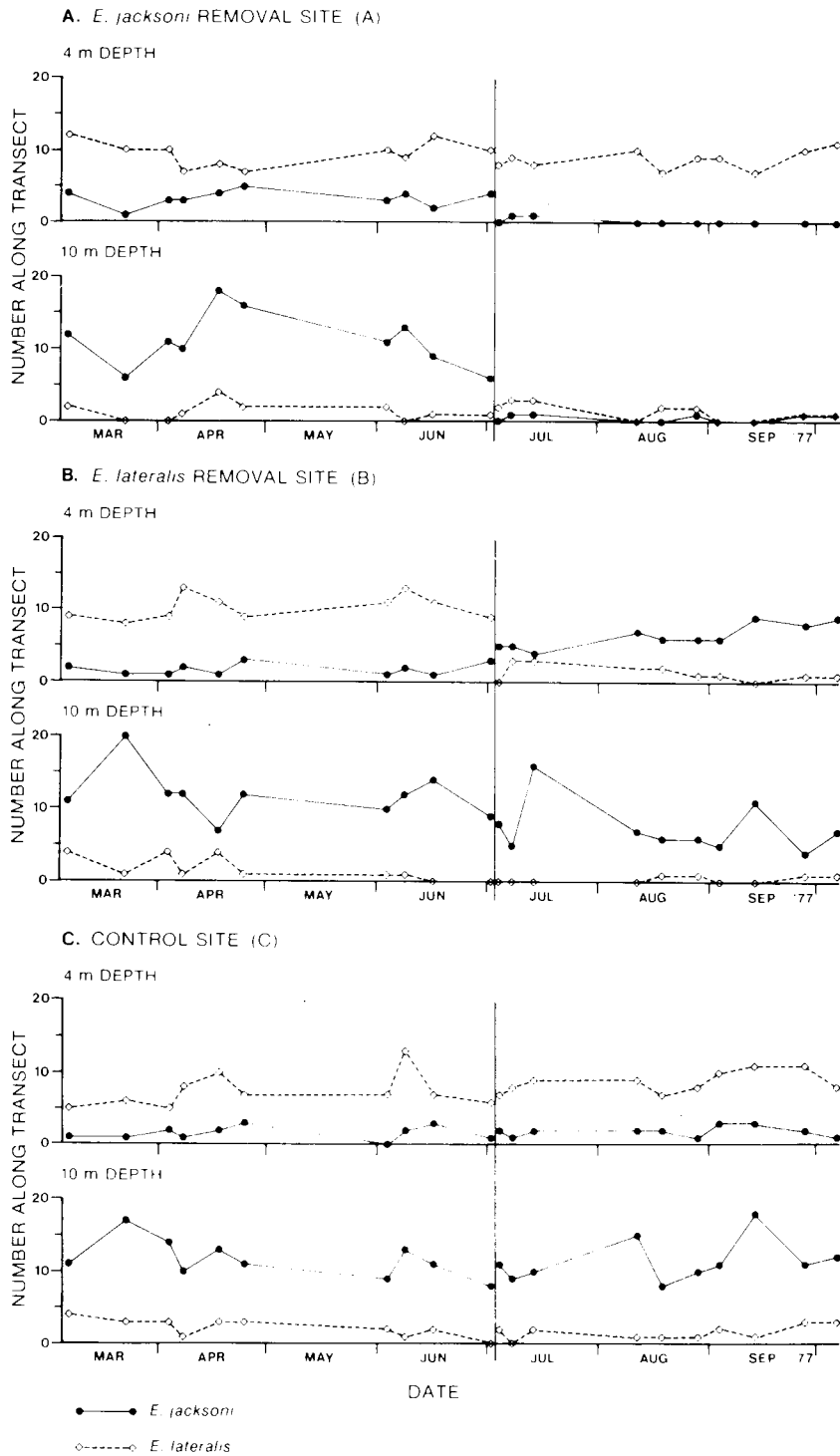
FIG. 5. Transect counts of the *Embiotoca* congeners off Santa Cruz Island before and after population removals. The vertical line midway along the abscissa indicates the date on which the manipulations took place. A: removal of *E. jacksoni* at Site A; B: removal of *E. lateralis* at site B; C: control site C.

lateralis closely paralleled that of algae, while *E. jacksoni* occurred mainly where turf was most abundant (Table 2).

