

An Experimental Analysis of Territoriality in the California Reef Fish *Embiotoca jacksoni* (Embiotocidae)

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Certain large males of *E. jacksoni* defend reef caves as mating sites off Santa Barbara, California. Some are territorial only during the breeding season, when they defend only the area immediately surrounding the cave entrance from other males, and forage over broadly overlapping undefended home ranges. Larger, and perhaps older, fish defend sites approximately 25 m² in area from both conspecifics and confamilials the year-round, and forage only within the well-defined boundaries of their territories. When caves were experimentally occluded, the occupants abandoned or shifted their territories. Fish that were removed from territories were quickly replaced by other males. The territory site rather than its occupant apparently determines whether the area is to be temporarily or permanently defended. The size of permanent territories varied inversely with experimentally manipulated food availability, and occupants selectively excluded potential food competitors of the same foraging guild. When overgrazed by sea urchins, permanent territories were abandoned and subsequently became the sites of temporary territories. The juxtaposition of a suitable cave and a sustainable food supply apparently makes an area valuable enough to be economically defendable throughout the year. Since their territories occur only around caves, *E. jacksoni* males competitively dominate other members of their guild only in areas with suitable caves. Their range of dominance is further restricted by sea urchins, which are superior exploitative competitors.

TERRITORIAL behavior, in the general sense of an animal excluding others from all or part of its home range, may occur when any limiting resource is "economically defendable" (Brown, 1964). Among vertebrates, territoriality is most often attributed to the defense of a food supply, a shelter, and/or a mating/nesting site (Brown and Orians, 1970; Myrberg and Thresher, 1974; Brown, 1975; Wilson, 1975; Davies, 1978). For fishes, the identities of intruder species excluded from the territory are usually used to deduce the adaptive significance of territoriality. Thus, purely intraspecific defense probably involves mating activities (Buckman and Ogden, 1973), while the intensity of defense directed toward other species may be correlated with the level of shared microhabitat preference (Moran and Sale, 1977), dietary similarity (Low, 1971; Ebersole, 1977), or both (Clarke, 1970; Thresher, 1976), in addition to potential egg predation. Most studies stress that territoriality among fishes is probably a multi-functional phenomenon (Myrberg and Thresher, 1974).

A more direct but difficult approach to determine which major resource categories are

the object of territorial defense is to experimentally manipulate the resource in question. Presently, such experiments have been reported for only two species of fish. In both cases, manipulated food supplies resulted in changes in territory size consistent with the food defense hypothesis (Slaney and Northcote, 1974; Syrop, 1974).

Embiotoca jacksoni, the black surfperch, is a common year-round resident of subtidal rock reefs off southern California (Limbaugh, 1955; Quast, 1968a; Feder et al., 1974). It attains a maximum length of about 35 cm (Miller and Lea, 1972), and is commonly observed swimming within a meter of the reef substrate and feeding on small benthic animals (Quast, 1968b). It is strictly diurnal, becoming inactive near the reef substrate at night (Ebeling and Bray, 1976). It eats various species of small, sedentary invertebrates (mainly crustacea) that inhabit a diverse aggregate "turf" of small plants and colonial benthic animals covering much of the reef bottom (Limbaugh, 1955; Quast, 1968b; Ellison et al., 1979). The primary prey are tube-dwelling gammarid amphipods (detritivorous and planktivorous crustaceans

averaging several millimeters in length). Because these prey brood their young, and their home sites (tubes) are fixed, they probably maintain local populations and thus constitute a potentially sustainable food supply. Like other members of the viviparous Embiotocidae, *E. jacksoni* exhibits internal fertilization. Except for a small copulatory organ located on the anal fin of males, which facilitates sex determination in the field, there is no sexual dimorphism (Tarp, 1952).

Preliminary field observations indicated that certain large males of this species were territorial, especially during the fall breeding season (Sept.–Jan.). This paper provides experimental as well as observational evidence that such territoriality primarily maintains an exclusive mating site, and may secondarily insure a sustainable food supply at that site. These data are discussed in terms of both the reproductive biology of this species and the economics of defending a food supply. Finally, competitive interactions between territorial *E. jacksoni* and other reef animals, including a large invertebrate grazer, are considered in terms of relative interference and exploitative competitive dominance.

METHODS

Study area.—The study took place primarily at Naples Reef, located 1.6 km offshore near Santa Barbara, California, and near the center of the coastal geographical range of *E. jacksoni* (Miller and Lea, 1972). This relatively large reef measures approximately 2.2 hectares and consists of siltstone rock ridges emerging diagonally from a subtidal sand and rock cobble plateau about 15 m deep. Depths across the reef flat average 6 to 9 m, although some ridges project to within 5 m of the surface. Water temperatures range between about 10 and 20 C, being warmest in fall and coldest in spring, and effective underwater visibility averages about 6 m. Ebeling and Bray (1976) and Ebeling et al. (1980) detail the general community structure of fishes that inhabit the reef.

Observations.—By necessity the entire study was conducted using SCUBA, which greatly limited effective field time. I could recognize many territorial fish by their unique color patterns, fin cuts, body scars, etc. However, most nonterritorial and several territorial individuals were identified by color-coded anchor tags inserted

through the base of the dorsal fin. During the summer of 1975, I tagged 25 males in situ using various trapping techniques and a waterproof tagging gun (Thorson, 1967). This procedure appeared to cause few short-term deleterious effects on the animals.

