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CHAPTER 17

Competition

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Introduction

Competition occurs when organisms inhibit each other's access to shared resources that are actually or potentially in short supply (Birch, 1957), and thereby have negative effects on each other at the individual or population level (Odum, 1953). Because overlap in resource use is usually greater within than between species, intraspecific (within-species) competition is typically thought to be more intense than interspecific (between-species) competition, all else being equal. Competition, especially within species, can be a major mechanism regulating populations (reviews by Murdoch, 1994; Hixon et al., 2002), and interspecific competition may additionally be an important interaction structuring ecological communities (reviews by Strong et al., 1984; Diamond and Case, 1986).

To my knowledge, the earliest substantial discussion of competition involving a California marine fish is Sette's (1943) description of a comprehensive research program to understand population dynamics of the Pacific sardine (*Sardinops sagax*). He speculated that "the basic influence tending to keep the population in check [before fishing] must have been competition within the population." In accepting this assumption, Sette followed the then evolving fundamental tenet of classic fisheries biology: within-species competition is the primary factor limiting population size before exploitation (review by Smith, 1994). This tenet laid the foundation for the concept of maximum sustainable yield, the attempted application of which has since proven disastrous (Larkin, 1977). Clearly, understanding the role of competition in marine fishes not only contributes to basic ecological knowledge, but also is of fundamental importance to managing and sustaining fisheries.

This chapter explores the existence, mechanisms, and ecological importance of competition in California marine fishes (excluding diadromous species). Following an overview of relevant definitions and concepts, I examine representative case studies in detail, and conclude with a brief discussion of the significance of studies of competition to fisheries.

Competition: Definitions and Concepts

The simple definition stated above belies the complexity of the meaning of competition, the evidence gathered to detect and understand the mechanisms and effects of competition, and resulting controversy in interpretation of that evidence. Ample jargon has developed in the study of competition, so this section provides a primer (see Keddy, 1989, for a review). Key words from the definition of competition that require further explanation include "inhibit," "shared resources," and "short supply." What are "resources" and when are they "shared"? A resource is any consumable entity—be it food, shelter, etc.—and it is shared when targeted by more than one consumer. Importantly, just because two organisms share a resource does not necessarily mean that they compete for it (e.g., all marine fishes share oxygen as a resource). The shared resource must be in "short supply," meaning that its abundance limits the reproductive success of the individual (via growth, survival, and reproductive output), and thus the distribution or abundance of the population (either within or between species). Ultimately, a resource in short supply limits the population growth rate in a density-dependent manner (i.e., the per capita population growth rate varies inversely with population size).

There are basically two ways that competing organisms of the same or different species can "inhibit" each other: interference and exploitation (Birch, 1957; see Schoener, 1983, for further subdivisions). Interference competition is a direct interaction involving some form of aggression. One common form is territoriality (chapter 19), whereby an animal defends an area and the resources within it. Exploitation competition occurs simply when one organism consumes a resource that is in short supply, thereby rendering that resource unavailable for another organism. In this case, there is no direct aggressive interaction, so that exploitation competition is actually an indirect effect between two consumers using the same limiting resource (Holt, 1984).

Unlike predation (chapter 16), mutualism (chapter 21), and other ecological interactions, competition is often not self-evident in nature. Competition within species can be demonstrated by documenting demographic density dependence that is not caused by predation in the broadest sense (which includes parasitism and disease). Density dependence occurs when the per capita birth rate decreases and/or the per capita death rate increases as population size or density increases. When density dependence occurs in such ways that the population growth rate varies inversely with population size, the population is said to be regulated (reviews by Murdoch, 1994; Hixon et al., 2002).

Within or between species, a typical manifestation of competition for food in fishes is density-dependent growth that causes either 1) density-dependent survival (proximally often due to predation) or 2) density-dependent fecundity (review by Myers, 2002). Territoriality, which is usually a within-species phenomenon but sometimes occurs between species, is self-evidently a mechanism of competition if resources other than eggs are defended (review by Grant, 1997).

Between species, the existence and strength of ongoing competition can be detected unequivocally only by logistically difficult experimental manipulations in the field (see Connell, 1983; Schoener, 1983, for general reviews). Note that this assertion raised major debate during the late 1970s and early 1980s (e.g., the exchange in *The American Scientist* by Wiens, 1977; Diamond, 1978; Schoener, 1982; Conner and Simberloff, 1986). Overall, there is a spectrum of evidence for interspecific competition. In order of increasingly strong inference, there are four basic categories (Connell, 1975): 1) observations of resource partitioning, 2) comparisons of resource use in sympatry vs. allopatry (so-called natural experiments), 3) observations of direct competitive displacement via interference, and 4) true field experiments.

Resource Partitioning

Between-species competition occurs by definition within guilds, which are groups of species—often but not always closely related—that share the same general categories of resources within the same general habitat. Ebeling and Hixon (1991) review the basic guilds of demersal marine fishes, including many examples from California. Resource partitioning occurs when species within a guild utilize shared resource categories in at least slightly different ways (review by Schoener, 1974). For example, five species of embiotocid surfperch form a guild of demersal microcarnivores inhabiting rocky reefs off California, and each has a detectably different combination of diet and foraging microhabitat (see below). Within this and other guilds, one often finds niche complementarity, whereby species that overlap greatly in diet tend to forage in different microhabitats, and vice versa.

The conventional interpretation of resource partitioning is that between-species competition has selected for divergence in resource use between species in ecological and possibly evolutionary time. Observations of resource partitioning are abundant in studies of marine fish communities in general (reviews by Helfman, 1978; Sale, 1979; Ross, 1986; Ebeling and Hixon, 1991). The interpretation that such patterns are caused by competition is problematic because different species are different by definition. Therefore, the specific use of resources by members of a guild is bound to be somewhat different regardless of whether or not those species have ever competed. Resource partitioning resulting from evolutionary divergence due to competition—sometimes called the "ghost of competition past" (Connell, 1980)—is particularly problematic because it is usually impossible to document unequivocally (Abrams, 1983).

Natural Experiments

Whether resource partitioning is caused by ongoing competition can be tested by examining patterns of resource use of a species in the presence vs. the absence of its presumed competitor. A natural experiment accomplishes this comparison by observing species where they occur together (sympatry, more specifically syntopy) vs. where each naturally occurs alone (allopatry). For example, the striped seaperch (*Embiotoca lateralis*) and the black perch (*E. jacksoni*) partition shallow and deep foraging zones on reefs where they are sympatric in the Santa Barbara Channel (see below). However, where each species occurs in allopatry outside of this region, each forages over both reef zones. The conventional interpretation of such patterns is that each species in sympatry is constrained by competition to use a subset of the resources it uses in allopatry (Diamond, 1978). The key assumption of a natural experiment is that the only relevant difference between sympatry and allopatry is the presence or absence, respectively, of the presumed competitor. This assumption is rarely tested by field experiments (but was in the surfperch case, see below).

Direct Observation

Occasionally, between-species competition can be directly observed in nature when its manifestation is self-evident. The two most obvious cases are 1) interspecific territoriality, when it is known that territorial individuals clearly prevent intruders from using shared resources (accepting the argument that territoriality between species occurs only when resources are actually or potentially limiting, in accordance with Brown's, 1964, concept of economic defendability); and 2) direct displacement of one species by another, as occurs when sea urchins overgraze the territories of kelp-forest fishes (see below).

Note that an inverse relationship between the abundances of two species through time does not necessarily imply direct displacement due to interspecific competition. For example, the Pacific sardine fishery in California collapsed in the late 1940s due to a combination of overfishing and environmental shifts (review by Murphy, 1966). One of the proposed mechanisms contributing to this decline was competition with the northern anchovy (*Engraulis mordax*), which increased in abundance following the decline in sardines (Ahlstrom, 1966). From the perspective of competition, this "biomass dominance flip" (sensu Sherman, 1990) was interpreted as a direct species replacement. However, competition between these species has not in fact been demonstrated. Scale deposits in stratified seafloor sediments dated over the past two millennia have demonstrated that the relative abundance of sardine and anchovy alternate in cycles lasting several decades (Soutar and Isaacs, 1974; Baumgartner et al., 1992; see fig. 17-3, chapter 25). These cycles are correlated with oceanic environmental regime shifts that affect similar species worldwide (Lluch-Belda et al., 1989, 1992). Sardines are more abundant during warmer periods and vice versa. There are thus two alternative explanations for biomass dominance flips: 1) environmental variation shifts competitive dominance between species (similar to Hutchinson's, 1961, "paradox of the plankton") or 2) environmental variation shifts the relative abundance of species via mechanisms other than competition, be they biotic (e.g., concomitant shifts in predator and prey species) or abiotic (e.g., via physiological constraints linked with water temperature). This issue remains unresolved.

Field Experiments

The most rigorous test for detecting and understanding ongoing interspecific competition is to manipulate the density of putative competitors or their resources via true field experiments, which include controls for the secondary effects of the manipulation, and preferably, site replication (Connell, 1974, 1975). If competition is occurring, then a species should expand its resource use (and ultimately its population size) in the experimental absence of the other species. In the parlance of Diamond (1978), one observes a niche shift when comparing the ecology of a species when its competitor is removed (fundamental niche) compared to when its competitor is present (realized niche). The extent of both the niche shift and the expansion of population size and distribution following experimental manipulations provide a measure of the relative strength of competition, as well as mechanisms of coexistence. If both species respond fairly equally to removal of the other species, then the interaction is relatively symmetrical between evenly matched competitors, a case of what Colwell and Fuentes (1975) have called either the coextensive niche model (fig. 17-1A) or the niche overlap model with competitive symmetry (fig. 17-1B). If one species responds more than the other, but both undergo substantial niche shifts, then the niche overlap model with competitive asymmetry is occurring (fig. 17-1C).

