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CHAPTER 16

Predation

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Introduction

Common sense suggests that predation must play some, probably important, role in the ecology of marine fishes. Many fishes are piscivorous, and virtually all fishes are vulnerable to predation at some point in their lives. Until recently, however, the effects of predation on the ecology of populations and communities of marine fishes were poorly known, although the subject of widespread speculation (Hixon, 1991). A recent spat of experimental work, reviewed in this chapter, has advanced considerably our understanding of the role of predators in the ecology of marine fishes, yet much remains to be done before we have a better sense of the general importance of predation. Coincidentally, much of the recent work on fish predation has been done on California's temperate reef fishes. To provide context and evaluate the generality of studies from California, we compare this body of work to similar studies conducted elsewhere, mainly on tropical coral reefs. We conclude by highlighting several aspects of predation in particular that are in need of more detailed study.

Predation is just one of the many processes (see other chapters in this book) that affects individuals, populations, and communities of marine fishes. Ideally, one would like to know how important these processes are relative to one another (Welden and Slauson, 1986). Are some of them trivial in nature, and therefore better ignored to instead focus our energies and resources on the more important ones? Frankly, there are too few data available to definitively judge the relative importance of predation. Nevertheless, a number of studies tell us that predation should be studied concurrently with other processes (e.g., competition) because of potential interactions, which cause the importance of one process to depend upon the level of another.

In this chapter, we focus on field studies to explore the role that predators play in nature. As practicing field ecologists, we believe that such studies, although logistically more challenging, provide the best tools available for exploring the workings of nature. We also discuss laboratory studies that we believe are particularly enlightening and provide insight not available from field studies. There are a number of topics related to predation that we do not discuss in detail, either because they do not provide much insight into the effects of predators or they lack a strong empirical basis. For example, we do not cover gut contents studies in detail, certainly the most prevalent form of the study of predation in fishes. These studies, although essential for determining who eats whom and for questions of prey selectivity, often offer little insight into the ecological effects of predators.

Evolutionary Influence of Predation: The Arms Race

Anti-predatory Adaptations

Being eaten by a predator obviously reduces future reproductive value to zero, hence reducing lifetime fitness. So, it is no surprise that marine fishes have evolved a variety of color patterns, morphological features, and behaviors that reduce their risk of being eaten. These adaptations provide compelling evidence that predation is an important process driving evolutionary change, and they imply that predation is important ecologically to fishes.

COLORATION AND MORPHOLOGY

Marine fishes have evolved a wide range of color patterns and morphological specializations that are thought to reduce the risk of predation. Although we are aware of no work that demonstrates the efficacy of these adaptations in fishes of California, we expect that the general effects of anti-predator adaptations of fishes from other regions should be similar to those of fishes in California. Here, we briefly discuss some of the adaptations that reduce the risk of predation in fishes.

One of the most widespread anti-predatory adaptations is crypsis—the use of camouflage—which reduces detection by predators and thus the risk of being eaten. Crypsis in fish can be achieved by color pattern alone or, often, by combining coloration with morphology and behavior. A very common cryptic color pattern in aquatic animals is countershading, in which the upper surface of the body is dark and the lower surface is light. In well-lit surface waters, such coloration blends in with the dark background when viewed from above and the light background when viewed from below. Further, when viewed from the side the well lit but darkly colored dorsum and poorly lit but lightly colored ventrum creates the impression of uniform shading that blends in with the background. Most open-water fishes such as the Pacific chub mackerel (*Scomber japonicus*) are counter-shaded. The California sardine (*Sardinops sagax*), the northern anchovy (*Engraulis mordax*), and a number of other species combine counter-shading with highly reflective, mirror-like scales that reflect back ambient light, enhancing their ability to blend with their environment when viewed from the side. Flatfishes match the color of the surrounding substrate and use their unique morphology to conform to or bury within the sea floor, rendering them nearly invisible to both prey and predators. The bay pipefish (*Syngnathus leptorhynchus*) matches both its shape and color (green to brown) to the eelgrass that it normally inhabits in California's embayments. That most fishes employ some form of crypsis indicates that it has been a particularly effective evolutionary tactic for evading detection by both predators and prey.

The selective pressure of predation also appears to have driven the evolution of physical defenses. For example, many of California's marine fishes have spines, which are thought to deter predators. The sharp spines (modified fin rays) that are common in the dorsal, pelvic, and anal fins of many teleosts certainly would be unpleasant to swallow; they also increase the effective size of the fish when flared, thus causing gape limitation of predators at smaller prey body sizes. The California scorpionfish (*Scorpaena guttata*) and many rockfishes (*Sebastes* spp.) take matters a step further by possessing venomous spines. In addition to fin spines, these scorpaenids also have spiny projections on their heads and opercula. Cartilaginous fishes also make use of spines, as seen in the horn shark (*Heterodontus francisci*), spiny dogfish (*Squalus acanthias*), bat ray (*Myliobatis californica*), and round stingray (*Urobatis halleri*). The spines of both bat rays and round stingrays are venomous.

GROUP LIVING

In addition to morphological defenses and crypsis, many fishes live in groups, which can reduce the risk of predation (Pitcher and Parrish, 1993). There are a variety of benefits that may be accrued from group living (and a number of costs), but foremost among the benefits is reduced risk of predation. The likelihood of being eaten may be reduced in a variety of ways, some of which are particularly effective in a certain type of group: a school. The terms school and shoal are sometimes used interchangeably, but we will follow the strict definitions given for them by Pitcher: A shoal is any group of fish, whereas a school is a special sort of shoal, one in which the orientation of individuals within the group is polarized. That is, they are oriented in the same general direction, maintain relatively uniform spacing, move at the same speed on average, and are of similar size.