I constructed a detailed map of the study area using a grid of small numbered floats anchored by concrete blocks and spaced about 5 m apart over a 40 m by 40 m section of the reef. I observed the movements of the tagged fish and plotted their locations during periodic visual surveys of this area. A total of 11 surveys were completed between July and November of 1975, by which time most of the tags had become fouled and unrecognizable. However, several fish whose tags remained unfouled were subsequently tracked up to 3 years. I estimated undefended home range sizes of those tagged individuals I had sighted on at least ten different occasions by means of the convex polygon method (Southwood, 1966). Home range boundaries were mapped by connecting the outermost sighting locations such that there were no concavities in the resulting polygon. The area of the polygon was then measured with a planimeter.

I mapped defended territory boundaries by hovering in midwater and dropping small colored weights at the sites of agonistic encounters. I then plotted the distances and angles between the weights on a plastic slate. I considered an "agonistic encounter" to be any display, escort or outright chase by the territory occupant immediately followed by the intruder leaving the territory. During outright chases, which were by far most common, I marked the endpoint of the chase. Locating and marking a sufficient number of interaction sites to accurately define the perimeter of the territory (at least ten) usually required about a half an hour of observation during periods when the fish were maximally aggressive. Additional observation time (up to 3 hours) did not result in a larger mapped area. After fitting a smooth curve to the plotted points by eye, I measured the resulting area with a planimeter. Thus, the measurement of territory size reflected the actual "defended area" (sensu Noble, 1939). There was no evidence of "serial territories" (sensu Myrberg and Thresher, 1974).

I recorded data on the activity budgets of territorial fish on an approximately weekly basis from March 1977 to August 1978. To account for temporal variations in behavior, I divided

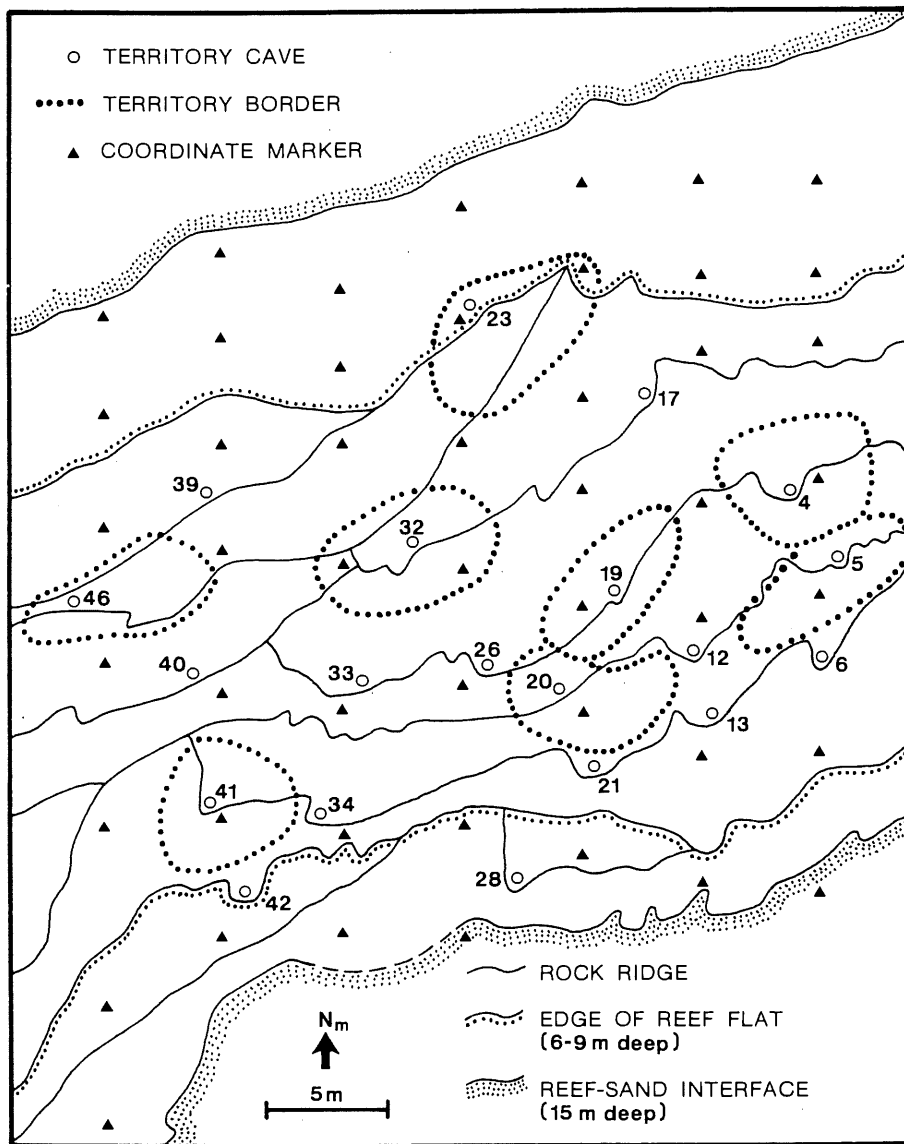


Fig. 1. Map of the Naples Reef study area showing the locations of all caves (numbered) within the territories of *E. jacksoni* males. Caves surrounded by dotted boundaries are permanent territories; others are sites of temporary territories, each of which included only a small area around the cave entrance. The territories were mapped during 1975 and 1976, before any experimental manipulations were made.

each year into the four solar seasons. Similarly, I divided each day into 2-hour intervals covering the 10 to 14 hours between sunrise and sunset. Within each time interval, I observed six (occasionally four) haphazardly chosen individuals for 5 minutes each. In all, a grand total of 615 minutes quantitative observation time was evenly distributed over all seasons and daylight hours. During each sample period, I tallied the number and species of excluded intruders and other activity data using a specially designed activity-event recorder.