If only one species undergoes a substantial niche shift, then that species is an inferior competitor and relative generalist normally confined to a competitive refuge by the superior competitor and relative specialist—the included niche model (fig. 17-1D). In ecological jargon, the fundamental niche of the competitively-subordinate generalist in the absence of competition is broader than its realized niche (competitive refuge) in the presence of competition (Colwell and Fuentes, 1975). For the competitively superior specialist, the fundamental and realized niches are similar in the included niche model. As reviewed in detail below, several of the most complete examples of the logistically challenging experimental approach to understanding competition in nature have focused on marine fishes of California.

Evidence Regarding Intraspecific Competition

Data indicating within-species competition in California marine fishes are of two kinds: the first an effect of competition (density-dependent growth) and the second a mechanism (intraspecific territoriality).

Density-dependent Growth

Density-dependent growth is well documented in fishes, and is generally assumed to be the result of competition for food (reviews by Weatherley, 1972; Wootton, 1990). Reduced growth due to increasing competition at higher population densities can ultimately regulate a population via two mechanisms: 1) density-dependent survival due to size-selective mortality, especially via predation (review by Sogard, 1997) and/or 2) density-dependent fecundity (review by Lorenzen and Enberg, 2002). Although I found no explicit studies from California per se, density-dependent growth has been documented off the Pacific coast of Canada in various species that range into California, including Pacific herring (*Clupea pallasii*) (Tanasichuk, 1997) and English sole (*Parophrys vetulus*) (Peterman and Bradford, 1987).

Off California, there is evidence for intraspecific competition in the feeding, growth, and fecundity patterns of striped seaperch, a benthic microcarnivore (Holbrook and Schmitt, 1992). At Santa Cruz Island, some individuals apparently specialize on caprellid amphipods, whereas others specialize on gammarid amphipods (Alevizon, 1975a). The caprellid specialists have fuller guts, are larger at age, and consequently, have higher calculated fecundity than gammarid specialists, with generalists lying midway between these extremes (fig. 17-2). Importantly, this pattern appeared to be maintained by aggressive displacement of smaller fish by larger fish from the foraging microhabitat that harbored caprellids (the red alga, *Gelidium*), rather than from active prey selection by different fish (see also Hixon, 1980a). Unknown was what came first: differential aggressive dominance between individuals of initially the same size that ultimately led to differential growth, or differential birth sizes that led to differential dominance.

Intraspecific territoriality

A variety of nearshore California fishes exhibit obvious territorial behavior (table 17-1), a clear form of within-species interference competition when resources other than demersal eggs are defended (review by Grant, 1997). Chapter 19 examines territorial behavior in detail. Typically, individual territories are permanent, cover the entire small home range, involve defense of both shelter and food (and often nests and eggs), and are defended mostly against members of the same species. Note that species with demersal eggs almost invariably defend clutches during the spawning season (e.g., cottids and hexagrammids), but this behavior is defense against egg predation rather than competition.

The question here is whether territoriality has significant effects on local population size within a species. This issue has been examined most explicitly in five species: the mussel blenny (*Hypsoblennius jenkensi*) (Stephens et al., 1970), the garibaldi (*Hypsypops rubicundus*) (Clarke, 1971), the black-and-yellow rockfish (*Sebastes chrysomelas*) and gopher rockfish (*S. carnatus*) (Larson, 1980ab), and the black perch (Hixon, 1981). In each case, local population sizes were manipulated then observed to return to original densities.

MUSSEL BLENNY

Mussel blennies defend individual subtidal crevices and abandoned invertebrate burrows, from which they feed on benthic and planktonic invertebrates (see table 17-1 for other details). Stephens et al. (1970) conducted a population enhancement manipulation on pier pilings off Palos Verdes. A total of 42 fish (the 10 largest were tagged) were translocated from one piling to another inhabited by 17 fish (the 12 largest were tagged). After about 50 days, the local population returned to its original size, 27% of the enhanced population being lost in the first 3 days, and 50% lost by 18 days. Although uncontrolled and unreplicated, this manipulation indicated that the local adult population was saturated, suggesting regulating within-species competition for territory sites.

GARIBALDI

Adults of the garibaldi (the California State marine fish) defend permanent territories in kelp forests off southern California (Clarke, 1970; see table 17-1 for other details). All territorial individuals defend a shelter site and a food supply

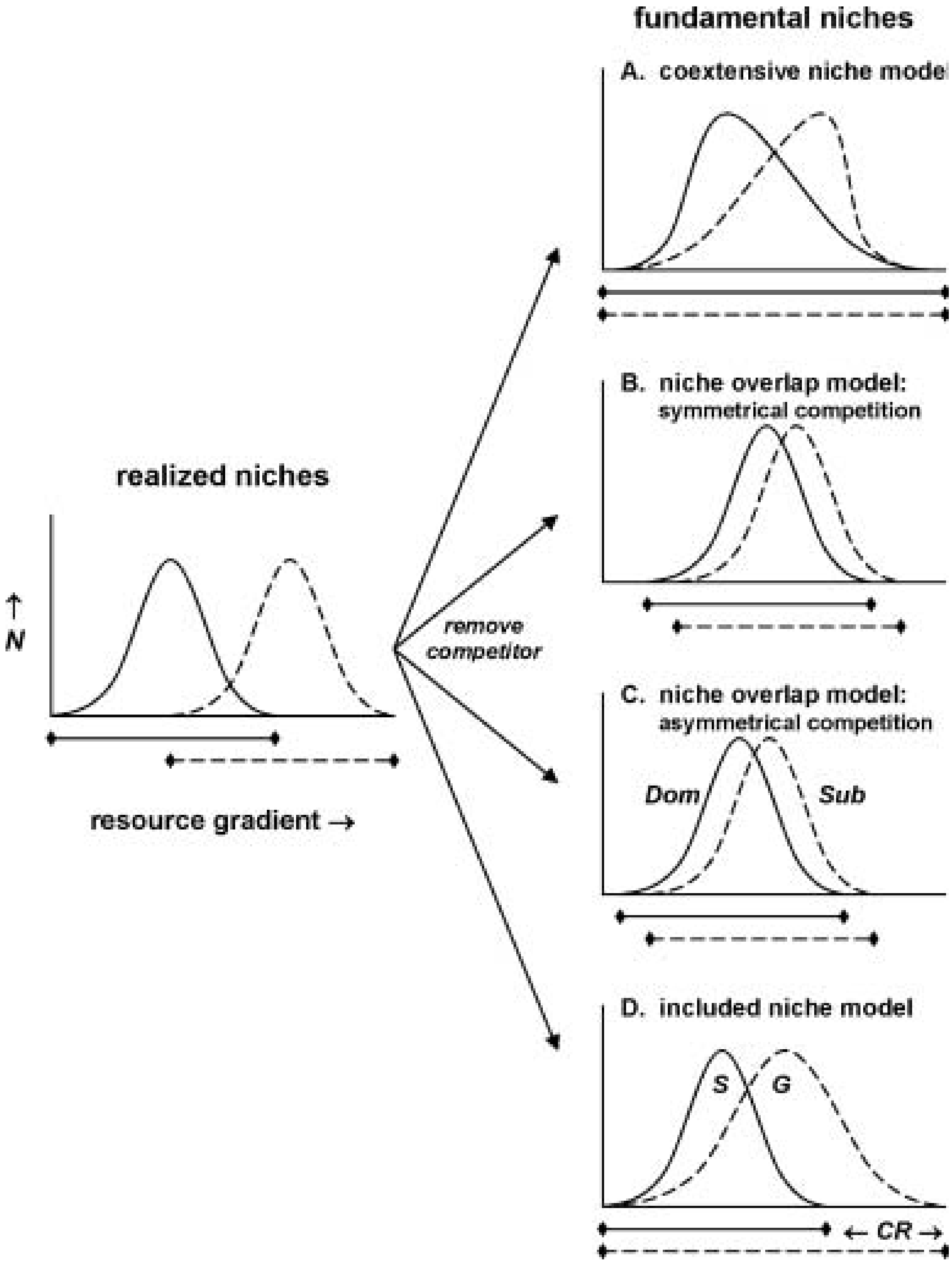


FIGURE 17-1 Niche shifts demonstrating competition between two species (solid and dashed curves). The "realized niches" (left) depict the distribution of two species (resource use measured typically as abundance or density (*N*) along some resource gradient, e.g., reef depth), where both species occur in the same general habitat (e.g., kelp forest) yet manifest some kind of resource partitioning (note low niche overlap). Bars along the x-axis depict niche breadths. Following the experimental removal of each species, one observes the "fundamental niche" of the remaining species, and both species can again be plotted on the same axes for comparison (right). The null outcome, indicating no interspecific competition, occurs when the realized and fundamental niches of each species are identical (not pictured). Four alternative outcomes indicate the presence and strength of interspecific competition (note greater overlap in fundamental compared to realized niches), as well as the mechanisms of coexistence: (A) Coextensive niche model, where each species can use the same range of resources in the absence of its competitor, yet each is the dominant competitor at opposite ends of that range. Each species excludes the other from opposite ends of the resource gradient in a fairly symmetrical way. (B) Niche overlap model with symmetrical competition, where both species undergo fairly equal niche shifts. (C) Niche overlap model with asymmetrical competition, where the dominant competitor (*Dom*) undergoes a substantially smaller niche shift than the subordinate competitor (*Sub*). (D) Included niche model, where a dominant specialist (*S*) eliminates a subordinate generalist (*G*) from most of the region of niche overlap, leaving the generalist to survive in a competitive refuge (*CR*).