A number of studies have demonstrated that the presence of predators, or even just their cues (e.g., sounds; Wilson and Dill, 2002), induces schooling in prey fishes (Pitcher and Parrish, 1993). In schools and shoals, the risk of predation may be reduced by three different mechanisms: the dilution effect, enhanced vigilance, and predator confusion. In the case of the dilution effect, the risk of predation that an individual faces is reduced by the presence of other prey (the schoolmates). In the simplest case, if there is one predator that will only capture and eat one prey item, then the risk of predation for a school member is reduced to 1/x, where x is the number of individuals in the school, relative to a solitary prey fish. Whether the dilution effect actually works in nature depends on the responses of predators to prey density. If predators exhibit density-dependent behavioral responses (functional or aggregative responses, described later in the chapter), then the dilution effect may produce no reduction in risk of predation. For example, if many predators aggregate to large schools of prey and feed on them until the entire school is devoured, a dilution effect is nonexistent. Some predators show a preference for large schools, whereas others prefer small schools. For example, Axelsen et al. (2001) found that Atlantic puffins focused their efforts on large schools of herrings (*Clupea harengus*) instead of small schools, whereas Nottestad and Axelsen (1999) found that killer whales focused their efforts on small schools of herrings, ignoring larger ones. The difference between the two predator species was likely a result of their very different hunting styles (Axelsen et al., 2001). The implication is that the benefit of associating with a school of a particular size will depend upon the foraging tactics of the predators encountered.

Enhanced vigilance and predator confusion are more likely to consistently benefit schooling fishes. Schools are more vigilant than individuals because there are more sensory systems (eyes, inner ears, lateral lines, etc.) available to detect predators. Thus, larger groups of fish detect predators at greater distances than smaller groups or individuals (Pitcher and Parrish, 1993). This early detection capability allows individuals within schools to initiate anti-predator behaviors earlier than solitary individuals.

The predator-confusion effect occurs because it is very difficult to focus on an individual within a school, and this is usually necessary to capture prey. A variety of studies have shown that with an increase in school size, capture rate per strike declines (Pitcher and Parrish, 1993), presumably because of the confusion effect. Moreover, a common response of schooling fishes is to reduce the inter-individual spacing within the school when faced by predators (e.g., Nottestad and Axelsen, 1999), making a very compact school in which it is even more difficult to single out individuals. Some predators have altered their hunting tactics in ways that overcome the predator-confusion tactic. For example, killer whales slap their flukes, which stun schooled prey, billfishes slash their bills as they pass through schools of prey, which injures or kills the prey, and some predatory species switch to ram feeding and simply swim through dense schools at high speeds with their mouths open.

There are potential costs to group living (schooling and shoaling), including increased risk of detection by predators, increased rates of disease transmission, and competition for resources. Little evidence of increased rates of disease transmission has been found in groups of reef fishes. There is some evidence that large groups attract more predators than do small groups (see Webster, 2003 for an example involving a coral-reef fish). There is widespread suggestive evidence that competition for food occurs in dense groups of both temperate (reviewed in chapter 17) and tropical reef fishes (Jones, 1991), but definitive tests showing that density dependence is eliminated by enhancing food abundance have not been made to our knowledge. Two recent studies on coral-reef fishes, however, have clearly shown that large groups suffer higher mortality than small groups when shelter space is limited. Holbrook and Schmitt (2002) found that dense populations of an anemonefish (Pomacentridae) suffered greater rates of mortality than sparse ones because of interference competition, in which dominant, aggressive individuals forced less aggressive individuals from the safe central zone of the anemone into the dangerous periphery or away from the anemone. The displaced individuals were then eaten, mainly by a suite of nocturnal predators. Studying a coral-reef goby, Forrester and Steele (2004) found that individuals in large groups died (due to predation) at higher rates than individuals in small groups in areas lacking abundant shelter, but in areas with abundant shelter, group size (density) did not affect mortality rate.

BEHAVIORAL RESPONSES

Many fishes alter their behavior when predators are near, thereby reducing their risk of being eaten. These behavioral changes typically reduce the risk of being detected by predators, reduce the probability of encountering a predator, or reduce the probability of capture once detected. Although schooling behavior can be induced or enhanced by the presence of predators, the most common behavioral responses of prey to predators are to reduce the rate of movement or move to a safer microhabitat. Typically, these behavioral changes come at the cost of reduced foraging success for the prey, and the trade-off between foraging success and risk of predation has been studied in detail, often in the context of optimal foraging theory and usually in the laboratory (Lima and Dill, 1990).

Schmitt and Holbrook (Schmitt and Holbrook, 1985; Holbrook and Schmitt, 1988a,b) explored the combined effects of predators and food availability on the behavior of juvenile black perch (*Embiotoca jacksoni*; Embiotocidae) (fig. 16-1) in a series of lab and field studies done at Santa Catalina Island. In a field experiment conducted in a large (50 m^2) enclosure, they (Schmitt and Holbrook, 1985; Holbrook and Schmitt, 1988a) manipulated the presence of the primary piscivorous predator at Catalina Island, the kelp bass, *Paralabrax clathratus* (Serranidae) (fig. 16-1). Kelp bass were either present or absent, and when present they were kept from eating young-of-year black perch by placing them in plastic mesh tubes. Within the enclosures, a natural array of microhabitats that differed in both prey (crustacean) abundance and suitability as shelter from predators was present. Prey abundance and shelter quality did not covary. The rate of foraging, duration of foraging bouts, number of visits, and time spent in each microhabitat were recorded during replicate trials. The general effect of the predator on microhabitat choice was to weaken the strength of the preference of black perch for microhabitats that contained high densities of crustacean prey.

The details of the changes in microhabitat use in this study are informative. *Phyllospadix torreyi*, a vascular plant, provided the highest quality shelter, but harbored very few crustacean prey. This microhabitat was seldom used in the absence of predators and the presence of predators did not cause any increase in its use. Apparently, a high rate of food intake, which could not be obtained in this prey-poor microhabitat, was valued too highly to make use of it. Instead, black perch switched from using the alga *Zonaria farlowii* as the favored microhabitat when predators were absent to using the algae *Cystoseira* sp. and *Sargassum palmeri* when predators were present. All three algae contained similar densities of crustacean prey, but *Zonaria* is shorter and has less finely divided blades than the other two species. This structural difference likely makes *Zonaria* an easier substrate from which to harvest prey, but also makes it less suitable as shelter from predators. The amount of time spent in the *Sargassum/Cystoseira* microhabitats increased when predators were present because the black perch would visit them more often and spend more time per visit there, consequently taking more bites per visit. Also, black perch would move among microhabitat patches less frequently when predators were present than absent, presumably reducing their risk of detection by predators. Further, the effect of predators on microhabitat choice was greatest at dusk, when risk of predation by many piscivores, including kelp bass, is thought to be highest (e.g., Hobson, 1965, 1972).