Experiments.—I investigated the adaptive significance of territoriality in *E. jacksoni* by manipulating both the territory occupants and their potential defended resources: reef caves and food. To determine if and how rapidly territory occupants would be replaced during the breeding season, I speared all territorial fish from the eastern half of the mapped study area (Fig. 1). The other half of the area served as a control. Between breeding seasons, I sequentially removed territorial individuals to determine if and how rapidly single fish would be replaced.

Non-neighboring territories served as controls for these manipulations.

I reduced the number of reef caves by blocking their entrances with boulders. Non-neighboring control territories were disturbed by the presence of a diver but not manipulated. I increased the number of caves by stacking large boulders and by placing a meter-long section of 30 cm diameter brick pipe at various locations on the reef. The artificial caves were placed in areas where territories were not already established and where food was apparently abundant.

If the absolute amount of food within a territory is important as a defended resource, one might expect the size of the territory to vary with food availability. This prediction, in turn, relies on the assumption that the occupant forages throughout its territory, or at least near the perimeter. I tested both prediction and assumption with the following experiment. I established meter-square grid patterns on two spatially isolated territories located about 5 m apart, using plastic surveying tape attached to the reef surface to mark the corners of each quadrat. For baseline data, I observed each fish during May of 1976 for a total of 4 hours divided into 15-min sample periods. I controlled for the time of day and the influence of any general variations in environmental factors by sequentially alternating my observations between the test and control fish. During 3 of the 4 hours, I recorded the number of foraging bites per quadrat made by the territory occupant, the number and species of territory intruders, and the number of agonistic encounters. During the fourth hour I measured the size of the territory as described above.

Following these baseline observations, I artificially reduced food availability in the test territory. Three quadrats were covered with 0.5 mm nylon netting tied to the reef surface and anchored along the edges with bricks. This effectively prevented the fish from foraging within the quadrats. These particular quadrats were covered because the territory occupant had taken exactly one-third of its total foraging bites from these areas during the baseline observations. To control for the presence of netting in the test territory, five quadrats in the control territory, which also accounted for one-third of the occupant's baseline foraging effort, were circumscribed with the same quantity of netting. This was accomplished by clustering the netting along the perimeter of each quadrat,

thus leaving it uncovered. Following this manipulation, during May and June of 1976, I again observed each fish for a total of 4 hours. As before, the sizes of the territories were measured during the final hour of observation. In June, the treatment was replicated, with two additional quadrats covered in the test territory, and three circumscribed in the control. This time, the manipulated quadrats accounted for half the number of foraging bites made by each fish during the baseline period.

During August of 1977, I artificially increased the availability of food organisms within territories. I anchored m^2 plastic trays in unproductive sand-cobble patches located within each of two spatially isolated territories located about 10 m apart. The territories were then measured (as described above) and the number of foraging bites made by each occupant was recorded during 45-min observation periods. After the baseline measurements, I filled the tray in one territory with food-rich reef substrates removed from the territory of a garibaldi, *Hypsypops rubicunda* (Pomacentridae). Garibaldi are large and very aggressive damselfish that defend permanent territories and are strongly dominant over *E. jacksoni* (Clarke, 1970). However, garibaldi eat mostly sponges and bryozoans (Quast, 1968b; Clarke, 1970), so their territories at the study site retained rich concentrations of tube-dwelling amphipods, the primary prey of *E. jacksoni* (Quast, 1968b). Subsequently, I observed and measured the control and test territories at intervals of 1 hour, 2 days, and 8 days after the manipulation. In September of 1977, I reciprocally replicated this experiment by switching treatment and control between the territories.

RESULTS

Spatial and seasonal patterns.—Territories were mostly noncontiguous and located on the reef flat, at depths ranging from 6 to 9 m, each centered around a single small reef cave (Fig. 1). Two types of territories could be distinguished. "Temporary" territories existed only during the fall breeding season, from late September through early January of each year. The occupants defended only the area immediately surrounding the cave entrance, from which they excluded other males and occasionally other embiotocids. Since the occupants limited their aggressive behavior to such small areas, the 12 temporary territories are mapped on

Fig. 1 solely by the locations of the defended caves.

Of the 25 fish tagged at the beginning of the study, nine were never seen again, twelve were nonterritorial within the mapped study area and four established temporary territories within the area. All four temporary territory occupants (206–217 mm SL) were larger than the nonterritorial tagged fish (116–188 mm SL). Nonterritorial fish appeared to spend most of their time foraging over the entire reef, and they were often excluded from both temporary and permanent territories.

Temporary territory occupants periodically left the immediate area of their caves and foraged over broadly overlapping undefended home ranges. During the 1975 breeding season, the calculated home ranges of the four tagged individuals ranged from 187 to 481 m² in area, with a mean size of 292 m². On several occasions, I observed these fish being excluded from other territories while they were foraging. None of the tagged fish, nor several others I recognized by natural color variations, defended the same cave during subsequent breeding seasons. One tagged occupant of a temporary territory was recognizable throughout the 3-year study, during which time it never established another territory within the study area. The turnover rate of temporary territory occupants thus appeared to be quite high.