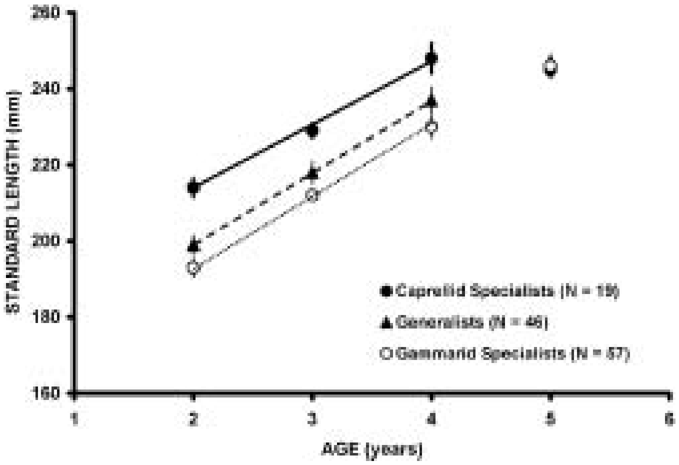


FIGURE 17-2 Size at age (mean ± SEM) of striped seaperch (*Embiotoca lateralis*) in each dietary category at Santa Cruz Island, California. Size at age differed significantly among the dietary groups for ages 2–4, but growth rates did not. After Holbrook and Schmitt (1992).

TABLE 17-1

Representative Examples of Territoriality in Marine Fishes of California

Family *Common Name* (*Scientific name*)	*Territory Size* (m^2)	*Intruders Chased*	*Resources Defended*	*Reference*
Scorpaenidae Black-and-yellow rockfish (*Sebastes chrysomelas*) Gopher rockfish (*Sebastes carnatus*)	ca.5–10	conspecifics, congenerics, some others	shelter, food	Larson, 1980ab
Embiotocidae Black perch (*Embiotoca jacksoni*)	ca.20–30	conspecifics, confamilials, some others	shelter/mating site, food	Hixon, 1981
Pomacentridae Garibaldi (*Hypsypops rubicundus*)	ca.6–12	conspecifics, egg predators	shelter, food, eggs	Clarke, 1970, 1971
Blenniidae Mussel blenny (*Hypsoblennius jenkinsi*)	ca.0.04	conspecifics, congenerics	shelter, eggs, (food?)	Stephens et al.,1970
Gobiidae Bay goby (*Lepidogobius lepidus*)	no data (small)	conspecifics	shelter, food, eggs	Grossman, 1980

of benthic invertebrate prey, and some males additionally defend cultivated mats of red algae that serve as nest sites for demersal eggs. Clarke (1971) noted that there was no evidence for fluctuations in adult population sizes off San Diego over 3 years, and that recruitment of new settlers more than balanced adult mortality. Given that the maximum life span of the garibaldi exceeds a decade, these patterns suggested that local populations were both saturated and regulated. To test these ideas, Clarke (1971) removed most adults at three sites (19, 15, and 71 fish), then re-censused the removal areas over 21 months, ultimately finding 39, 14, and 43 adults, respectively. Thus, two sites fully recovered from the removals (one doubling in density), and one was partially repopulated. Most of the immigrants were smaller than the removed fish, and were either females or bachelor males that had not been defending well-developed nests. These results suggested that within-species interference competition played a role in regulating local populations of adult garibaldi.

ROCKFISHES

On subtidal rocky reefs in the Santa Barbara Channel, adult black-and-yellow rockfish and gopher rockfish (very similar sibling species) defend permanent territories that include benthic prey and individual shelter holes, although some individuals are nonterritorial floaters and commuters (Larson, 1980a; see table 17-1 for other details). As part of a comprehensive study of competition within and between these species (see below), Larson (1980b) tested whether adult density was limited by territorial behavior. At three sites, he removed 2, 2, and 4 territorial fish, respectively, with an additional 2 fish disappearing naturally at the third site (all but 2 of the removed individuals were gopher rockfish). Relative to control territories, intrusion rates into the 10 emptied territories increased significantly. Neighboring conspecific or congeneric adults recolonized all of the emptied territories, and all but one of the colonizers thereby obtained a smaller and more exclusive home range. These results were consistent with the

TABLE 17-2

Representative Examples of Resource Partitioning in Marine Fishes of California

Guild	*Study Area*	*Partitioned Resources*	*Reference*
Rocky intertidal sculpins (3 species)	Pescadero Point	space, food	Yoshiyama, 1980, 1981
Coastal blennies (3 species)	Palos Verdes	space, food	Stephens et al., 1970
Breakwater surfperches (5 species)	Redondo Beach	food	Ellison et al., 1979
Rocky-reef planktivores (8 species)	Catalina Island	space, food, time	Hobson and Chess, 1976
Rocky-reef microcarnivores (3 species)	Santa Barbara Channel	space, food	Bray and Ebeling, 1975
Rocky-reef surfperches (5 species)	Santa Barbara Channel	space, food	Alevizon, 1975a; Ebeling and Laur, 1986
Rocky-reef macrocarnivores (3 species)	Santa Barbara Channel	space, food	Love and Ebeling, 1978
Rocky-reef rockfishes (6 species)	Carmel Bay	space, food	Hallacher and Roberts,1985
Deep-sea thornyheads (2 species)	Central California	space	Jacobson and Vetter, 1996

hypothesis that competition via territorial behavior limited local adult density.

BLACK PERCH

Large male black perch, a viviparous species, defend reef caves as courtship and mating sites (Hixon, 1981). On a rocky reef off Santa Barbara, 12 territorial fish were experimentally removed, and all were replaced by other males within 4 days such that the number and distribution of territories was identical to that before the manipulation. During the same period, there was no change in the configuration of 8 adjacent control territories, suggesting the existence of a pool of non-territorial floaters (sensu Brown, 1969). Natural disappearances were also followed by rapid replacements. These results indicated that the population density of mating males was limited by competition for a fixed number of courtship and mating sites. However, this result did not necessarily indicate overall population regulation because those males holding territories could nonetheless have fertilized all available females.

Evidence Regarding Interspecific Competition

The evidence that competition is an ecologically significant interaction between species of California marine fishes runs the full spectrum, from purely circumstantial to experimentally compelling. This review focuses on representative case studies that illustrate this spectrum.

Resource Partitioning

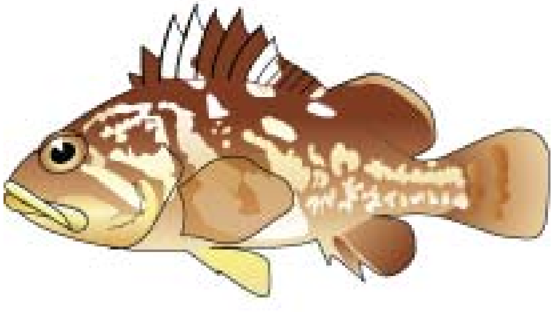
There are numerous examples of resource partitioning among marine fishes of California (review by Ebeling and Hixon, 1991). These studies have taken two perspectives: the entire community or a specific guild. Examination of an entire community always detects differences in resource use among species because such comparisons include between-guild contrasts (e.g., bay fishes: Allen, 1982; rocky intertidal fishes: Grossman, 1986; kelp-forest fishes: Larson and DeMartini, 1984; nearshore sand-bottom fishes: Hobson and Chess, 1986; pelagic fishes: Allen and DeMartini, 1983; mesopelagic fishes: Lavenberg and Ebeling, 1967). There is also temporal partitioning between diurnal and nocturnal species at the community level in nearshore California fishes, which has been ascribed to competitive interactions in the evolutionary past (Ebeling and Bray, 1976; Hobson et al., 1981). Such community-level surveys certainly provide valuable insight on the organization of entire assemblages. However, it is the within-guild perspective that offers the strongest inference regarding the possibility of ongoing competition between species.

As summarized in table 17-2, studies within guilds of demersal California fishes have invariably detected between-species differences in microhabitat use and/or diet, often in complementary ways (i.e., high overlap in space with low overlap in food, or vice versa). As discussed above, these patterns can be used to hypothesize which species are likely competitors, but do not actually demonstrate competition. More convincing evidence of competition requires one to build a case by combining observational data from a variety of sources, observing overt competitive displacement, or conducting a field experiment.

Direct Observation

Self-evident competition involving California marine fishes is of two kinds: (1) between-species territoriality where resources other than eggs are defended, and (2) displacement of territorial fish by sea urchins.

black-and-yellow rockfish



gopher rockfish

FIGURE 17-3 *Sebastes* congeners experimentally demonstrated to compete with each other in kelp forests at Santa Cruz Island, California: the shallow-water black-and-yellow rockfish (*S. chrysomelas*) and the deep-water gopher rockfish (*S. carnatus*).

INTERSPECIFIC TERRITORIALITY

Fishes that defend permanent territories from members of the same species almost invariably also exclude other species that are potential threats to food or shelter (reviews by Grant, 1997; chapter 19). In studies of within-species territoriality in California marine fishes, there is often evidence of such between-species interference (table 17-1). For example, laboratory behavioral observations indicated that the territorial mussel blenny is aggressively dominant over a nonterritorial congener, the bay blenny (*H. gentilis*), and may therefore limit habitat use by the bay blenny where these species co-occur (Stephens et al., 1970). Large males of the viviparous black perch defend permanent territories that include courtship and mating sites, as well as surrounding foraging areas (Hixon, 1981). Although most aggression is among conspecific males, permanently territorial males also exclude intruding members of the same foraging guild (including 4 other species of perch—see below) in proportion to interspecific overlap in diet. The mechanism underlying this correlation is that territorial males tend to chase only intruders that actively forage within their territories—non-feeding intruders are generally ignored. The fact that food supplies comprise a defended resource was confirmed by manipulations of foraging substrata that demonstrated an inverse relationship between territory area and food availability (see also Hixon, 1980b).