These findings were further supported by supplemental laboratory experiments in mesocosms, which also evaluated whether black perch could distinguish a predatory species from a non-predatory species and between two different species of predators (Schmitt and Holbrook, 1985; Holbrook and Schmitt, 1988a). The young black perch easily distinguished the non-predatory species, the giant kelp fish, *Heterostichus rostratus* (Clinidae) (fig. 16-1), which is somewhat similar in size, shape, and color pattern to the predatory kelp bass but does not prey upon black perch (Schmitt and Holbrook, 1985). The general reaction of black perch to predators was to move slowly away while continuing to forage. There was no difference between the reaction to another predatory species, the grass rockfish (*Sebastes rastrelliger*; Scorpaenidae), and the kelp bass (Holbrook and Schmitt, 1988a). This result is somewhat surprising because grass rockfish are encountered by black perch much less frequently than kelp bass because they are much less abundant, cryptic, and nocturnal, whereas kelp bass are abundant and active during diurnal and crepuscular periods, when black perch are active.

In these studies, food abundance (crustacean density) was allowed to vary naturally. In a later study done in laboratory mesocosms, Holbrook and Schmitt (1988b) manipulated food abundance and predator presence while holding habitat structure constant by using only one species of alga. Predators (kelp bass) were again placed in plastic mesh tubes to keep them from consuming the young black perch. When predators were present at all food patches, the preference of black perch for high-food-density patches was reduced relative to when predators were absent at all patches. In other words, black perch were less selective in foraging. The black perch were most selective when predator presence and food availability were manipulated concurrently so that choices could now be made between low-food-density patches with predators and high-food-density patches without predators. Not surprisingly, the majority of black perch were found in patches with abundant food and no predators. Interestingly, black perch did not respond to predators by reducing their rate of foraging when predators were present: in all treatments, the rate of foraging was the same. In the field, however, the presence of predators did reduce the rate of foraging by black perch by about 28% (Schmitt and Holbrook, 1985; Holbrook and Schmitt, 1988a), so it appears that the laboratory finding of no effect of predators on foraging rate cannot be extrapolated to the field. Overall, Holbrook and Schmitt (1988b) suggested that the flexible responses of black perch (e.g., more selective in some situations and less selective in others) have evolved to allow the latitude necessary to minimize the lethal and nonlethal effects of predators under the highly variable conditions typically found in nature.

The only other studies on the effects of predators on the behavior of California marine fishes were also done at Santa Catalina Island. Steele (1998) explored the effects of predators on the behavior of two small gobies (Gobiidae), the bluebanded goby, *Lythrypnus dalli*, and the blackeye goby, *Rhinogobiops nicholsii* (formerly *Coryphopterus nicholsii*) (fig. 16-1). The study was done on an array of small (1 × 1 m) artificial reefs built of

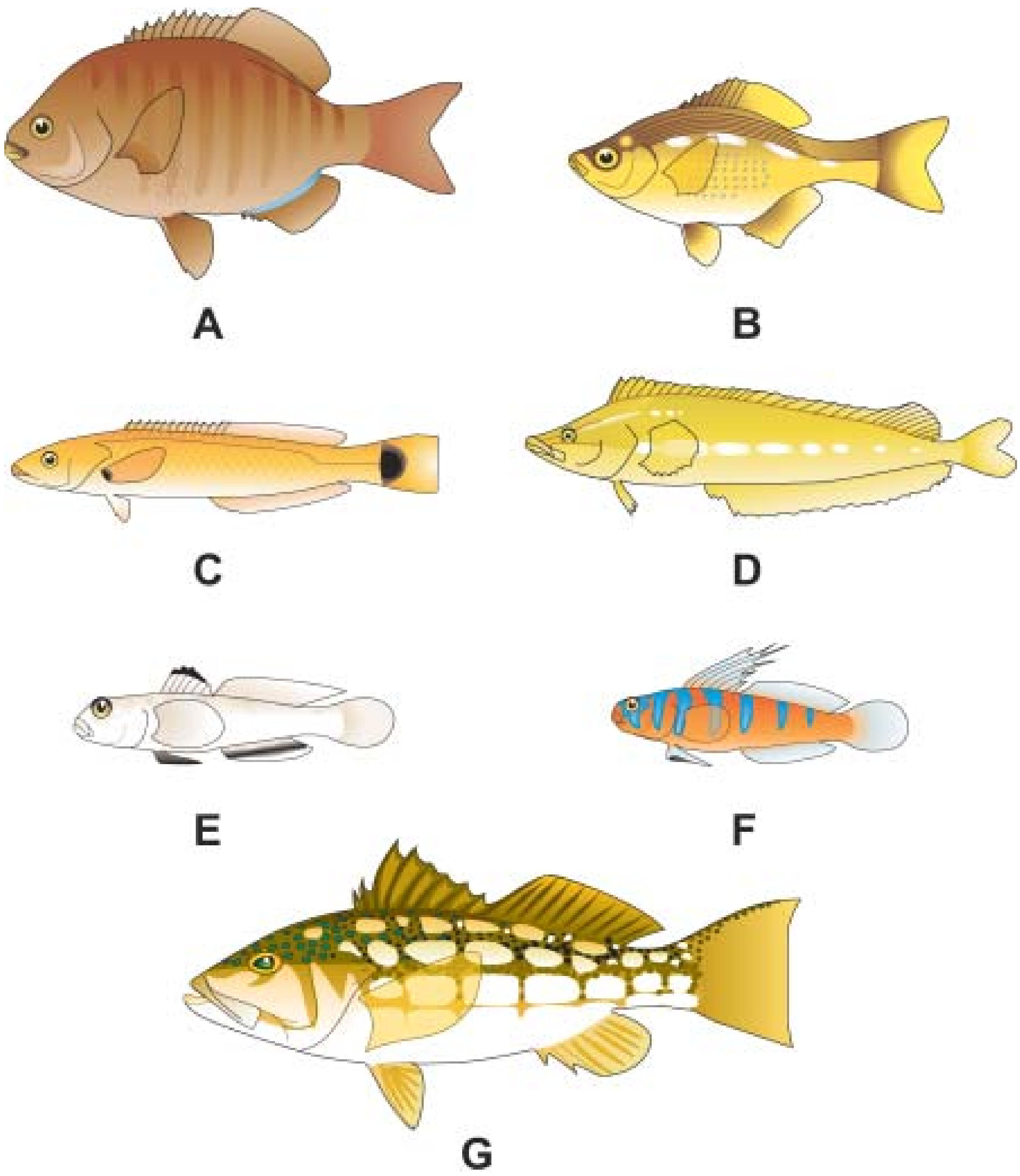


FIGURE 16-1 Seven California reef fishes for which experimental studies of predation have been conducted: a) black perch, *Embiotoca jacksoni*, b) kelp perch, *Brachyistius frenatus*, c) senorita, *Oxyjulis californica*, d) giant kelpfish, *Heterostichus rostratus*, e) blackeye goby, *Rhinogobiops nicholsii*, f) bluebanded goby, *Lythrypnus dalli*, and g) kelp bass, *Paralabrax clathratus*.