"Permanent" territories existed throughout the year and were characterized by well-defined defended areas surrounding the cave entrance (Fig. 1). Where territories were contiguous, neighboring occupants occasionally interacted along a common boundary. Boundaries were often located along the edges of meter-high rock ridges which occur throughout the reef (Fig. 1). The eight permanent territories mapped in Fig. 1 ranged from 21.2 to 30.7 m² in area, with a mean size of 25.4 m². Each occupant foraged exclusively within its territory and rarely swam beyond its boundaries.

Frequencies at which the occupants of permanent territories excluded various species are presented in Table 1. A four-year monitoring study by Ebeling et al. (1980) indicated that the relative abundances and distributions of all species listed in Table 1 (except *Hypsurus caryi*, see below) remain quite stable at this reef. Thus, between-season differences in chase frequencies can be safely attributed to changes in the aggressive response of territorial *E. jacksoni*. During the fall breeding season, the territories

were mainly defended against any intruding conspecific males. Other embiotocid species were usually excluded only when they foraged within the territory, entered the cave, and/or intruded during courtship. Occasionally, various non-embiotocid species, mainly young adults of the piscivorous serranid *Paralabrax clathratus* (kelp bass) and the planktivorous pomacentrid *Chromis punctipinnis* (blacksmith), were also excluded, but only after entering the cave and/or interrupting courtship. Between breeding seasons (winter through summer), female as well as male conspecifics were excluded at a relatively high rate. Non-embiotocids were rarely chased during this period, and other embiotocids were excluded at a much lower rate. An apparent exception to this trend was that the embiotocid *Hypsurus caryi* (rainbow surfperch) was excluded only during the spring and summer (Table 1). However, this was because this species inhabited the reef only during these months.

The turnover rate of permanent territory occupants appeared to be much lower than that of temporary territory occupants. Of the eight territories mapped on Fig. 1, three (5, 32 and 46) were occupied by fish with very distinctive natural color patterns. These individuals retained their territories for at least 30, 23 and 20 months, respectively. While I could recognize other permanent occupants for a number of months by fin cuts, body scars, etc., such ephemeral features precluded unequivocal long-term identification. (Permanent territory occupants would not enter traps and proved impossible to capture unharmed for tagging.)

Five randomly selected permanent territory occupants were significantly larger than five temporary territory occupants (mean SL: 235 mm vs. 224 mm, $P < 0.05$, Mann-Whitney U-test). Aged by scale annuli, the permanent occupants averaged 6–7 years old, compared to 5–6 years for temporary occupants, although this difference was not quite significant ($0.10 > P > 0.05$, Mann-Whitney U-test). Cave dimensions of five randomly selected temporary territories did not differ significantly from those of five permanent territories. These dimensions included mean entrance height (40 cm vs. 34 cm, respectively), mean entrance width (88 cm vs. 78 cm), mean cavity depth (106 cm vs. 90 cm), and approximate mean volume (0.36 m³ vs. 0.24 m³, $P > 0.2$ for all comparisons, Mann-Whitney U-test). Thus, while permanently territorial individuals were significantly larger and

TABLE 1. SEASONAL VARIATION IN FISH SPECIES EXCLUDED FROM TERRITORIES.

Season: Total observation time (min): Number of sample periods:	No. of agonistic encounters observed				Total 615 123
	Fall 135 27	Winter 150 30	Spring 150 30	Summer 180 36	
Embiotocids:					
<i>Embiotoca jacksoni</i>	61	33	58	50	202
<i>Embiotoca lateralis</i>	16	2	5	1	24
<i>Damalichthys vacca</i>	9	2	1	1	13
<i>Rhacochilus toxotes</i>	7	1	2	2	12
<i>Hypsurus caryi</i>	0	0	4	3	7
<i>Phanerodon furcatus</i>	0	0	1	0	1
Total:	93	38	71	57	259
Non-embiotocids:					
<i>Paralabrax clathratus</i> (Serranidae)	9	1	0	0	10
<i>Chromis punctipinnis</i> (Pomacentridae)	7	0	0	0	7
<i>Sebastes atrovirens</i> (Scorpaenidae)	2	0	0	1	3
<i>Sebastes chrysomelas</i> (Scorpaenidae)	0	1	0	0	1
<i>Sebastes mystinus</i> (Scorpaenidae)	0	0	1	0	1
<i>Oxylebius pictus</i> (Hexagrammidae)	1	0	0	0	1
Total:	19	2	1	1	23

perhaps older than temporary territory occupants, I could detect no difference in the size, location, or any other quality of the caves they defended.

Caves as a resource.—During the breeding season, both temporary and permanent territory occupants actively courted any females entering their territories. The primary courtship display consisted of the male assuming a "head-stand" position, quivering his pectoral and caudal fins, and usually orienting his copulatory organ directly in front of the female's face. During courtship the male would gradually lead the female toward his cave, where I observed copulation on three occasions. Only one of the observed copulations, which involved a permanent territory occupant, occurred within the study area. I never observed a complete mating sequence from the initial courtship display to copulation. After mating, the female would voluntarily leave or be chased from the territory.