DISPLACEMENT OF TERRITORIAL FISH BY URCHINS

In the absence of predation by sea otters and other predators, sea urchins (*Strongylocentrotus* spp.) often attain high densities along the California coast, sometimes overgrazing the seafloor and causing barrens (reviews by Dayton, 1985; Schiel and Foster, 1986). Two studies at Naples Reef off Santa Barbara indicated overgrazing of fish territories, which are cases of a morphologically defended and superior exploitative competitor (an urchin) locally displacing an ineffective interference competitor (a fish). Hixon (1981) witnessed a foraging front of *S. purpuratus* slowly denude two permanent territories of adult male black perch to the point where the fish eventually abandoned their territories. Breitburg (1987) documented that urchins and territorial blackeye gobies (*Rhinogobiops nicholsi*) used the same rocky microhabitats, yet their co-occurrence at the same specific location was <3% vs. an expected value of 36%. It appeared that urchins dislodged demersal eggs defended by male gobies, suggesting local competition for space as well as possible egg predation.

Experimental Evidence

Between-species competition and its ecological ramifications have been explored experimentally in three pairs of fish species inhabiting rocky reefs off southern California. To my knowledge, these labor-intensive studies comprise the most complete investigations to date of competition in any marine fishes. Because scientists at the University of California at Santa Barbara (UCSB) conducted all these studies, I present them in temporal sequence as a historical narrative.

ROCKFISHES

Alfred Ebeling started the first field studies of marine fishes based at UCSB, shifting emphasis from deep-sea to kelp-forest systems in the late 1960s. His doctoral student, Ralph Larson (1980c), was the first to provide unequivocal evidence for population-level, between-species competition in marine fishes: a sibling pair of rockfishes (fig. 17-3). In the Santa Barbara Channel, the black-and-yellow rockfish dominates shallow reef areas, whereas the gopher rockfish dominates deeper areas (fig. 17-4). The transition depth between the species is about 10-15m. The specific transition depth between sites is inversely correlated with shading by seaside cliffs, which probably affects the density of benthic invertebrate prey. In any case, prey density decreases with depth. Overlap in diet is high, so these congeners partition space and not food.

In 1974 at Santa Cruz Island, Larson (1980c) cleared one site of black-and-yellow rockfish (removing 209 fish), and cleared another site of gopher rockfish (removing 159 fish), leaving a third site as an unmanipulated control. Over the next 3 years, the treatments were maintained by additional removal of 125 black-and-yellow rockfish and 59 gopher rockfish. In response to these population manipulations, the deep-living gopher rockfish moved into shallow water where the shallow-living black-and-yellow rockfish had been removed, and the black-and-yellow rockfish moved slightly into deeper water where the gopher rockfish had been removed, while the distributions of both species did not change at the control site (fig. 17-5). The fish that moved were slightly smaller than average, and by the time new recruits could be identified to species, they had already segregated by depth. In

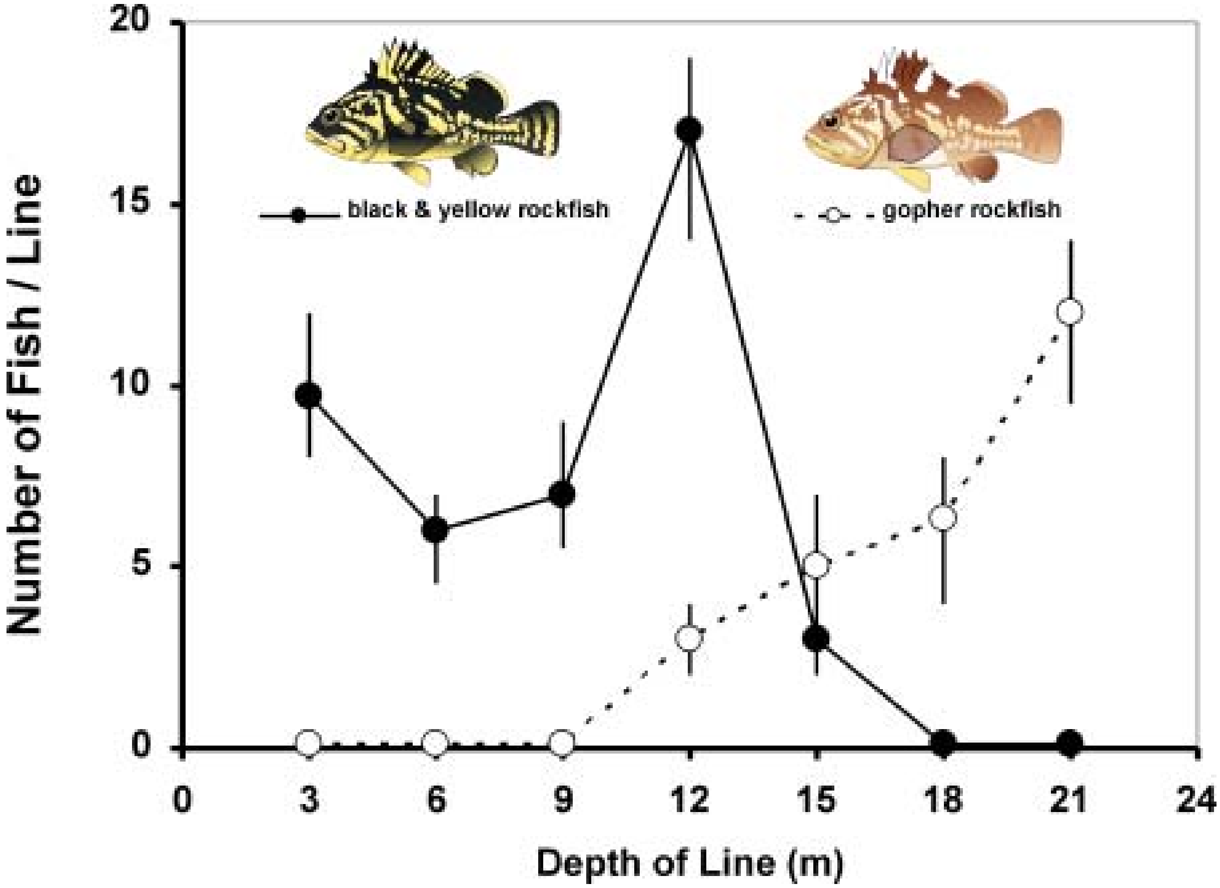


FIGURE 17-4 Segregation by depth of the black-and-yellow rockfish (*Sebastes chrysomelas*) and the gopher rockfish (*S. carnatus*) off Santa Cruz Island, California. Data are median number of fish (± quartile range) along 30 × 2 m transects (n = 30 censuses per transect). After Larson (1980c).

paired contests over shelter holes in the laboratory, black-and-yellow rockfish tended to dominate gopher rockfish, winning 69% of 48 trials.

Larson (1980c) concluded that between-species competition was partly responsible for the bathymetric segregation of these species. He speculated that this segregation begins with differential larval settlement by depth, and is then reinforced by territorial behavior, with a strong prior residency effect (i.e., territory residents win encounters). What allows these species to coexist without one species eliminating the other? Larson suggested that black-and-yellow rockfish are the aggressive dominant, but may be constrained to occupy food-rich shallow zones. If so, gopher rockfish have a competitive refuge in food-poor deeper zones. As such, this system fits the included niche model of coexistence of competing species (Colwell and Fuentes, 1975). In the parlance of niche jargon reviewed above, the fundamental niche of a relatively specialized dominant competitor (black-and-yellow rockfish) is a subset of the fundamental niche of a relatively generalized subordinate competitor (gopher rockfish). This situation results in the dominant having a realized niche similar to its fundamental niche, and the subordinate being restricted to the portion of its fundamental niche that does not overlap with that of the dominant (i.e., a competitive refuge). This scenario allows coexistence of species despite ongoing between-species competition (fig. 17-1D).

SURFPERCHES

Concurrent with Larson's work on rockfishes, another of Ebeling's graduate students, Bill Alevizon, began observational studies of a guild of two congeneric pairs of kelp-forest surfperches, which are viviparous demersal microcarnivores. Alevizon (1975b) showed that the congeners that were more dissimilar in feeding morphology—the pile perch (*Rhacochilus vacca*) and the rubberlip seaperch (*R. toxotes*)—overlapped substantially in microhabitat use, whereas the more trophicly similar *Embiotoca* congeners—the striped seaperch and the black perch—showed greater microhabitat segregation. These patterns were later substantiated in much greater detail by Schmitt and Coyer (1982), Laur and Ebeling (1983), Schmitt and Holbrook (1984), Ebeling and Laur (1986), and Holbrook and Schmitt (1986).