Table 3 presents data on the distributions of young-

of-the-year juveniles (hereafter, simply "juveniles") of each species at Santa Cruz Island and Naples Reef during the summer of 1978. Like the adults of their species, *E. lateralis* juveniles were primarily found in
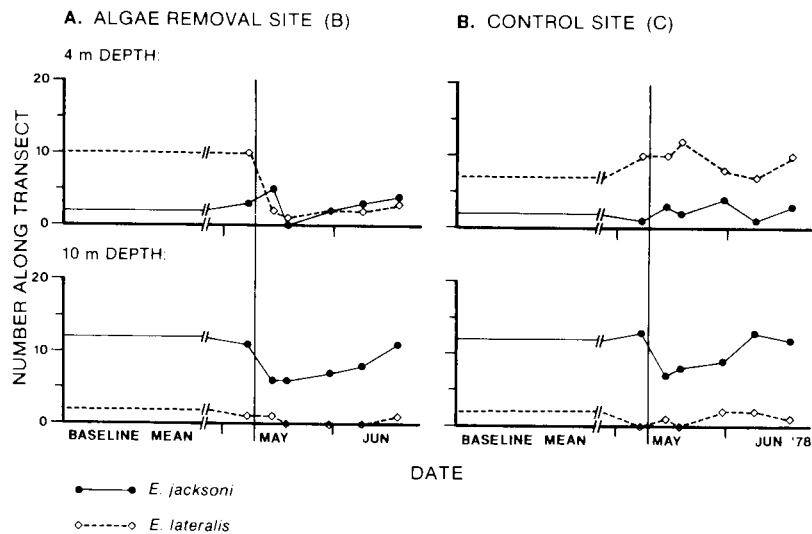
FIG. 6. Transect counts of the *Embiotoca* congeners off Santa Cruz Island before and after the removal of shallow algal food substrates. The given baseline means are of data presented in Fig. 5. The vertical line midway along the abscissa indicates the date on which the manipulation took place. A: test site B; B: control site C.

areas $< \approx 6$ m deep and appeared to forage mainly over algae. *E. jacksoni* juveniles, however, occurred at all depths, though they too were most abundant in shallow water. Qualitative field observations revealed that they commonly foraged over algae as well as turf. This pattern contrasted sharply with that of adult *E. jacksoni*, which mainly inhabited deeper areas and foraged over turf.

Thus, although the *Embiotoca* congeners exhibit substantial dietary overlap where they are sympatric, they tend to occupy different reef zones and forage over different food substrates. *E. lateralis* dominates shallow reef areas covered by dense stands of medium-sized algae, from which it picks its prey. *E. jacksoni* adults dominate deeper areas and normally forage over benthic turf. Juvenile *E. jacksoni*, however, occur at all depths and commonly forage over algae as well as turf.

To determine if each of these fishes exhibits a different bathymetric distribution toward more central parts of its geographic range, where the other species is rare, I collected transect data on a northern population of *E. lateralis* at Lone Black Reef off Avila and a southern population of *E. jacksoni* off Anacapa Island (Fig. 1). The lower depth limit of dense algal stands at these sites was ≈ 6 m, the same as Santa Cruz Island. However, where either species occurred nearly alone it occupied all reef microhabitats, from shallow water to the reef base (Fig. 4). Note that where *E. lateralis* was numerically dominant, *E. jacksoni* occurred only at the deep base of the reef (Fig. 4A), while where *E. jacksoni* was most abundant, *E. lateralis* occurred only at the shallow reef crest (Fig. 4B). These distributions resemble those reported from other reefs off northern (*E. lateralis*) and southern (*E.*

jacksoni) California (Miller and Geibel 1973, Haldorson 1978, E. S. Hobson, *personal communication*). Moreover, qualitative field observations revealed that, where each species occurred nearly alone, it commonly foraged over both food substrates.

Experimental data

During the food substrate "preference" experiment in the zone of sympatry, when algae and turf were offered side by side in shallow water, *E. lateralis* still foraged almost exclusively over the tray containing algae (Table 4), a result consistent with the activity budget data (Table 1). When presented both food substrates in deep water, on the other hand, *E. jacksoni* readily fed from both (Table 4). There was, in fact, no significant difference between the mean number of bites per foraging pass from the two substrates ($P > .5$, t test), although the activity budget data had indicated that *E. jacksoni* normally forages over turf (Table 1).

Fig. 5 presents the results of the initial population removal experiments. Depth-specific fish counts before and after each removal were compared by approximate t tests (Sokal and Rohlf 1969). There was no significant change in the bathymetric distribution of either species at the control site (C) between baseline and experimental periods ($P > .1$). Also, where *E. jacksoni* was removed (site A), the distribution of *E. lateralis* remained unchanged ($P > .2$). *E. lateralis* did not move into deep areas formerly occupied by *E. jacksoni*.