rock rubble on a sandy plain, with kelp bass again the most common predator. Smaller numbers of its congener, the barred sand bass (*Paralabrax nebulifer*), were also present. Observations of prey (goby) behavior were made as time budgets on haphazardly chosen focal individuals and they were divided into two categories: observations made while predators were present or absent. During the observations, divers recorded the number of foraging attempts (bites) and the time spent moving, perching on top of rocks, clinging to the sides of rocks, sitting beside rocks, hiding under rocks, or sitting on the sand away (>5 cm) from rocks.

Predators had dramatic effects on the behavior of the two small gobies. The general response of both species to predators was to stop feeding, move less, hide under rocks, and remain motionless (fig. 16-2). The rate of foraging was reduced by 86% in the bluebanded goby and 90% in the blackeye goby in response to predators. These behavioral responses to predators also had effects on the growth rates of the gobies, described later in the chapter.

A comparison between the responses of the black perch studied by Holbrook and Schmitt and the gobies studied by Steele offers some insight into the potential causes of differences in

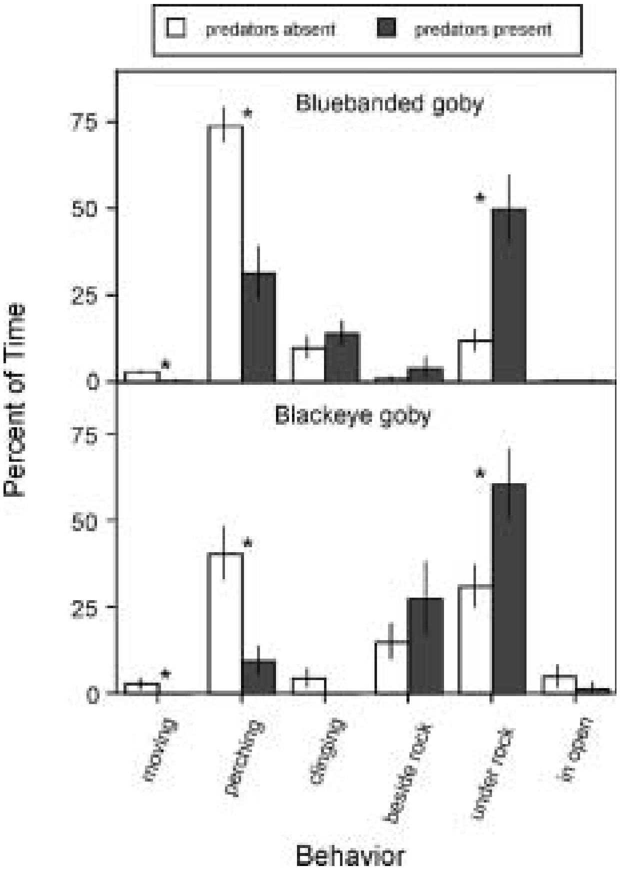


FIGURE 16-2 The effects of predators on the behavior of bluebanded and blackeye gobies. Data are from time budgets of focal individuals. Shown are means and standard errors. Significant differences (based on *t*-tests) are denoted by asterisks (from Steele 1998 with kind permission of Springer Science and Business Media).

behavioral responses to predators among prey species. In the field, all three species responded to predators by decreasing their foraging rates. The two gobies, however, reduced their rates of foraging much more dramatically than the black perch, essentially ceasing foraging, whereas the black perch continued to forage, albeit at about 72% of the rate when predators were absent. Moreover, the gobies generally ceased moving and hid under rocks when predators were present, whereas the black perch continued to move about and forage. We suspect these differences stem from differences in the risk of predation faced by the three species. Black perch grow much larger than either of the goby species, and even the young-of-year black perch used in Holbrook and Schmitt's studies were larger than all of the bluebanded gobies and most of the blackeye gobies studied by Steele. Since piscivores are generally gape limited, it seems likely that the two gobies, by virtue of their smaller size, faced greater risk of predation, and therefore exhibited more extreme behavioral responses to predators.

Like the study by Steele (1998), a study by Hastings (1991) in the Gulf of California revealed that signal blennies (*Emblemaria hypacanthus*) at a site where predators were abundant spent more of their time in shelters and reduced their movement relative to blennies at a site with fewer predators. This study also showed than male blennies courted females less vigorously and with less intense courtship coloration at the site with more predators.

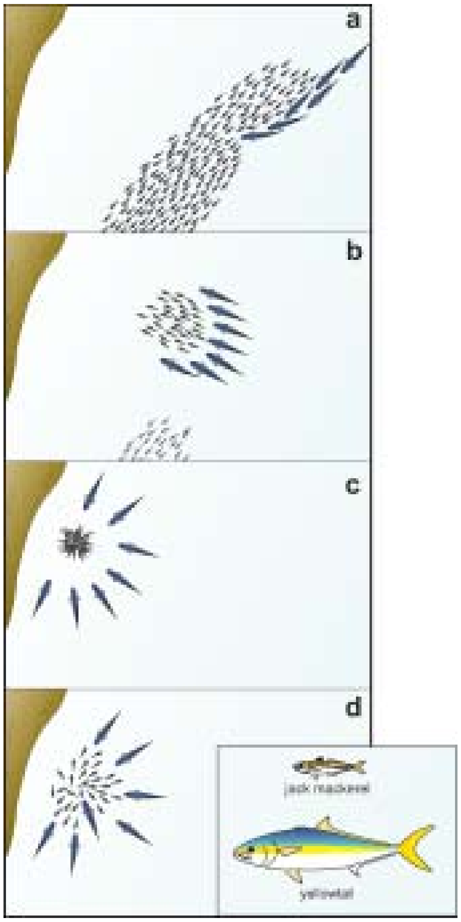


FIGURE 16-3 A diagrammatic representation of the cooperative foraging sequence of yellowtail hunting jack mackerel at Santa Catalina Island. The emergent cliff face is on the top left. a) Yellowtail aligned along the seaward flank of the prey school. Leading predators have begun to turn into the prey. b) After splitting a small group of jack mackerel from the main school, yellowtail have fanned into a crescent formation to herd the prey shoreward. c) The prey, pressed against the shore in shallow water, form a dense aggregation. Yellowtail surround the prey and orient toward the group. d) A single yellowtail rushes through the tight prey aggregation, scattering the jack mackerel in a radiating fashion (after Schmitt and Strand, 1982).