Ebeling and Laur (1986) most thoroughly quantified the two contrasting modes of niche complementarity in this guild at Naples Reef off Santa Barbara: the *Rhacochilus* congeners overlapped only 32% in diet but 84% in foraging microhabitat, whereas the *Embiotoca* congeners overlapped 56% in food but only 35% in space (fig. 17-6). These patterns of complementarity are especially impressive given that, first, dietary data were gathered during the relatively food-rich summer period when competition was least likely, and second, microhabitat use data were gathered on a relatively small rocky reef lacking the substantial vertical relief of more

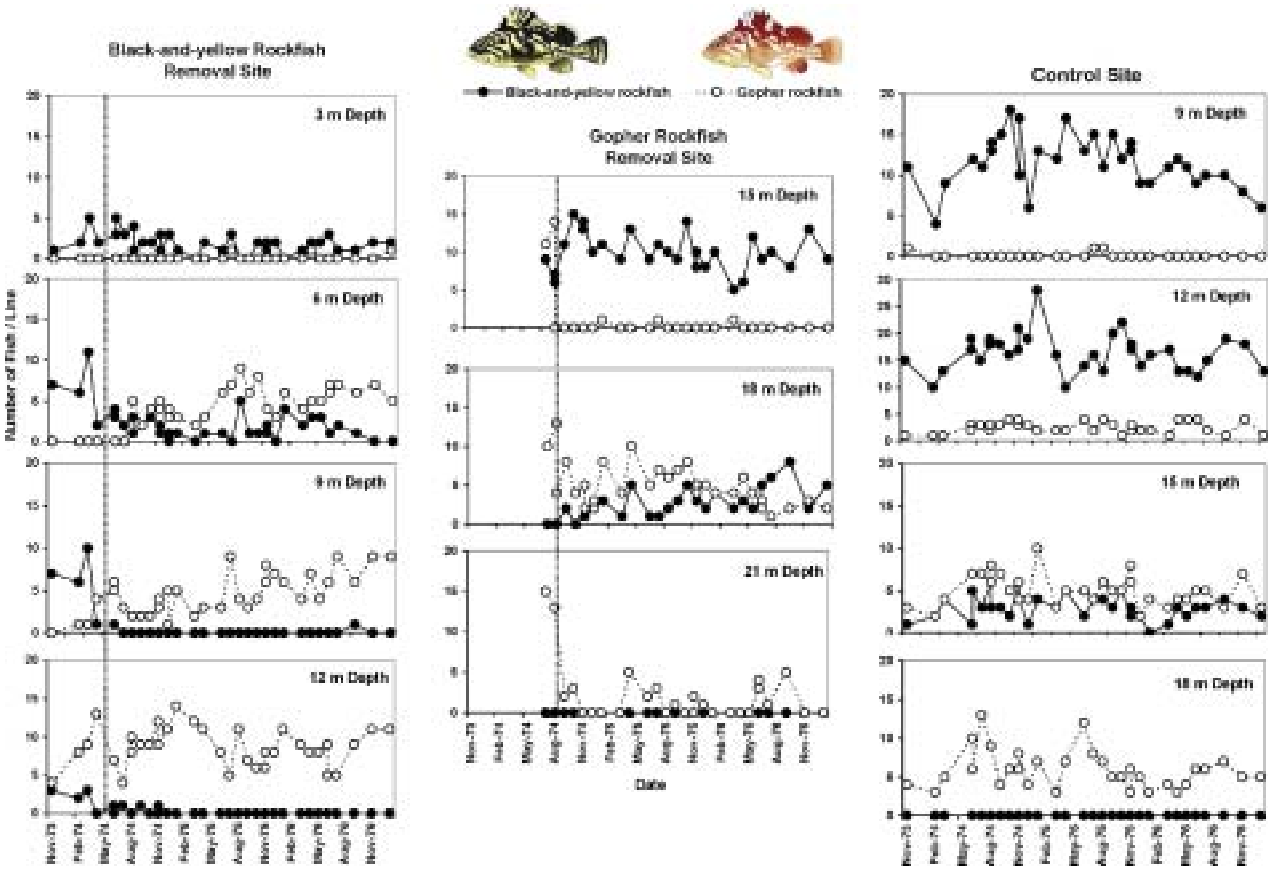


FIGURE 17-5 Responses of rockfish (*Sebastes*) species to reciprocal removals of congeners at Santa Cruz Island, California. Vertical dashed lines show dates of manipulations. Data are number of fish along 30 × 2 m transects, and error bars give mean ± range of 5 counts repeated on the same date. After Larson (1980c).

continuous habitats at the California Channel Islands (see below). Note, however, that not all pairwise comparisons within the guild showed complementarity, leading Ebeling and Laur (1986) to conclude that resource overlap of most pairs of species within this guild were not influenced by competition. In particular, a fifth species, the rainbow seaperch (*Hypsurus caryi*), overlapped substantially in both food and space with both rubberlip seaperch and black perch (fig. 17-6), but the rainbow seaperch is a seasonal resident of kelp forests during only the food-rich summer months. Overall, these patterns suggested the hypothesis that between-species competition organized patterns of resource use in at least the two congeneric pairs of species in the kelp-forest surfperch guild.

As another of Ebeling's students, I combined Alevizon's observational approach with Larson's experimental approach, focusing on the *Embiotoca* congeners (fig. 17-7). Like Larson's rockfishes, these surfperches were segregated by depth where they co-occurred at Santa Cruz Island (fig. 17-8A). This spatial separation was clearly correlated with the distribution of the major foraging microhabitats of these species, from which they picked small invertebrate prey: striped seaperch on shallow understory algae, especially *Gelidium robustum* (from which they took 96% of their foraging bites), and black perch on deeper benthic turf (from which they took 85% of their foraging bites) (fig. 17-8B). In a natural experiment, each species occupied and foraged over the full range of depth zones where each naturally occurred in the near-absence of the other species (Hixon, 1980a): striped seaperch to the north of Pt. Conception (fig. 17-8C, see also Haldorson and Moser, 1979) and black perch to the south of Santa Cruz Island (Fig. 17-8D, see also Schmitt and Coyer, 1983). From this perspective, the niche relations of the species are coextensive (fig. 17-1A).

The small benthic prey of these fishes, mostly amphipods, were more abundant on shallow than deep substrata (Schmitt and Holbrook, 1986). When shallow algae and deep turf were offered side-by-side on experimentally translocated trays, striped seaperch at shallow depths still took significantly more bites from algae, whereas black perch in deeper water foraged over both substrata more equally, expanding their foraging microhabitat to include prey-rich shallow algae (Hixon, 1980a). Schmitt and Coyer (1983) observed that black perch consumed a broader range of prey taxa and sizes in allopatry than in sympatry. Moreover, the diet of black perch in allopatry was similar to that of striped seaperch in sympatry (i.e., more free-living amphipods and fewer tubiculous amphipods), even accounting for between-site differences in prey availability. Balanced time-budget analyses in sympatry, stratified by species, time of day, and season, showed that striped seaperch were aggressive toward black perch about 3.5 times as much as the converse, and a statistical spacing analysis suggested that black perch avoided striped seaperch (Hixon, 1980a).

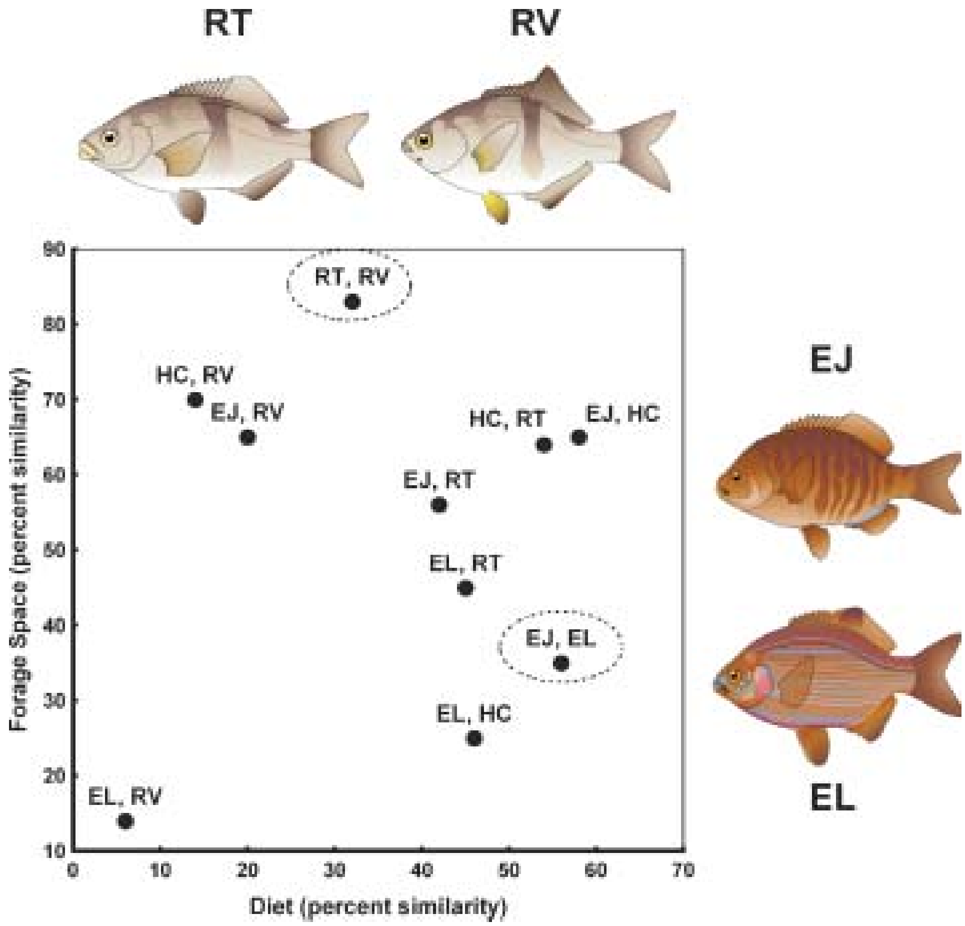


FIGURE 17-6 Percent overlap in foraging space and diet within a guild of five surfperches at Naples Reef, California. Species are the black perch (EJ, *Embiotoca jacksoni*), the striped seaperch (EL, *E. lateralis*), the pile perch (RV, *Rhacochilus vacca*), the rubberlip seaperch (RT, *Rhacochilus toxotes*), and a seasonal guild member, the rainbow seaperch (HC, *Hypsurus caryi*). Note niche complementarity in the two pairs of congeners (EJ, EL and RT, RV). After Ebeling and Laur (1986).

Combined, these observational data were consistent with the hypothesis that the *Embiotoca* congeners competed with each other.