However, where *E. lateralis* was removed (site B), the distribution of *E. jacksoni* changed rather dramatically. The number of *E. jacksoni* not only increased significantly in shallow water ($P < .001$), but also de-
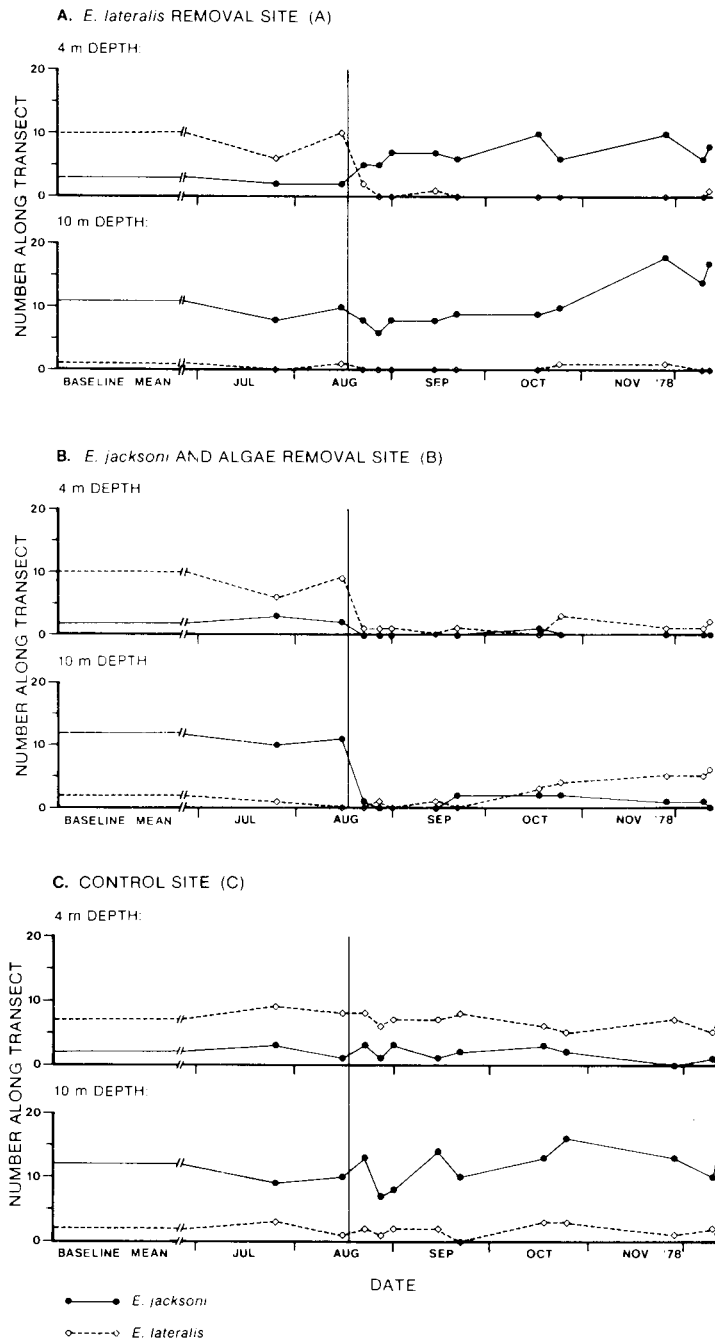
FIG. 7. Transect counts of the *Embiotoca* congeners off Santa Cruz Island before and after population and/or shallow algal food substrate removals. The given baseline means are of data presented in Fig. 5. The vertical line midway along the abscissa indicates the date on which the manipulations took place. A: removal of *E. lateralis* at site A; B: removal of *E. jacksoni* and algae at site B; C: control site C.

creased significantly in deep water ($P < .05$), indicating a probable net movement of resident fishes into areas formerly dominated by *E. lateralis* (Fig. 5B). When this manipulation was later replicated at Site A, the same results were obtained in shallow water ($P < .001$), although the abundance of *E. jacksoni* did not

significantly decrease along the deep transect ($P > .5$; Fig. 7A). As before, there was no significant change in distribution of either species at the control site ($P > .2$; Fig. 7C). In this case, it appeared that a net movement of resident individuals from the base of the reef had occurred. During both replicates, individual *E.*
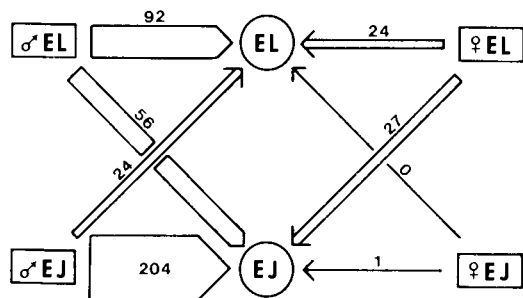
FIG. 8. Number of agonistic encounters observed among the *Embiotoca* congeners. Symbols within rectangles represent the species and sex of the aggressors; those within circles represent the species receiving the aggression, regardless of sex. EJ: *Embiotoca jacksoni*; EL: *E. lateralis*.

jacksoni occupying shallow water were commonly observed foraging over algae.