Cave removal experiments tested the importance of these mating sites to the existence of a territory. When I occluded the caves in two permanent and two temporary territories during the 1977 breeding season, the occupants immediately altered their behavior while fish in unmanipulated control territories did not, as detailed by Hixon (1979). One occupant shifted its permanent territory (46 in Fig. 1) and in-

cluded a relatively small cave near the occluded one that was previously unoccupied. When the original cave was reopened 2 months later, the fish reestablished its original territory boundaries. Another manipulation produced a chain reaction. The affected occupant completely abandoned its permanent territory (4) and displaced its neighbor from permanent territory 5 (Fig. 2). The excluded neighbor, in turn, displaced the occupant of temporary territory 12, who subsequently disappeared. When the occluded cave was reopened 5 days later, both the permanently territorial fish reestablished their original boundaries (4 and 5) within several hours, and a new fish occupied cave 12. During the manipulations of temporarily defended caves, the affected occupants disappeared and were never seen again. When reopened, the caves were reoccupied by other males.

Between the 1977 and 1978 breeding seasons, when only permanent territories were defended, I again occluded the caves in territories 4 and 46 (Fig. 1). The results were nearly identical to those during the breeding season: each fish shifted its territory boundaries, occupying a nearby open cave, and reestablished its original boundaries when the original cave was reopened. Artificial caves built from natural or man-made materials proved unsuitable to the fish and were never occupied.

While it was apparent that small reef caves

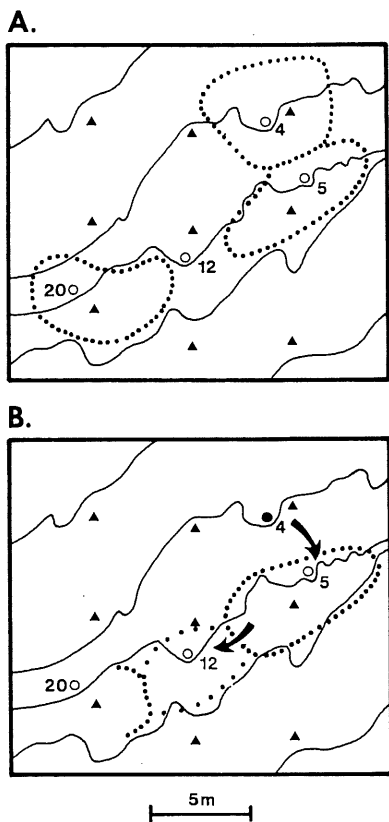


Fig. 2. Shifts in territory occupants and boundaries following the experimental occlusion of a territory cave. Symbols are the same as in Fig. 1. A) Boundaries of permanent territories 4, 5 and 20 and the location of temporary territory 12 before the manipulation. B) Territory boundaries after the occlusion of cave 4 (solid circle) and the directions of shifts in occupants. Note that the boundary of territory 12 was relatively vaguely defined. Territory 20 was not remapped completely after the manipulation.

constitute mating sites, reproductive success could not be estimated and compared among males, since *E. jacksoni* is viviparous and copulation was rarely observed. Yet, nearly every small cave located within the study area was occupied and defended during the breeding season, so the availability of suitable sites could potentially limit the number of reproductively successful males. Indeed, when I removed five permanent and seven temporary occupants from half the study area during the 1978 breeding season, all 12 fish were replaced by new males within 4 days. The number and distribution of territories was, in fact, identical to that before the removal. During this same period, there was no change in the configuration of the eight control territories (three permanent and five temporary) located on the other

half of the study area. However, I was unable to recognize every occupant in the control area, so some may have exchanged territories. Additionally, when I sequentially removed two permanently territorial fish from outside the study area between the 1977 and 1978 breeding seasons, each was permanently replaced by another male within several days. Finally, at the end of the food removal experiments in June of 1976 (see below), the test fish disappeared from its territory and was soon replaced by another.

Food as a resource.—Occupants of permanent territories apparently defended food supplies as well as mating sites. While nonterritorial males foraged throughout the reef, and temporary territory occupants foraged both near their caves and over relatively large undefended home ranges, permanent occupants appeared to forage exclusively within their territories.

Sequential manipulations of food availability within a permanent territory (19, Fig. 1) resulted in the occupant increasing the size of its territory and included foraging range as more food-bearing substrate was covered (Fig. 3). The test fish increased the area of its territory disproportionately in relation to the area of the covered quadrats. When three m^2 quadrats were covered the territory expanded by $9.6 m^2$ (experiment #1), and when two more quadrats were covered the territory expanded by an additional $8.2 m^2$ (experiment #2, Fig. 3). However, the newly acquired quadrats were subsequently utilized much less extensively than the covered quadrats had been (Fig. 3). The size of the control territory (4, Fig. 1) changed very little during this period, and the occupant continued to forage over those quadrats outlined by netting, indicating that the mere presence of netting did not affect quadrat utilization. Both the test and control fish continued to forage throughout their territories (Fig. 3). Unfortunately, an intervening period of foul weather removed the netting and the quadrat markers before the effects of re-exposing the covered quadrats could be observed. By the time repairs were completed, the test fish disappeared. However, the site was soon reoccupied by another fish, so one month after the experiment I remeasured both territories. The uncovered test territory now measured $21.2 m^2$, which approximated its original size of $17.4 m^2$ and was much smaller than the sizes during the