In 1977 at Santa Cruz Island, the critical experimental test for competition was conducted by clearing one reef of striped seaperch (removing 56 fish), and clearing another reef of black perch (removing 130 fish), leaving a third reef as a control (Hixon, 1980a). Over the next 3 months, the treatments were maintained by the additional removal of 45 striped seaperch and 63 black perch. During this period, striped seaperch did not change their distribution in response to the removal of black perch, but black perch immediately expanded their distribution into shallow water in response to the removal of striped seaperch (fig. 17-9). There were no changes at the control reef. Despite the lack of site replication, these results demonstrated that striped seaperch competitively excluded black perch from food-rich shallow habitats, but did not explain why striped seaperch did not colonize deeper areas formerly occupied by black perch. In 1978, shallow algae were removed from one reef, leaving another reef as a control (Hixon, 1980a). In response, striped seaperch abandoned the denuded reef rather than displacing black perch from deeper water (with no changes at the control site). Later that year, the original experiment was repeated, this time switching species-removal treatments among reefs and additionally denuding shallow algae at the site where black perch were removed. Over the next 3 months, striped seaperch finally did shift their distribution into deeper water, abandoning the denuded shallow zone and colonizing the deep zone formerly occupied by black perch (fig. 17-10). At the reef where striped seaperch were removed, black perch again quickly shifted their distribution into the shallow zone, as had occurred the previous year at another site (fig. 17-10). As before, no change occurred at the control reef.

Based on both experimental and observational results, I concluded that interactions between the *Embiotoca* congeners at Santa Cruz Island fit the included niche model of coexisting competitors (fig. 17-1D) in a scenario similar to Larson's rockfishes (see above). Striped seaperch were the dominant competitors and occupied only the food-rich shallow zone preferred by both species. Why did striped seaperch not also competitively exclude black perch from the deep zone, as indicated by the natural experiment reviewed above? I speculated that the abundance of striped seaperch was limited by factors other than competition here at the southern limit of its contiguous geographical range. This geographical limit is probably associated with water temperature because the Santa Barbara Channel is a major biogeographic transition zone, separating the cold-temperate Oregonian Province north of Point

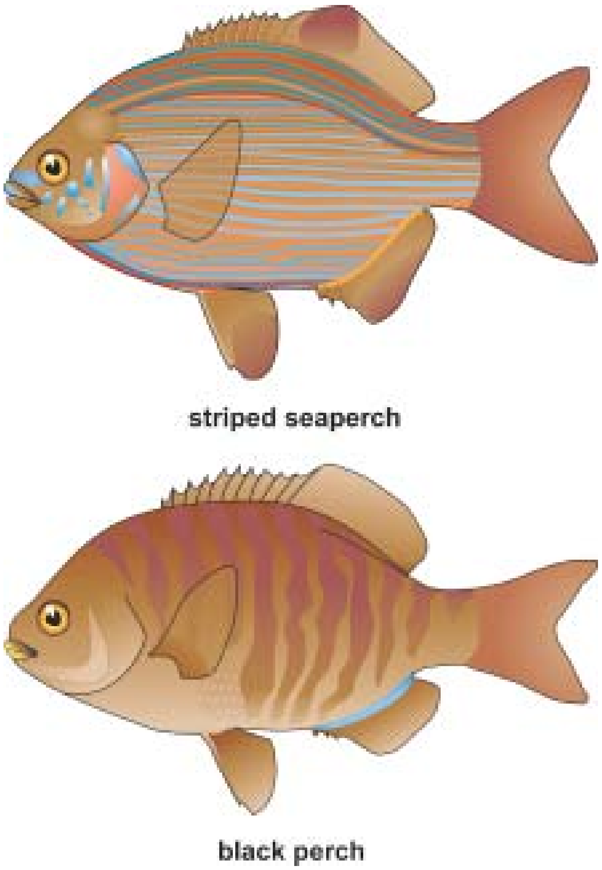


FIGURE 17-7 *Embiotoca* congeners experimentally demonstrated to compete with each other in kelp forests at Santa Cruz Island, California: the shallow-water striped seaperch (*E. lateralis*) and the deep-water black perch (*E. jacksoni*).

Conception from the warm-temperate Californian Province to the south (Briggs, 1974). South of the Santa Barbara Channel, the striped seaperch is found only in areas of intense year-round, cold-water upwelling along the Baja peninsula (Love, 1996).

In any case, striped seaperch populations limited by temperature or some other factor did not shift to the food-poor deep zone over the 3-month duration of my experiments, even if the black perch there were removed, unless the shallow zone was denuded of prey-bearing algae, thereby exacerbating competition (Hixon, 1980a). In ecological jargon, the black perch was the subordinate competitor relegated to a competitive refuge provided by the food-poor deep zone (realized niche), and readily inhabited the shallow zone as well whenever striped seaperch were removed (fundamental niche). Therefore, in sympatry, the striped seaperch was the competitively dominant specialist and black perch was the competitively subordinate generalist, allowing coexistence despite ongoing between-species competition (fig. 17-1D). However, in allopatry north of Point. Conception, striped seaperch occupied and foraged over both reef zones, being more abundant in the more central portion of their geographical range. Black perch also inhabited both reef zones in allopatry south of Pt. Conception, so that the fundamental niches of the two species where each naturally occurred alone were relatively coextensive (fig. 17-1A).

In the early 1980s, the surfperch project was taken over by Russell Schmitt and Sally Holbrook, who repeated and extended previous research on the *Embiotoca* congeners with unparalleled thoroughness. Schmitt and Holbrook (1986) duplicated much of Hixon's (1980a) study at Santa Cruz Island, independently corroborating patterns of resource partitioning (bathymetric segregation and foraging patterns) and repeating the short-term population manipulations. However, unlike the previous study, they were able to include site replication in their experiments, and overall, documented patterns in much greater detail. Importantly, this was perhaps the first time an experimental field study of competition had been replicated by two different research groups, providing the kind of independent repeatability often advocated but seldom accomplished in the science of ecology (Fretwell, 1981; Connell, 1983).

Besides confirming previous research, Schmitt and Holbrook greatly extended the duration of the population-removal experiments at Santa Cruz Island, providing unprecedented insight on the role of competition in seasonal and regional patterns of resource use and long-term population dynamics. Regarding seasonal patterns, there was four times as much invertebrate prey available in the summer as during the winter, so the intensity of competition was greater during the winter (Holbrook and Schmitt, 1989). This cycle affected seasonal patterns of overlap in use of foraging microhabitats (algae *vs*. turf) between the two surfperches. High overlap occurred in the food-rich shallow zone during the summer, when competition was least intense. Low overlap occurred in the depleted shallow zone during the winter, as well as in the relatively food-poor deep zone year-round.

Long-term changes in the abundance of giant kelp (*Macrocystis pyrifera*) during the 1980s indirectly altered competitive interactions between the *Embiotoca* congeners. Comparisons among 18 reefs at Santa Cruz Island had shown that the abundance of striped seaperch was correlated with the cover of shallow *Gelidium* algae, whereas the abundance of black perch was correlated with the cover of deeper benthic turf (Hixon, 1980a; Holbrook et al., 1990ab). When kelp became abundant, *Gelidium* declined and the turf increased in cover, and consequently, striped seaperch declined and black perch increased in abundance (Schmitt and Holbrook, 1990a). Repeating and extending Hixon's (1980a) manipulations of foraging habitat, Holbrook et al. (1990b) reduced *Gelidium* cover by 80% at two sites by clipping algal holdfasts in 50 m × 15 m plots. They also increased turf cover fourfold on four 2m × 2m plots by removing overlying seaweeds, with the same number of replicates used as controls in each case. In response, the striped seaperch decreased in abundance and black perch increased in abundance, with no change in the controls (fig. 17-11). Thus, variation in food availability in both time and space clearly affected the intensity of competition and the local abundance of the two surfperches.

Complimentary to these patterns, after a severe storm removed kelp, and urchins subsequently overgrazed turf from Naples Reef off Santa Barbara, the *Embiotoca* congeners converged in their foraging effort on the remaining *Gelidium* (Stouder, 1987). The density of striped seaperch at Naples Reef (40 per hectare) was apparently so low that black perch (327 per hectare) could effectively overwhelm them (data from Ebeling and Laur, 1986). As the abundance of surfperch declined after the storm, and subsequently as the turf recovered, partitioning of foraging microhabitat by the *Embiotoca* congeners resumed (Stouder, 1987).