The algae removal experiment was run in an attempt to increase the "economic density" (sensu Elton 1927) of *E. lateralis*, thus "forcing" it to utilize deeper microhabitats which it had ignored during the initial removal of *E. jacksoni*. When algae were removed at site B, however, almost all *E. lateralis* left the reef and remained away during the 2-mo duration of the experiment ($P < .001$; Fig. 6A). Presumably, these fish crossed some 100 m of open water in swimming to the nearest neighboring reef. The distribution of *E. jacksoni* did not change substantially during this experiment, but for unknown reasons, its abundance did significantly decrease along the deep transect line ($P < .02$; Fig. 6A). There was no significant change in the distribution of either species at the control site between the original baseline period and the test period ($P > .05$; Fig. 6B). Within 3 mo of the completion of this experiment, most of the algae at the test site had regrown and *E. lateralis* had returned.

To test the possibility that *E. lateralis* would utilize deep reef microhabitats only if both food was limiting and *E. jacksoni* was absent, I ran the final experiment involving the removal of both shallow algae and all *E. jacksoni*. Initially, as before, almost all *E. lateralis* left the test site ($P < .001$; Fig. 7B), while their distribution at the control site remained unchanged throughout the experiment ($P > .2$; Fig. 7C). Within ≈2 mo, however, *E. lateralis* returned to the reef and subsequently occupied only deep microhabitats (Fig. 7B). Although there was an increase in the mean number of *E. lateralis* at the deep transect between baseline and test periods, the initial emigration of the fish rendered this change statistically insignificant ($P > .2$). However, this mean increase was significant if the initial test counts are ignored ($P < .01$). Individual *E. lateralis* occupying deep water were commonly observed foraging over turf as well as occasional small patches of algae.

Aggression and avoidance patterns

Fig. 8 depicts the total number of agonistic encounters observed between the *Embiotoca* congeners over all seasons and daylight hours between March 1977 and August 1978. Of a total of 428 chases over 41 h of observation, 321 or 75% were directed toward conspecifics. Within each species, males were always much more aggressive than females. *E. jacksoni* males engaged in conspecific chases more than twice as frequently as *E. lateralis* males (204 vs. 92 chases). The relatively high level of within-species aggression exhibited by male *E. jacksoni* is explained by the fact that these fish display territorial behavior, which is primarily a response to intraspecifically limiting mating sites (Hixon, *in press*).

Between species, *E. lateralis* was observed chasing *E. jacksoni* on 83 occasions, while *E. jacksoni* chased *E. lateralis* only 24 times. As with intraspecific encounters, interspecific aggression was primarily expressed by males. Female *E. jacksoni* were never interspecifically aggressive, while males only chased those *E. lateralis* that occasionally entered their territories. The shallowest *E. jacksoni* territory occurred below 6 m, which was deeper than those reef areas numerically dominated by *E. lateralis*. Both male and female *E. lateralis* behaved aggressively toward *E. jacksoni*, though males did so more than twice as frequently as females (56 vs. 27 chases).

While activity budget data clearly indicated that *E. lateralis* is aggressively dominant over most *E. jacksoni*, at any given time at least one *E. jacksoni* individual could be found foraging within those shallow reef areas numerically dominated by *E. lateralis*. However, *E. jacksoni* appeared to enter shallow areas primarily when *E. lateralis* individuals were not in the immediate vicinity, suggesting that *E. jacksoni* may often avoid *E. lateralis*. In fact, data from the comparative nearest neighbor analysis indicated that the mean distance between an intruding *E. jacksoni* and the nearest *E. lateralis* (2.9 m) was significantly greater than that expected if the fishes were distributed at random (1.8 m, $P < .001$, approximate t test).

DISCUSSION

The existence of competition

The *Embiotoca* congeners are very similar morphologically and overlap extensively in their diet of small benthic crustaceans and bryozoans. Within their major zone of sympatry, they are spatially segregated along a food density gradient extending from shallow reef zones dominated by dense stands of relatively food-rich algae, to less productive deep reef microhabitats dominated by benthic "turf." *E. lateralis* numerically dominates shallow areas and forages almost exclusively over algae, while *E. jacksoni* dominates deeper zones and normally forages over turf. Alevizon (1975a) additionally noted that these fishes segregate

along a vertical dimension, since *E. lateralis* forages in the kelp canopy more frequently than *E. jacksoni*. Thus, the basis of sympatric resource partitioning between these species involves the utilization of different food substrates which occur at different depths. Where each species occurs nearly alone in other geographical areas, however, it occupies all reef microhabitats and forages over both food substrates.