Adaptations of Predators

Just as natural selection should favor prey that are better at avoiding predation, predators that are better at catching their prey should also have a selective advantage. Many of the adaptations that are used by prey in avoiding detection by predators should be equally effective at allowing predators to avoid detection by their prey. For example, the counter-shading and silvery scales of white seabass (*Atractoscion nobilis*; Sciaenidae) likely render them more difficult for their piscine and cephalopod prey to detect. Similarly, the California halibut (*Paralichthys californicus*; Paralichthyidae), an ambush predator, surely benefits from the crypsis provided by matching the color of and burying into the substrate, remaining motionless until small prey fish swim in close proximity.

Other adaptations that increase success of predators have been noted in fishes found in California waters. Schmitt and Strand (1982) observed yellowtail (*Seriola lalandi*; Carangidae) using an organized, cooperative hunting behavior when attacking schools of smaller fish, which allowed them to overwhelm the defenses of their prey (fig. 16-3). The billfishes

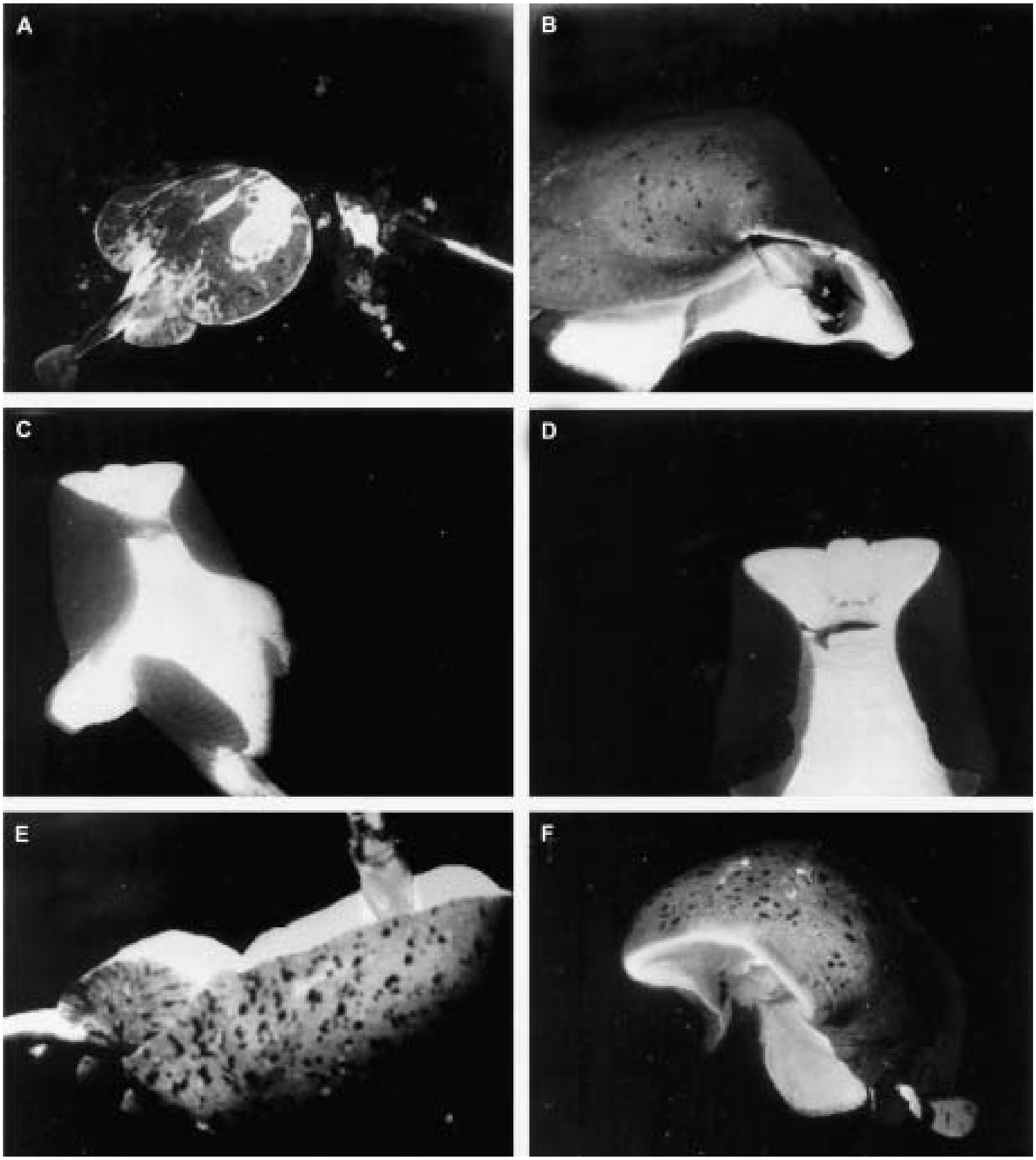


FIGURE 16-4 Prey capture at night by the Pacific electric ray. a) A female ray presented a reef fish while swimming above the reef. b) Posture of an electric ray after lunging on a prey fish. c) A ray near the completion of a forward somersault. The prey has been positioned near the mouth by peristalsis-like foldings of the disk. d) Prey being swallowed headfirst, while the disk is still folded. e) A stunned jack mackerel partially enveloped in the disk of an upside-down electric ray. f) The same ray as in (e) at the completion of the somersault. The prey is now near the mouth while fully enveloped by the disk. These rays are about 750 mm long (from Bray and Hixon 1978, with permission from the American Association for the Advancement of Science).