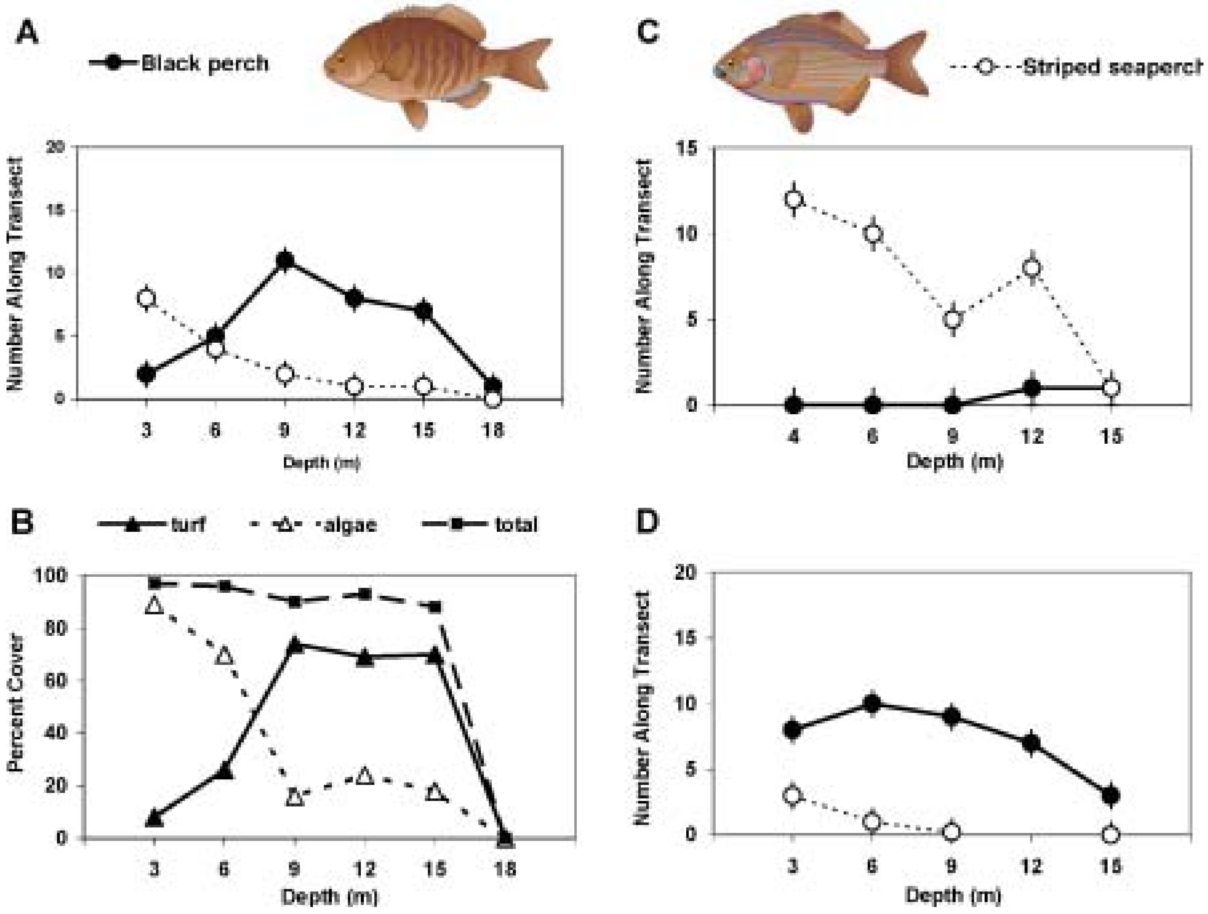


FIGURE 17-8 (A) Segregation by depth of the striped seaperch (*Embiotoca lateralis*) and the black perch (*E. jacksoni*) off Santa Cruz Island, California. (B) The depth distribution of these species at Santa Cruz Island is closely correlated with the distribution of shallow algae and deep turf foraging substrates. (C) Depth distribution of these species at Lone Black Reef, north of Pt. Conception, where the striped seaperch predominates and occupies all depth zones. (D) Depth distribution of these species at Anacapa Island, south of Pt. Conception, where the black perch predominates and occupies all depth zones. Data in plots A, C, and D are number of fish along 30 × 4 m transects (mean ± range, n = 3, 5, and 5 transects, respectively). Data in plot B are percent cover (line intercept) along 10 m lines (mean ± range, n = 10 lines). After Hixon (1980a).

Sustaining the population-removal experiments for multiple years, Schmitt and Holbrook (1990b) found that competitive effects between the *Embiotoca* congeners were more symmetrical than the short-term manipulations of Hixon (1980a) and Schmitt and Holbrook (1986) had indicated. In fact, the abundance of each species increased approximately 40% in the absence of its congener over 4 years (fig. 17-12), a pattern best described as coextensive niches (fig. 17-1A). Schmitt and Holbrook speculated that release from interference competition explained the short-term results manifested as behavioral shifts in depth distribution, whereas release from exploitation competition appeared over a longer time frame that involved population shifts in abundance. From this perspective, coexistence of these species was ensured by the effective ability of each to exploit different foraging microhabitats when prey are scarce: striped seaperch on the alga *Gelidium* as superior visual predators, and black perch on benthic turf as superior "winnowing" predators (Laur and Ebeling, 1983). In any case, it was clear that striped seaperch were superior at utilizing the mutually preferred foraging substratum (*Gelidium*) that normally covered shallow reef surfaces (Holbrook and Schmitt, 1995).

GOBIES

It is important to mention at least one case where the presence of competition within and between-species was examined experimentally and found to be negligible. One of Holbrook's graduate students, Mark Steele, conducted a thorough study of potential competition involving two species of goby (Gobiidae): the blackeye goby and the bluebanded goby (*Lythrypnus dalli*). It was known that blackeye goby are territorial (Cole, 1984) and that bluebanded goby compete for shelter holes (Behrents, 1987). Steele (1997, 1998) constructed a matrix of 36 meter-square rock reefs on a sand bottom adjacent to the main reef in Big Fisherman Cove, Catalina Island. Gobies of each species were added to these reefs in a variety of combinations of abundance, both in the presence or absence of predatory fishes (using cages). The recruitment and fates of gobies on the reefs was subsequently monitored for about 3 weeks during each of three experiments. Overall, any effects of competition were minor compared to the strong effects of predation (chapter 16). Regarding within-species competition, blackeye gobies suffered no effects on growth, but survival was slightly lower at higher densities. Growth of bluebanded gobies was slightly lower at

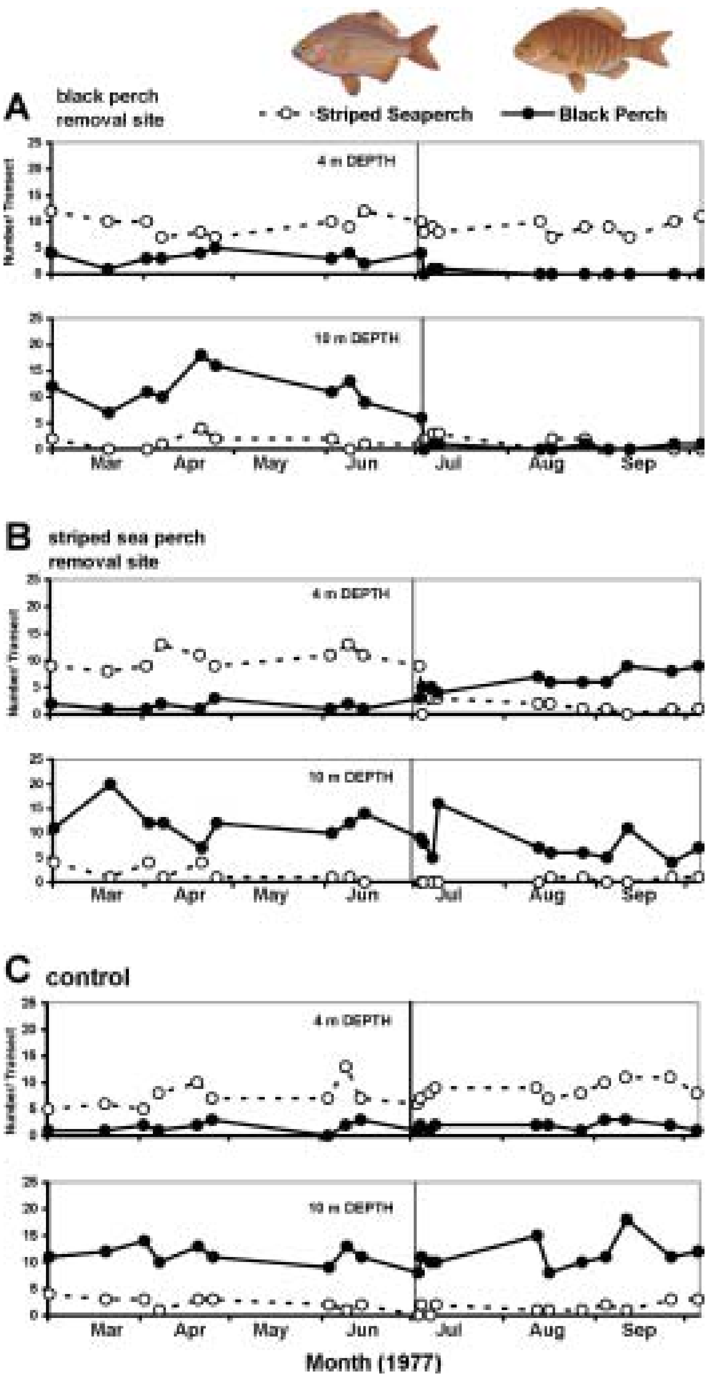


FIGURE 17-9 Responses of surfperch (*Embiotoca*) species to reciprocal removals of congeners at Santa Cruz Island, California. Vertical lines show dates of manipulations. Data are number of fish along 30 × 4 m transects. After Hixon (1980a).

higher densities, but there was no effect on survival. Recruitment was actually enhanced at higher conspecific densities for bluebanded gobies, with no effects for blackeye gobies. There was no detectable-between-species competition.