Such differences between sympatric and allopatric populations are said to constitute a "natural experiment" demonstrating the existence of competition between species (Diamond 1978). Because such evidence is circumstantial, however, alternative hypotheses are not falsified. For example, since these viviparous fishes do not have dispersive planktonic larvae, different populations could constitute distinct gene pools (Alevizon 1975*b*, Haldorson 1978). If so, the sympatric populations may have specialized on different food substrates (*E. lateralis* on algae and *E. jacksoni* on turf) to a level where neither species is capable of utilizing both substrates. Thus, interspecific competition would not presently influence the within-habitat distributions of these species.

Such alternatives can be falsified only by controlled field experiments (Connell 1974, 1975). Food substrate translocations within the zone of sympatry clearly indicated that *E. jacksoni* will readily feed from algae as well as turf. And when *E. lateralis* was removed from two different reefs, *E. jacksoni* quickly occupied shallow areas vacated by *E. lateralis* and foraged over algae. *E. lateralis*, on the other hand, did not forage over turf translocated to shallow water, and resident fish did not move to deep areas vacated by *E. jacksoni*. Therefore, the *Embiotoca* congeners do actively compete with each other in sympatry, with *E. lateralis* limiting the within-habitat distribution of *E. jacksoni* by exclusively occupying food-rich shallow reef zones. This system supports the "compression hypothesis" of MacArthur and Wilson (1967), since the presence of *E. lateralis* results in restricted microhabitat use by *E. jacksoni*, although dietary overlap between the species remains quite high.

Mechanisms of exclusion

Activity budget and comparative nearest neighbor analyses indicated that the behavioral mechanism of competitive exclusion in this system is a combination of occasional overt aggressive dominance by *E. lateralis* and covert subordinate avoidance by *E. jacksoni*. Thus, the *Embiotoca* system is basically an example of "interference" competition (sensu Miller 1967). While avoidance behavior is, for all practical purposes, impossible to document unequivocally in the field, its theoretical selective advantage is straightforward. As long as the energetic and temporal cost of avoiding a dominant competitor is less than the cost of being aggressively excluded by that competitor, then, all other factors being equal, avoidance behavior

should be favored by individual selection (see also Morse 1974). By avoiding the dominant competitor itself, rather than the competitor's preferred microhabitats, a subordinate individual can possibly spend some time exploiting resources within such preferred areas. Thus, *E. jacksoni* will readily forage over food-rich shallow reef algae when *E. lateralis* is temporarily absent, as well as when *E. lateralis* is experimentally removed or when shallow algae are translocated to deep reef areas.

Interestingly, however, interactions between the *Embiotoca* congeners apparently do not involve juvenile fish. Not only do the bathymetric distributions of such individuals broadly overlap, with juveniles of both species commonly foraging together nonaggressively over shallow algae, but also adults were never observed behaving aggressively toward juveniles of either species. These observations suggest that resource limitation may not occur among juveniles and/ or between juveniles and adults of either species. This should be especially true for *E. jacksoni*, since territorial aggression in this species is closely linked with adult reproductive activities (Hixon, *in press*). Additionally or alternatively, it may simply not be worthwhile energetically for an adult fish to exclude juveniles aggressively since they are less abundant than and presumably consume much less food per unit time than adults. As *E. jacksoni* juveniles grow, they probably reach a critical size at which subordinate agonistic encounters with *E. lateralis* become common, this forcing them to move to deeper reef areas. In the *Embiotoca* system, therefore, juveniles do not appear to exhibit an active role in the overt competitive interactions that occur among adults.

Mechanisms of coexistence

If *E. lateralis* is the dominant competitor in this system, why does it not exclude *E. jacksoni* from all reef microhabitats? The major zone of sympatry of these species (the Santa Barbara Channel) is located at the southern margin of the geographical range of *E. lateralis*. Within this area, the population density of *E. lateralis* on different reefs varies between ≈5% and 22% of that of populations north of this area, and ≈ 17–50% of that of sympatric *E. jacksoni* populations (data from Miller and Geibel 1973, Ebeling et al., *in press*). Exactly what limits marginal populations of *E. lateralis* is unknown, but warmer water is probably an important factor (Hubbs 1948, Neushul et al. 1967, Haldorson and Moser 1979, see also Brett 1956, Terry and Stephens 1976). Populations of *E. lateralis* occur south of Santa Barbara only in localized areas of intense cold water upwelling (Haldorson 1978, Haldorson and Moser 1979).