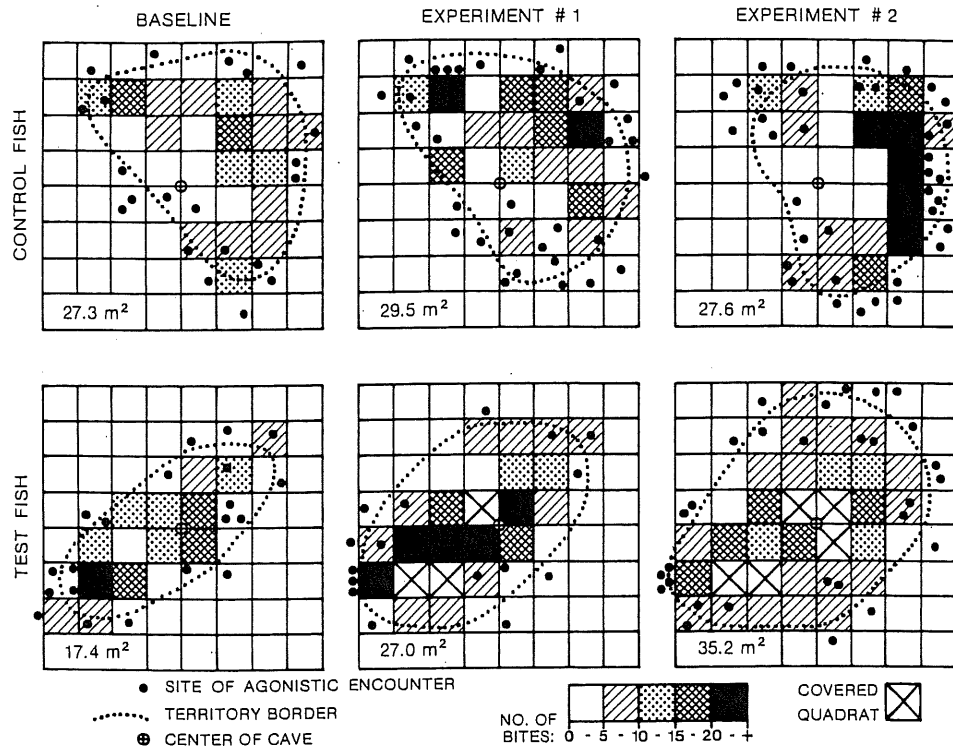


Fig. 3. Effect of successive food substrate removals on permanent territory size. Each of the six frames summarizes data from 4 hours observation of the occupant's foraging patterns, including 1 hour observation of the sites of agonistic encounters with intruding fishes, from which the given territory boundaries and areas were calculated. At the beginning of each experiment, those meter-square quadrats from which the test fish took one-third (expt. #1) and one-half (expt. #2) of its foraging bites during the baseline period were covered with fine-mesh netting. These experiments were run during May and June of 1976.

food removals (27.0 and 35.2 m², Fig. 3). The control territory now measured 27.2 m², nearly the same as during the experimental period (Fig. 3).

E. jacksoni belongs to a foraging guild of five embiotocid species (A. W. Ebeling, pers. comm.). Within this guild, pooled aggression data from these experiments compared with dietary data previously gathered at this reef

(Ebeling, pers. comm.) revealed a significant correlation between the proportion of intruders of a species that were chased from the territory and the proportional dietary overlap between that species and *E. jacksoni* (Table 2; $P < 0.02$, Kendall's tau test).

The introduction of amphipod-rich substrates resulted in the occupants reducing the size of their territories within one hour (Table

TABLE 2. NUMBER AND PROPORTION OF EMBIOTOCID INTRUDERS AGGRESSIVELY EXCLUDED BY TWO PERMANENT TERRITORY OCCUPANTS DURING THE 24 OBSERVATION HOURS OF THE FOOD REMOVAL EXPERIMENTS (FIG. 3). Proportional dietary overlap between each species and *E. jacksoni* provided by A. W. Ebeling (pers. comm.) using the index proposed by Colwell and Futuyma (1971).

Species	Number encountered	Number excluded	Proportion excluded	Proportional dietary overlap with <i>E. jacksoni</i>
<i>Embiotoca jacksoni</i>	504	385	0.75	1.00
<i>Embiotoca lateralis</i>	63	43	0.68	0.61
<i>Hypsurus caryi</i>	145	71	0.49	0.49
<i>Rhacochilus toxotes</i>	12	2	0.17	0.34
<i>Damalichthys vacca</i>	88	9	0.10	0.17

TABLE 3. CHANGES IN TERRITORY SIZE, NUMBER OF FORAGING BITES OFF AND ON FOOD TRAYS AND NUMBER OF AGONISTIC ENCOUNTERS DURING FOOD ADDITION EXPERIMENTS.

Time after food addition to test tray	Territory size (m ²)	No. of foraging bites in 45 min		Number of agonistic encounters in 45 min
		off tray	on tray	
Experiment #1:				
Test fish:				
Baseline	27.8	38	—	36
1 hour	14.3	15	34	40
2 days	23.0	21	6	30
8 days	26.8	19	0	20
Control fish:				
Baseline	23.7	25	—	29
1 hour	24.1	31	—	23
2 days	24.0	29	—	22
8 days	24.2	30	—	31
Experiment #2:				
Test fish:				
Baseline	24.2	30	—	31
1 hour	10.8	9	43	27
2 days	18.8	31	7	29
8 days	21.0	22	1	34
Control fish:				
Baseline	26.8	19	—	20
1 hour	26.9	27	—	22
2 days	27.7	20	—	25
8 days	25.2	36	—	31

3). However, this initial effect may have been due to increased intruder pressure per unit of defended area as well as increased food availability, since the recently filled food trays attracted many intruders from outside the territory (Brown, 1975; Verner, 1977). Moreover, the test fish initially foraged over the food trays more frequently than the remainder of their territories, taking 69% and 83% of their total foraging bites from the trays (Table 3).