Competition in Context

This review documents substantial evidence that competition is an ecologically significant interaction both within and between several species of Californian marine fishes. The majority of evidence has come from nearshore fishes along the coast of southern California, especially at SCUBA depths on rocky reefs and associated kelp forests. Perhaps the most exhaustive study of interspecific competition between any marine fish species worldwide was on California surfperches. Unfortunately, from the perspective of generality, surfperches are viviparous and thus have closed populations much different in demographic structure from most marine fishes (Caley et al., 1996). Surfperches are also not major fishery species. Thus, studies of competition most relevant to California marine fisheries have involved rockfishes. Because rockfishes are increasingly overfished (Parker et al., 2000), understanding and conserving natural mechanisms of population regulation, such as competition, is of great relevance to fisheries management (see also Hixon and Webster, 2002). The fact that there is substantial competition between at least two species of rockfishes lends credence to the concept of ecosystem-based

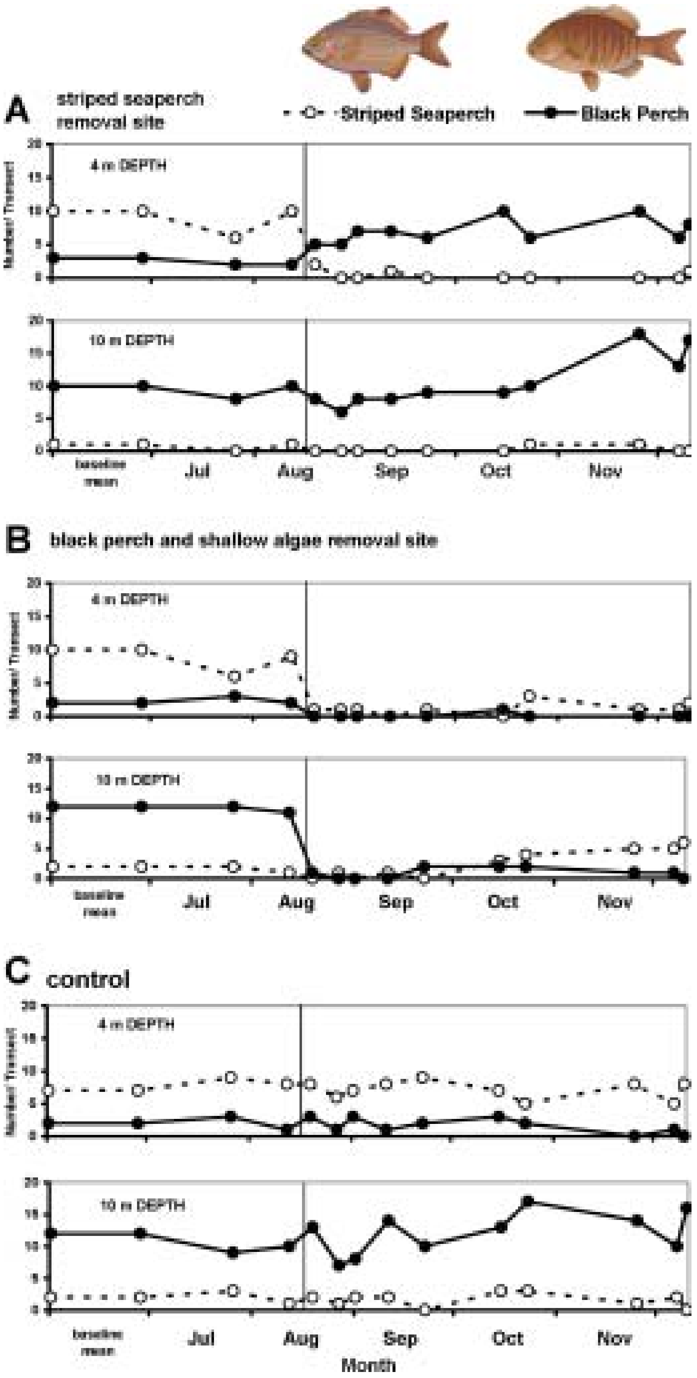


FIGURE 17-10 Responses of (A) black perch (*Embiotoca jacksoni*) to removal of striped seaperch (*E. lateralis*), and (B) striped seaperch to removal of both black perch and shallow algae, compared to (C) an unmanipulated control site, all at Santa Cruz Island, California. Vertical lines show dates of manipulations. Data are number of fish along 30 × 4 m transects. After Hixon (1980a).

precautionary management and less reliance on clearly ineffective single-species fishery models (Weeks and Berkeley, 2000).

Despite the relevance of studies of competition to fisheries management, there have been few studies of competitive interactions in California marine fishes since the 1980s. Has competition become irrelevant or out-of-date? Certainly, in general ecology, competition is no longer seen as the all-important predominant biotic interaction, as it was during the heyday of resource partitioning studies and niche theory in the late 1960s and early 1970s. However, competition is still common in nature (reviews by Connell, 1983; Schoener, 1983) and is now considered an interaction that occurs regularly when predation, physical disturbance, or harsh conditions do not preclude it. Clearly, there is much still to be learned regarding the role of competition in the dynamics of populations and the organization of natural communities of marine fishes of California and elsewhere.

Acknowledgments

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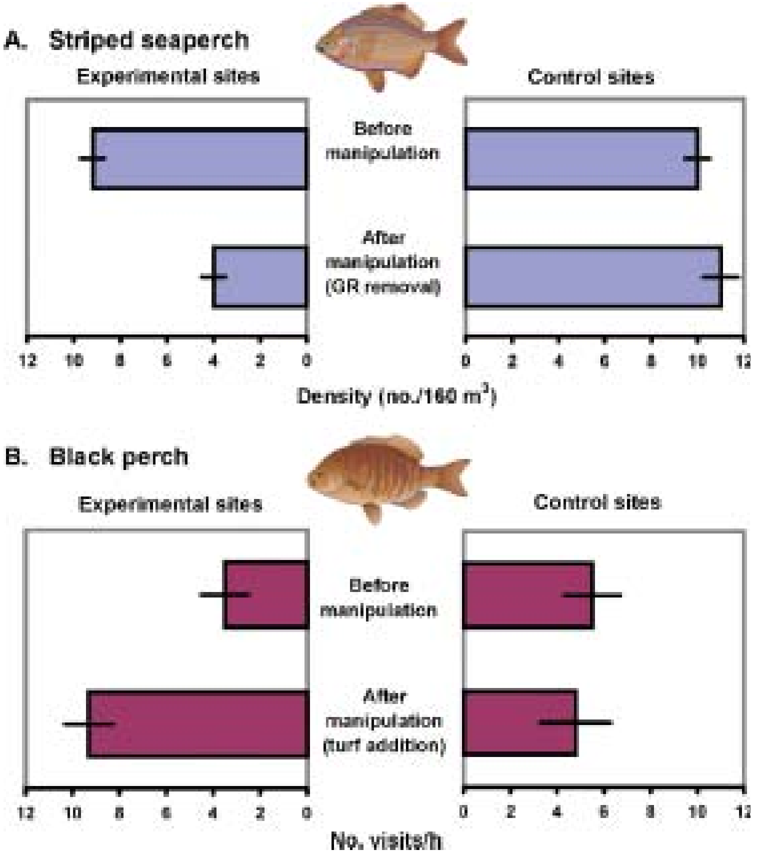

FIGURE 17-11 Responses of (A) striped seaperch (*Embiotoca lateralis*) following removal of its primary foraging substrate (the dominant shallow alga *Gelidium robustum*, GR) at Santa Cruz Island, California (mean ± SEM of two 40 × 2 × 2 m transects each), and (B) black perch (*E. jacksoni*) following addition of its primary foraging substrate (benthic turf) at Catalina Island, California (mean ± SEM of four 2 × 2 m plots each). After Holbrook et al. (1990b).

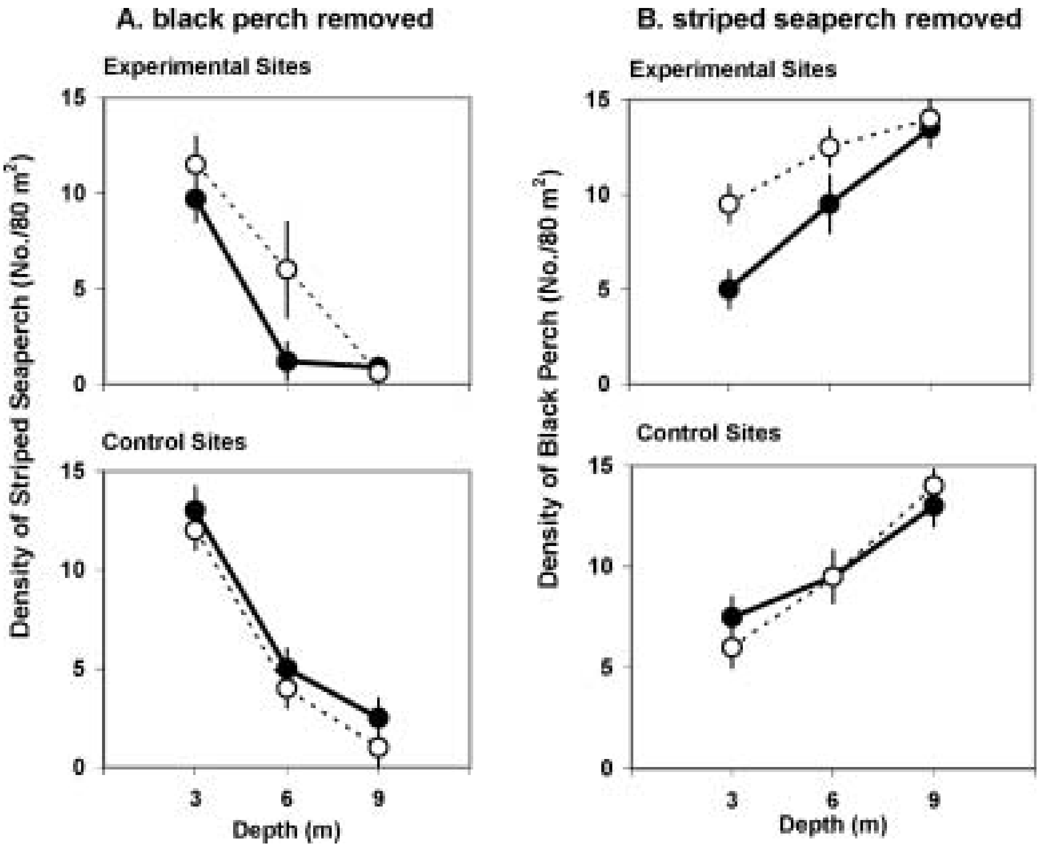

FIGURE 17-12 Long-term responses of surfperch (*Embiotoca*) species to reciprocal removals of congeners (“experimental sites”) compared to unmanipulated control sites at Santa Cruz Island, California. Solid symbols and lines are before manipulations, and open symbols and dashed lines are 4 years after manipulations. Data are number of fish along 40 × 2 m transects (mean ± SEM, n = 2 sites each). After Schmitt and Holbrook (1990b).

Alfred Ebeling, a true pioneer in subtidal studies of the ecology of marine fishes of California.

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