These data suggest that marginal population densities of *E. lateralis* may not be regulated by resource limitation as much as by unfavorable physical factors. As the dominant competitor, *E. lateralis* thus occupies
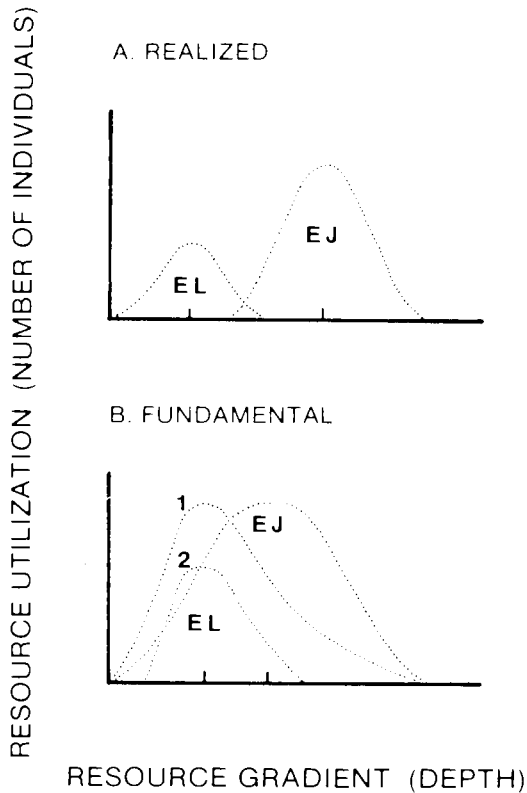
FIG. 9. Hypothetical spatial niche relations of the *Embiotoca* congeners. A: Realized niches representing the observed bathymetric distributions of the species within their zone of sympatry (cf. Fig. 3B). B: Fundamental niches representing the observed allopatric distributions of *E. lateralis* (curve 1; cf. Fig. 4A) and *E. jacksoni* (cf. Fig. 4B). These curves also represent the distribution of *E. lateralis* where both shallow algal food substrates and all *E. jacksoni* have been experimentally removed within the zone of sympatry, as well as the distribution of *E. jacksoni* where *E. lateralis* has been removed. In this case, the niches of the two species appear to be "coextensive," with *E. lateralis* being nearly as generalized as *E. jacksoni*. Curve 2 represents the distribution of *E. lateralis* where *E. jacksoni* (only) has been experimentally removed within the zone of sympatry. In this case, the niche of *E. lateralis* appears to be "included" within that of a relatively generalized *E. jacksoni*. EJ: *Embiotoca jacksoni*; EL: *E. lateralis*. See text for further explanation.

only the relatively food-rich shallow reef areas, and is subject to little or no within-species competition to exploit less productive deeper microhabitats. Indeed, although *E. jacksoni* readily enters shallow reef areas vacated by *E. lateralis*, *E. lateralis* remains in shallow water when *E. jacksoni* is experimentally removed. Thus, while the spatial "realized niches" (sensu Hutchinson 1957) of these species overlap little within their zone of sympatry (Fig. 9A), the "fundamental niche" of *E. lateralis* (Fig. 9B, curve 2) appears to be "included" within that of a relatively generalized *E. jacksoni* (see Colwell and Fuentes 1975).

However, given the marginal nature of *E. lateralis* populations in the zone of sympatry, such a classic example of a habitat specialist outcompeting a generalist (sensu MacArthur 1972) may, in fact, be fortuitous. One may hypothesize a situation where, in more favorable habitats north of Santa Barbara, increased population density and resulting within-species competition may effectively expand bathymetric habitat utilization by *E. lateralis* to the point where it does completely exclude *E. jacksoni* from the reefs. This hypothesis is supported by two lines of circumstantial evidence. First, while the competitively subordinate *E. jacksoni* is common off most of the California coast and frequently occupies reefs south of Santa Barbara, north of this area it is rare over reefs and mainly occupies sandy habitats (D. J. Miller and L. J. Haldorson, *personal communication*). Secondly, the competitively dominant *E. lateralis* not only exclusively occupies the reefs north of Santa Barbara, but also exhibits increased dietary breadth there (Haldorson and Moser 1979), indicating trophic as well as spatial niche expansion.

Thus, the relative position of a dominant competitor along the generalist-specialist continuum may be merely a function of its population density (sensu MacArthur's [1972] "principle of equal opportunity"), which may in turn be a function of some factor(s) independent of the competitive interaction itself.

Within the zone of sympatry, then, *E. lateralis* will eventually occupy deep reef areas only after both *E. jacksoni* has been removed and its own "economic density" (sensu Elton 1927) has been increased by the removal of shallow algal food substrates. Thus, the spatial fundamental niche of *E. lateralis* appears to expand (Fig. 9B, curve 1), and become "coextensive" with that of *E. jacksoni* (see Colwell and Fuentes 1975), a result compatible with the ubiquitous bathymetric distributions of these species in areas of geographic allopatry.