Two days after the trays were filled, however, the intrusion rate of nonterritorial fishes had returned to normal levels and the test fish were foraging over the trays no more frequently than over other productive portions of their territories, taking 22% and 18% of their total foraging bites from the trays (Table 3). At the same time, the test territories were still significantly smaller than usual, when compared with their baseline and control sizes ($P < 0.05$, t-test). Moreover, in each replicate the territory size of the test fish was significantly negative-

ly correlated with the number of bites the fish took on the food tray ($r = -0.98$ and -0.96 , $df = 2$, $P < 0.05$), but not with the number of agonistic encounters per unit time ($r = -0.60$ and -0.74 , $df = 2$, $P > 0.05$).

Eight days after the trays were filled, the test territories had returned to their original sizes and the trays were no longer utilized by the occupants (Table 3). Presumably the food organisms had been depleted by foraging and/or wave surge, which had continuously buffeted and shifted the positions of the rock substrates in the trays. Throughout both replicates, the sizes of the control territories remained nearly unchanged (Table 3).

A natural decrease in food availability that affected territory configurations occurred during an outbreak of sea urchins (*Strongylocentrotus purpuratus*) within the study area (Paine and Vadas, 1969; Lang and Mann, 1976; Schroeter, 1977). Early in 1977, the density of these echinoderms became noticeably greater than in previous years. By late summer, foraging fronts of urchins had grazed a significant portion of the reef to almost bare rock. Concurrently, the occupant of permanent territory 32 shifted its territory such that denuded areas were no longer defended (Fig. 4a, b). Within a year, denuded areas had expanded to the point where this fish abandoned its territory (Fig. 4c). During the same period, urchins completely denuded permanent territory 41 (Fig. 1), which also resulted in the occupant abandoning the area. These caves, which were now surrounded by bare rock, became the centers of temporary territories during the subsequent 1978 breeding season.

DISCUSSION

Territoriality and reproduction.—Field observations of mating behavior and the results of territory cave removals suggest that defense of reef caves utilized as mating sites is the primary reason for both temporary and permanent territoriality in *E. jacksoni* males. Territories occur only where caves are present and mating behavioral sequences generally progress toward and within caves. The adaptive significance of mating in caves may involve protection from predation or wave surge during courtship as well as avoidance of interference by other males. Caves are generally not occupied by embiotocids during nonmating activities (Ebeling and Bray, 1976).

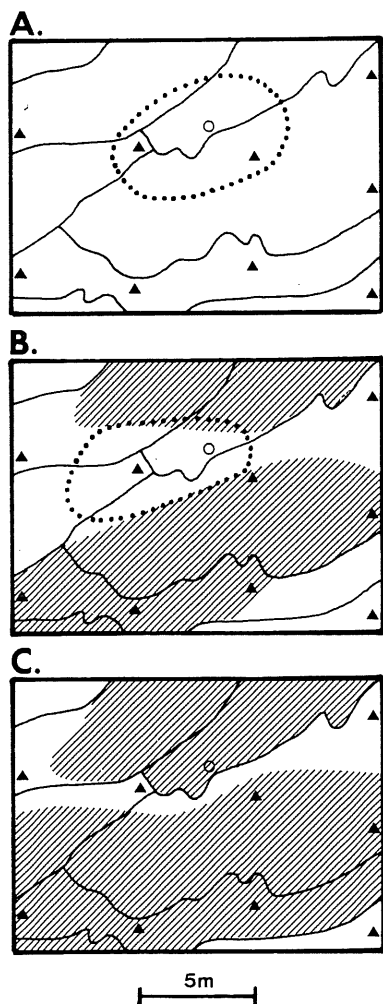


Fig. 4. Effect of sea urchin foraging on the configuration of permanent territory 32 (Fig. 1). Symbols are the same as in Fig. 1. Shading indicates areas totally denuded by overgrazing of sea urchin foraging fronts as of: A) early 1976; B) late 1977; C) mid 1978. By mid 1978, the fish had abandoned its territory.

Does the number of suitable caves on a reef limit the number of reproductively successful males? During the breeding season, nearly every small cave within a fairly narrow size range is defended by a male, although many caves of various sizes remain unoccupied. Moreover, when territory occupants are removed they are quickly replaced. Only the largest and perhaps oldest males are territorial, so dominance is apparently a function of size and/or experience. Smaller nonterritorial males very seldom court females. Thus, suitable reef caves appear to be essential for successful male courtship, and as mating sites such caves apparently constitute a limiting resource for males.

This situation does not, however, indicate that the number of mating sites limits the overall population size of *E. jacksoni*. Evidence for population regulation through territoriality requires a demonstration that mature females as well as males are prevented from breeding (Brown, 1969). While the existence of nonterritorial males and the rapid replacement of territory occupants indicates that male reproductive success may be limited by territoriality, there is no evidence that any females are kept from mating (see also Stewart and Aldrich, 1951; Hensley and Cope, 1951; Clarke, 1970). Territorial males actively court virtually every female passing through their territories at all daylight hours during the breeding season. Being viviparous, no parental care is required of the males, so successful territorial males probably mate many times during any given breeding season (Perrone and Zaret, 1979). Therefore, the mating system of *E. jacksoni* at this reef is probably sequential polygyny, with the formation of very brief pair bonds during courtship.