(in California waters, mainly the striped marlin, *Tetrapturus audax* [Istiophoridae] and the swordfish, *Xiphias gladius* [Xiphiidae]) stun or kill their prey with their bills before returning and consuming them. Bray and Hixon (1978) described the predatory behavior of the Pacific electric ray (*Torpedo californica*), which generates a shock with electric organs. After stunning its prey, this nocturnal predator envelops it by folding its disk and maneuvering it towards its mouth (fig. 16-4). Bray and Hixon suggested that the Pacific electric ray might be a major nocturnal predator of temperate reef fishes. As similarly concluded by Hixon (1991) for coral-reef fishes, the ubiquity of adaptations in prey that reduce predation and in predators that enhance prey capture provides compelling circumstantial evidence that predation has been a key force driving the evolution (see chapter 3) and ecology of marine fishes of California.

Effects of Predators on Prey Demography and Population Dynamics

Fluctuations in demographic rates cause populations to vary in size. Since Hjort's (1914) early observations that age-classes of fishes vary tremendously in abundance, fisheries biologists and fish ecologists have sought to understand what causes populations of marine fishes to vary in abundance over time. Predators may play an important role in generating dynamics in populations of their prey because they can affect prey demographic rates in a variety of ways. Moreover, predatory effects on prey populations may ultimately alter community and ecosystem structure.

Interest in predation, particularly in the fisheries literature, has been focused mainly on predators as consumers, and hence, has examined effects of predators on rates of mortality. Predators, however, can also influence other demographic rates such as growth and fecundity via effects on prey behavior or population density, which can dramatically impact prey populations (e.g., Werner and Gilliam, 1994). Exposure to predators can even modify the morphology of their prey (e.g., Bronmark and Miner, 1992) and alter competitive interactions among prey (e.g., Paine, 1966). In this section, we first discuss the effects of predators on growth, a demographic rate that can strongly influence population dynamics, but one that has received disproportionately little study in marine fishes. We then discuss the impacts of predators on settlement and recruitment of fishes, followed by the effects of predators on fish mortality.

Growth

Typically researchers study the lethal effects of predators on their prey. Predators, however, also have important nonlethal ("sublethal") effects. In the previous section, we discussed behavioral responses of prey to predators, one type of nonlethal effect of predators. By altering prey behavior, predators can influence their rate of food intake, thus affecting growth rates (e.g., Steele, 1998). Predators can also alter competitive interactions by reducing the density of their prey (prey thinning), thus alleviating competition for limited resources and enhancing growth rates of the remaining prey. Hence, predators can have both negative and positive effects on the growth rates of their prey, depending upon the mechanism involved: suppression of foraging or thinning of populations, respectively.

Nonlethal effects of predators on the growth of their prey matter primarily because body size strongly influences many demographic rates and biological processes (Werner and Gilliam, 1984). The importance of growth is exaggerated in fish relative to many other organisms because it is extremely labile and continues throughout life. Maturity in fishes typically is more closely related to size than to age, and once mature, body size has a dramatic influence on reproductive output (Bagenal, 1978; Wootton, 1979; Werner and Gilliam, 1984). Additionally, because the risk of mortality in fishes may decline with size (Sogard, 1997), any factor that influences growth rates may indirectly influence mortality. Moreover, many fishes change gender during their lifetime and the timing of sex change is often influenced by relative or absolute size. Consequently, factors that influence growth rates may affect the sex ratios of populations and thus their reproductive output (Sadovy, 1996). Overall, effects of predators on the growth of their prey may have important consequences for prey population dynamics. Few studies, however, have examined nonlethal effects of predators, especially in marine systems (for rare examples see Connell, 1998; Steele, 1998; Nakaoka, 2000; Steele and Forrester, 2002a). Some of these studies, however, focused on marine fishes in California.

Steele (1998) and Steele and Forrester (2002a) examined the effects of predators on the growth of bluebanded and blackeye gobies at Santa Catalina Island, where the main predator of these two species is the kelp bass. In the 1998 study, Steele explored the effects of predators on the growth of the two gobies on an array of 1 × 1 m artificial patch reefs built of rock rubble. Half of the reefs were enclosed in cages that excluded predators, and the other half were enclosed in partial cages that gave predators access to the reefs. Densities of the gobies were also concurrently manipulated.

Predators had different effects on the growth of the two gobies during this experiment. Bluebanded gobies grew more slowly on reefs exposed to predators than on reefs free of predators (fig. 16-5), but exposure to predators had little effect on blackeye gobies. Both species foraged at lower rates on reefs exposed to predators, so one might predict that they both would grow at slower rates on reefs with predator access. The proximate explanation for the difference between the two gobies is that the rate of growth in bluebanded gobies was related to their rate of foraging, but there was no such relationship in blackeye gobies. Why there was no relationship between foraging rate and growth rate in blackeye gobies is unknown.

In the later study, Steele and Forrester (2002a) found that predators caused blackeye gobies to grow more slowly during some periods but not others (fig. 16-5). This work was done at the same site and also used cages to manipulate the presence of predators. In two of three months studied, blackeye gobies on reefs exposed to predators (uncaged reefs) grew more slowly than those protected from predators. Population density also had a negative effect on goby growth rate, but this effect was independent of the predatory effect (i.e., the two processes did not interact statistically). The effects of predators on growth of the gobies declined from summer to winter, from relatively large effects to no effects, and this pattern mirrored a typical seasonal decline in predator abundance from summer to fall as kelp bass moved to deeper areas away from the reefs that the gobies inhabited. The authors speculated that nonlethal effects of predators on growth of their prey might normally be seasonal.

If predators suppress foraging and thus growth of their prey, and concurrently thin dense populations of competing individuals by eating them, they will have both positive and negative effects on prey growth. It is possible that these opposing effects of predators may balance so that there is no net effect of predators on the growth of their prey, but it is unlikely that these effects will exactly balance one another. Which effect will dominate can be determined graphically (fig. 16-5). For both species, the negative effect of predators on growth outweighed their positive effect mediated via thinning of the prey populations during the studies. During other studies, however, predators consumed more than enough of the two gobies to offset their suppression of growth (Steele et al., 1998; Forrester and Steele, 2000; Steele and Forrester, 2002b).