Interestingly, however, when only shallow algae are removed within the zone of sympatry, *E. lateralis* will leave the reef rather than exclude *E. jacksoni* from deeper areas. Perhaps it is more beneficial for these fish to move to another shallow reef than to compete aggressively with *E. jacksoni* for less productive deeper areas. This hypothesis is supported by the fact that certain large male *E. jacksoni* defend feeding (as well as mating) territories in deeper water, and do chase intruding *E. lateralis* individuals (Hixon, *in press*). In the experimental absence of *E. jacksoni* as well as shallow algae, the economic advantage may shift, so any *E. lateralis* entering the area will readily forage over deeper microhabitats. When resources are limiting for both the *Embiotoca* congeners, therefore, either species will attempt to utilize the full range of available reef microhabitats.

Thus, within the major zone of sympatry, the dominant competitor in this system (*E. lateralis*) is limited to relatively low population densities, being at the southern margin of its geographical range. It therefore

dominates only the richest end of a bathymetric food density gradient, a result predicted on theoretical grounds by Case and Gilpin (1974). This situation apparently provides a competitive refuge in less productive areas for the subordinate species (*E. jacksoni*), thus maintaining the coexistence of these ecologically similar congeners within the same California reef habitat.

Literature Cited

Alevizon, W. S. 1975a. Spatial overlap and competition in congeneric surfperches (Embiotocidae) off Santa Barbara, California. Copeia 1975:352–356.

———. 1975b. Comparative feeding ecology of a kelp-bed embiotocid (*Embiotoca lateralis*). Copeia 1975:608–615.

Birch, L. C. 1957. The meanings of competition. American Naturalist 91:5–18.

Bray, R. N., and M. A. Hixon. 1978. Night-shocker: predatory behavior of the Pacific electric ray (*Torpedo californica*). Science 200:333–334.

Brett, J. R. 1956. Some principles in the thermal requirements of fishes. Quarterly Review of Biology 31:75–87.

Briggs, J. C. 1974. Marine zoogeography. McGraw-Hill, New York, New York, USA.

Case, T. J., and M. E. Gilpin. 1974. Interference competition and niche theory. Proceedings of the National Academy of Sciences (USA) 71:3073–3077.

Cody, M. L. 1974. Competition and the structure of bird communities. Princeton University Press, Princeton, New Jersey, USA.

Colwell, R. K., and E. R. Fuentes. 1975. Experimental studies of the niche. Annual Review of Ecology and Systematics 6:281–310.

Colwell, R. K., and D. J. Futuyma. 1971. On the measurement of niche breadth and overlap. Ecology 52:567–576.

Connell, J. H. 1974. Field experiments in marine biology. Pages 21–54 in R. N. Mariscal, editor. Experimental marine biology. Academic Press, New York, New York, USA.

———. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. Pages 460–490 in M. L. Cody and J. M. Diamond, editors. Ecology and evolution of communities. Belknap Press, Cambridge, Massachusetts, USA.

DeMartini, E. E. 1969. A correlative study of the ecology and comparative feeding mechanism morphology of the Embiotocidae (surf-fishes) as evidence of the family's adaptive radiation into available ecological niches. Wasmann Journal of Biology 27:177–247.

Diamond, J. M. 1978. Niche shifts and the rediscovery of interspecific competition. American Scientist 66:322–331.

Ebeling, A. W., and R. N. Bray. 1976. Day versus night activity of reef fishes in a kelp forest off Santa Barbara, California. United States Fish and Wildlife Service Fishery Bulletin 74:703–717.

Ebeling, A. W., R. J. Larson, W. S. Alevizon, and R. N. Bray. In press. Annual variability of reef-fish assemblages in kelp forests off Santa Barbara, California. United States Fish and Wildlife Service Fishery Bulletin.

Ellison, J. P., C. Terry, and J. S. Stephens. 1979. Food resource utilization among five species of embiotocids at King Harbor, California, with preliminary estimates of caloric intake. Marine Biology 52:161–169.

Elton, C. S. 1927. Animal ecology. Sidgwick and Jackson, London, England.

Feder, H. M., C. H. Turner, and C. Limbaugh. 1974. Observations on fishes associated with kelp beds in southern California. Fish Bulletin 160, California Department of Fish and Game, Long Beach, California, USA.

Haldorson, L. J. 1978. Geographic variation in two surfperches (Embiotocidae): local differentiation in one-dimensional population structure. Dissertation. University of California at Santa Barbara, Santa Barbara, California, USA.

Haldorson, L., and M. Moser. 1979. Geographic patterns of prey utilization in two species of viviparous surfperch (Embiotocidae). Copeia 1979:567–572.