Why are some caves defended throughout the year, while others are defended only during the breeding season, regardless of changes in the territory occupants? There were no obvious differences between permanently and temporarily defended caves, and there was no way to determine if males that defend permanent territories experience greater reproductive success than others. However, permanently defended territories are occupied by the largest and perhaps oldest males on the reef. Assuming such males are social dominants, some unknown characteristic of permanently defended caves and/or surrounding food supplies apparently makes them valuable enough to be economically defendable throughout the year. Perhaps the juxtaposition of any suitable cave and a sustainable food supply simply allows these males to remain near their caves at all times. This would allow these fish not only to spend more time courting females, but also to retain their sites through dominance derived from prior residency (Braddock, 1949). This hypothesis is supported by the fact that, during a cave removal experiment, the displaced permanent occupant of a territory switched to a nearby unoccupied cave, but continued to defend most of the original area of its territory. Alternatively or additionally, females may be attracted to particular caves or an abundant food supply, although they appear to forage within and out-

side of territories with equal intensity. At any rate, the economic defense of permanent territories evidently requires an adequate food supply near the cave, since two such territories were abandoned when overrun by grazing urchins.

Territoriality and food.—While all territorial *E. jacksoni* males defend mating sites, those that maintain permanent territories secondarily defend food supplies. Such males regularly defend their territories from both conspecifics and several other embiotocid species that are members of the same foraging guild. Within this guild, the proportion of intruders of a species that are chased from the territory is positively correlated with the proportional dietary overlap between that species and *E. jacksoni* (see also Low, 1971; Thresher, 1976; Ebersole, 1977). The mechanism behind this correlation may be that, between breeding seasons, territorial *E. jacksoni* appear to chase only those heterospecific intruders that actively forage within the territory. Fish that simply pass through the territory are usually ignored. Thus, the more extensively these intruders overlap in diet with the territory occupant, the more often they would encounter and consume suitable prey within the territory, and subsequently, the more frequently they would be excluded.

It is obviously more advantageous energetically for a territory occupant to chase foraging heterospecific intruders between breeding seasons, and ignore nonforaging ones. Beyond this, an additional economic advantage would be realized by a fish maintaining a territory size that reflected some optimal net energetic gain between the cost of defending an area of a given size and the benefit of having exclusive access to the food within that area. While tests for such optimization require rigorous analyses beyond the scope of the present study (Hixon, 1980a), evidence that the occupant at least controls the amount of food it defends can be derived from manipulations of territory food supplies. Thus, if the animal forages throughout its defended area, territory size should usually vary inversely and proportionally with food availability (Hixon, 1980a). The results of such controlled experiments support this hypothesis for *E. jacksoni*. This relationship has also been demonstrated experimentally for limpets (Stimson, 1973), other fishes (Slaney and Northcote, 1974; Syrop, 1974), lizards (Simon,

1975) and birds (Miller et al., 1970). Although these experiments often (by necessity) manipulate food availability in a relatively unnatural patchy manner, such recurring patterns nonetheless indicate that these animals at least partially control the amount of food they defend.

Indirect evidence also suggests that *E. jacksoni* males may control the standing crop of their food supplies. For each m² of territory substrate covered during the food removal experiments, the test fish expanded its territory by about 3.5 m². This result indicates that the standing crop of food organisms within permanent territories may be greater than in surrounding areas, as has been shown for certain tropical reef fishes (Vine, 1974; Brawley and Adey, 1977), although this may possibly be due to different substrate qualities as well as the activities of fish.

Territoriality and competitive dominance.—*E. jacksoni* overlaps most extensively in diet with its congener, *E. lateralis*, the striped surfperch (A. W. Ebeling, pers. comm.). However, while individual *E. jacksoni* males readily exclude *E. lateralis* from their territories, *E. lateralis* (a non-territorial species) is competitively dominant over *E. jacksoni* and exclusively occupies the more productive shallow areas of the reef (Hixon, 1980b). This paradox may be partially resolved by the fact that small reef caves, the primary defended resource of *E. jacksoni* males, are relatively scarce in shallow areas where these studies took place. Thus, the distribution of suitable caves may limit potentially dominant large *E. jacksoni* males to less productive deeper reef areas, leaving *E. lateralis* to contend only with female and smaller male *E. jacksoni* in the food-rich shallow zone (Hixon, 1980b). This situation may facilitate the ability of *E. lateralis* to competitively dominate shallow reef areas.

While competitive interactions between territorial *E. jacksoni* and other fishes are clearly a form of "interference," overgrazing of territories by sea urchins is an example of "exploitation" competition (sensu Miller, 1967). Protected by sharp calcareous spines, urchins can forage within territories without interference from the occupants. Since urchins consume benthic food sources as they slowly pass through a territory in dense foraging fronts, they almost completely remove the occupant's food supply. Thus, the superior exploitative ability of urchins, combined with their morphological defenses, occasionally allows these

invertebrates to competitively dominate a territorial vertebrate. Such overt competition between distantly related groups may be an important although rarely documented determinant of reef community structure (see also Williams, 1979). Territorial *Embiotoca jacksoni* thus play a diverse competitive role in the structure of southern California reef communities.

ACKNOWLEDGMENTS

I am very grateful to the members of my doctoral committee for their constant support and inspiration: A. W. Ebeling (chairman), J. H. Connell, A. Oaten, P. F. Sale and R. R. Warner. R. J. Larson, D. R. Laur, R. N. Bray, M. E. Molina, R. Douglas and A. Foskett generously assisted me both in the field and in many other ways. This work was mainly supported by NSF grants GA-38588 (Ebeling) and OCE76-23301 (Ebeling and Warner) and a U.C. Patent Fund Grant. This paper is a chapter from a dissertation submitted in partial satisfaction of the requirements for a doctorate in biology.

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