Comparing studies of Californian fishes with studies conducted elsewhere is problematic due to the global rarity of such investigations. In the only other study on the effects of predators on growth of a marine fish of which we are aware, Connell (1998) manipulated the presence of predators with

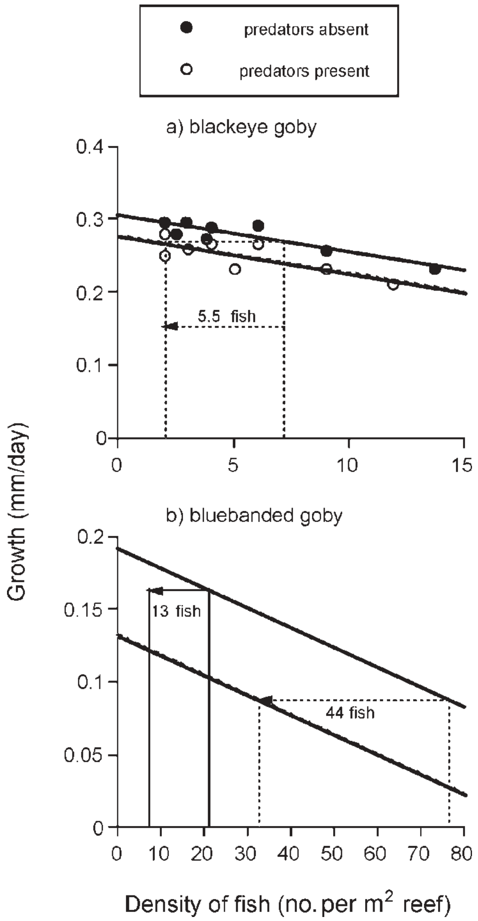


FIGURE 16-5 A graphical method for determining the magnitude of predation necessary to offset the negative nonlethal effects of predators on growth of intraspecifically competing prey. Shown are data for two prey species, a) blackeye goby and b) bluebanded goby. In both species, intraspecific competition caused growth to decline as prey population density increased, both in the presence and absence of predators. Predators, by eating prey, reduce population densities and thereby alleviate competition, enhancing prey growth. Shown by broken the broken lines are the average numbers of fish that must be eaten by predators in order for the prey-thinning effect of predators to balance the negative effect that their presence has on growth. Shown by solid lines in b) is the actual average number of bluebanded gobies thinned by predators, which is insufficient to make up for their negative effect on the growth of this species. For blackeye gobies, during the study shown, predators had no effect on the density of their prey, but in other studies they have greatly reduced blackeye goby density. Data for the blackeye goby come from Steele and Forrester 2002a. The slopes and elevations of the line in b) are derived from data presented in Steele, 1998.

cages and found that predators suppressed the growth of a small, coral-reef damselfish on the Great Barrier Reef, Australia. This one non-Californian study and its similar results, combined with the ubiquity of nonlethal effects in freshwater systems (e.g., Werner et al., 1983; Semlitsch, 1987; Skelly and Werner, 1990; Fraser and Gilliam, 1992; Peckarsky et al., 1993; Scrimgeour and Culp, 1994) lead us to suspect that such effects of predators will likely play an important role in the demography of other marine fishes.

Settlement and Recruitment

Input into local populations of most demersal marine fishes occurs when pelagic larvae or juveniles settle from the plankton and associate with benthic habitat. This transition from the pelagic to the benthic environment, defined as settlement, is very difficult to measure directly, and typically a proxy for it, recruitment, is measured. Recruitment is the number recent settlers left after some unknown amount of post-settlement mortality has occurred. (Note that this ecological definition of recruitment differs from the definition used in fisheries biology, which refers to the addition of individuals to the harvestable stock—normally large juveniles or adults). Depending on the magnitude and pattern of early post-settlement mortality, recruitment may or may not be an appropriate proxy for settlement. Studies on the effects of predators on input into populations of marine fishes have all measured recruitment, not settlement. Consequently, the exact causes of predatory effects on recruitment are not known with absolute certainty. When predators have negative effects on recruitment, these effects can arise by two different mechanisms: predators may eat settling and recently settled fishes (the typical interpretation), or settling fishes may detect predators and avoid settling in areas where predators are abundant.

To our knowledge, the possibility that settling fishes detect and avoid predators has been tested only once in marine fishes, and not in California. On small coral reefs in the Bahamas, Almany (2003) confined predators in cages, which kept them from eating settling fish, but still provided cues of their presence. He measured recruitment (every other day) to reefs with caged predators (with cues) and without predators (without cues). Although an earlier experiment had revealed effects of predators on reef fish recruitment, there was no difference in the rate of recruitment between reefs with and without caged predators. Thus, he found no evidence that settling fishes avoided reefs with predators. To our knowledge, no such study has ever been done in California or any temperate system but this phenomenon deserves examination because settling fishes certainly have the sensory capabilities and swimming abilities necessary to detect and avoid predators. Sweatman (1988) showed that a highly social coral-reef fish may detect chemicals emitted by conspecifics and use them as settlement cues, so it is plausible that settling fishes could detect, either through chemosensory, visual, or other means, the presence of predators and avoid areas where they are abundant. Even relatively weak swimmers like barnacle larvae are able to detect chemical cues from their predators and respond by altering their settlement choices (Raimondi, 1988). Piscivorous fishes, however, tend to be much more mobile than invertebrate predators, and this characteristic may make cueing on them less likely to occur in settling fishes than invertebrates.

Even though it has yet to be shown that predators directly influence settlement of marine fishes, it has been clearly demonstrated that predators often reduce their recruitment. The usual interpretation of this finding is that predators reduce recruitment by eating settling and recently settled fishes, but further studies on settlement choice are necessary before it can be accepted with certainty. Examples of predator-caused reductions in recruitment of marine fishes in California all come from Santa Catalina Island.