Hedgpeth, J. W. 1957. Marine biogeography. Pages 359–382 in J. W. Hedgpeth, editor. Treatise on marine ecology and paleoecology. Volume 1. Ecology. Memoir 67, Geological Society of America, Boulder, Colorado, USA.

Hixon, M. A. 1979. Competitive interactions and spatiotemporal patterns among California reef fishes of the genus *Embiotoca*. Dissertation, University of California at Santa Barbara, Santa Barbara, California, USA.

———. In press. An experimental analysis of territoriality in the California reef fish *Embiotoca jacksoni* (Embiotocidae). Copeia.

Horn, M. H., and L. G. Allen. 1978. A distributional analysis of California coastal marine fishes. Journal of Biogeography 5:23–42.

Hubbs, C. L. 1948. Changes in the fish fauna of western North America correlated with changes in ocean temperature. Journal of Marine Research 7:459–482.

Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology 22:415–427.

Jerlov, N. G. 1968. Optical oceanography. Elsevier, New York, New York, USA.

Larson, R. J. 1977. Habitat selection and territorial competition as the causes of bathymetric segregation of sibling rockfishes (*Sebastes*). Dissertation, University of California at Santa Barbara, Santa Barbara, California, USA.

Limbaugh, C. 1955. Fish life in the kelp beds and the effects of harvesting. IMR 55-9, University of California Institute of Marine Resources, Scripps Institute of Oceanography, University of California at San Diego, La Jolla, California, USA.

Low, R. M. 1971. Interspecific territoriality in a pomacentrid reef fish, *Pomacentrus flavicauda* Whitley. Ecology 52:648–654.

MacArthur, R. H. 1972. Geographical ecology. Harper and Row, New York, New York, USA.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey, USA.

May, R. M. 1973. Stability and complexity in model ecosystems. Princeton University Press, Princeton, New Jersey, USA.

Miller, D. J., and J. J. Geibel. 1973. A reef ecology study in Monterey Bay, California. Fish Bulletin 158, California

Department of Fish and Game, Long Beach, California, USA.

Miller, D. J., and R. N. Lea. 1972. Guide to the coastal marine fishes of California. Fish Bulletin 157, California Department of Fish and Game, Long Beach, California, USA.

Miller, R. S. 1967. Pattern and process in competition. Advances in Ecological Research 4:1–74.

Morse, D. H. 1974. Niche breadth as a function of social dominance. American Naturalist 108:818–830.

Neushul, M., W. D. Clarke, and D. W. Brown. 1967. Subtidal plant and animal communities of the southern California islands. Pages 37–55 in R. Philbrick, editor. Proceedings of the Symposium on Biology of the California Channel Islands, Santa Barbara Botanical Gardens, Santa Barbara, California, USA.

Pianka, E. R. 1976. Competition and niche theory. Pages 114–141 in R. M. May, editor. Theoretical ecology: principles and applications. Saunders, Philadelphia, Pennsylvania, USA.

Quast, J. C. 1968. Observations on the food of kelp-bed fishes. Pages 109–142 in W. J. North and C. L. Hubbs, editors. Utilization of kelp-bed resources in southern California. Fish Bulletin 139, California Department of Fish and Game, Long Beach, California, USA.

Robertson, D. R., H. P. A. Sweatman, E. A. Fletcher, and M. G. Cleland. 1976. Schooling as a mechanism for circumventing the territoriality of competitors. Ecology 57:1208–1220.

Sale, P. F. 1975. Patterns of use of space in a guild of territorial reef fishes. Marine Biology 29:89–97.

Schoener, T. W. 1974. Resource partitioning in ecological communities. Science 185:27–39.

Sokal, R. R., and F. J. Rohlf. 1969. Biometry. Freeman, San Francisco, California, USA.

Sverdrup, H. U., W. Johnson, and R. H. Fleming. 1942. The oceans: their physics, chemistry, and general biology. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

Tarp, F. H. 1952. A revision of the family Embiotocidae. Fish Bulletin 88, California Department of Fish and Game, Long Beach, California, USA.

Terry, C. B., and J. S. Stephens. 1976. A study of the orientation of selected embiotocid fishes to depth and shifting seasonal vertical temperature gradients. Bulletin of the Southern California Academy of Sciences 75:170–183.

Werner, E. E., and D. J. Hall. 1976. Niche shifts in sunfishes: experimental evidence and significance. Science 191:404–406.

———. 1977. Competition and habitat shift in two sunfishes (Centrarchidae). Ecology 58:869–876.

———. 1979. Foraging efficiency and habitat switching in competing sunfishes. Ecology 60:256–264.

Williams, A. H. 1978. Ecology of threespot damselfish: social organization, age structure, and population stability. Journal of Experimental Marine Biology and Ecology 34:197–213.