In the first study of a marine fish in California to directly manipulate the presence of predators, Behrents (1987) found that bluebanded gobies recruited to artificial habitats at higher rates if they were protected from predators. Unfortunately, she

a) experimental design

b) kelp bass recruitment

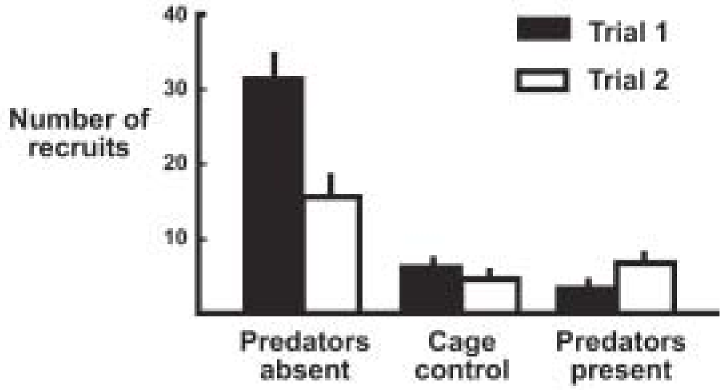


FIGURE 16-6 The experimental design a and b subsequent recruitment of kelp bass to reefs with the understory alga, *Sargassum palmeri,* on which predator access was manipulated. The data are means ± 1 standard error for each of three treatments (predator exclusion, predator access [no cage], and a cage control [half-cage]) over two experimental trials (after Carr, 1991).

could not rule out caging artifacts as the cause of the enhanced recruitment in caged areas. Later work by Steele (1997a, 1999), shown to be without substantial experimental artifacts, demonstrated a negative effect of predators on recruitment of this species, substantiating the results of Behrents' study.

Steele (1997a) also evaluated the importance of the effect of predators on recruitment relative to those of resident conspecifics (potential competitors or cues for settlement), potential interspecific competitors, and reef location (which can influence settlement rates). The presence of predators halved recruitment of bluebanded gobies but had little effect, on average, on the recruitment of blackeye gobies. For both species, however, the magnitude of the predatory effect varied with reef location. This pattern caused a statistical interaction between the effects of predators and reef location and made it impossible to quantify, in any meaningful way, the importance of predatory effects relative to other effects. Qualitatively, however, the effects of predators were much more important that those of any other process. In the absence of predators, reef location had strong effects on recruitment. Predators, however, completely eliminated this underlying spatial pattern of recruitment. This result implies that predators consumed the two gobies in a density-dependent manner. Notably, Steele and colleagues (Steele 1997a, 1999; Steele et al., 1998; Steele and Forrester, 2002b) have found the effects of predators on recruitment of blackeye gobies to be highly variable. Their studies have found predatory reductions in recruitment of this species as small as 14% over 21 days (Steele, 1997a) to as large as 90% within 24 hours of settlement (Steele and Forrester, 2002b). The cause of such variability in predatory effects has yet to be determined, but it is suggestive of temporally density-dependent predation given that per capita mortality rates generally increased with prey density (Steele and Forrester, 2002b).

Carr (1991) studied the effects of cannibalism on recruitment of kelp bass. He used replicate $1m^2$ plots of rocks with attached algae (primarily *Sargassum palmeri*) in three treatments: predator exclusion (full cage that allowed access only by new recruits), predator access (open plot), and a cage control (half-cage) (fig. 16-6). In two separate 2-wk trials, Carr allowed young kelp bass to settle and accumulate on the reefs and then recorded the number of recruits (fish 10-15 mm SL) in each plot at the end of a trial. He found greater recruitment to the predator exclusion treatment than to open plots, and there was no difference in recruitment between the open plots and cage controls, suggesting that the cages did not confound the experiment by either inhibiting or enhancing settlement (fig. 16-6). In laboratory mesocosm experiments, Carr (1991) also found that risk of cannibalism did not differ among algal habitats, suggesting that the experiments using *Sargassum* provided a general model of predator-mediated recruitment success in other algal habitats (e.g., giant kelp, *Macrocystis pyrifera*).

In recent work using an experimental design similar to Carr (1991), Anderson and Davenport (unpublished data) quantified recruitment of three kelp-associated fishes, the kelp bass, the senorita (*Oxyjulis californica*), and the giant kelpfish (*Heterostichus rostratus*) (fig. 16-1) to giant kelp. Despite variation in the magnitude of recruitment and the relative abundance of recruits over a two-year period, recruitment of all species was much higher in the absence of piscivorous kelp bass (there were no observed artifacts based on comparisons with cage controls). Moreover, there was evidence of size-dependent

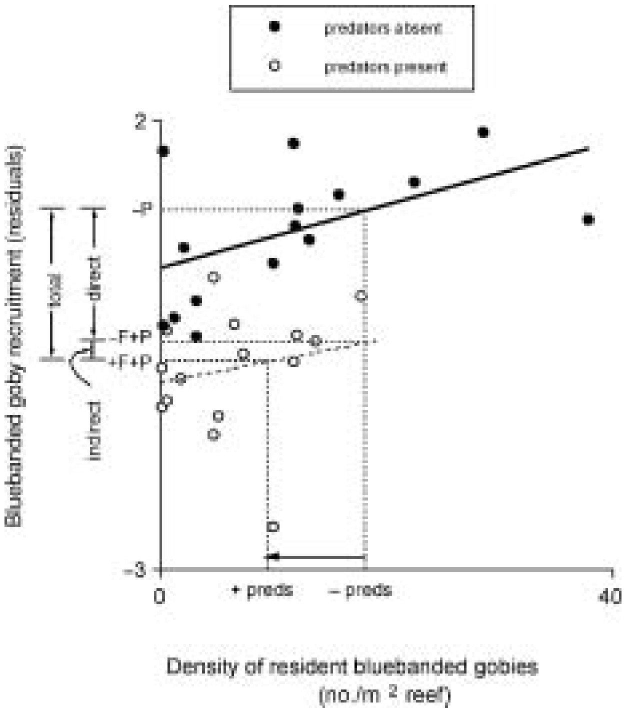


FIGURE 16-7 The direct and indirect effects of predators on recruitment of the bluebanded goby. This species experiences recruitment facilitation, and therefore, predation on resident individuals reduces the cue for recruitment of juveniles. The direct effect of predators is the difference between points – P (no predators) and – F+P (no facilitation, predators present) on the y-axis. The total effect of predators is the difference between points – P and +F+P (facilitation present, predators present). The indirect effect of predators caused by their consumption of residents (the difference between – preds and + preds on the x-axis) and the concomitant reduction of the cue for recruitment is the difference between points – F+P and +F+P (the natural condition) on the y-axis (from Steele 1997a with permission from the Ecological Society of America).

predation. Recruited kelp bass (the only species with enough recruitment for this analysis) were much larger in predator-exclusion plots than in plots that allowed access to predators. This finding is contrary to the bigger-is-better hypothesis, widely believed to apply to marine fishes (Sogard, 1997).

As noted earlier, some highly social fish use the presence and density of conspecifics as a cue for settlement (e.g., Sweatman, 1985; Booth, 1992; Schmitt and Holbrook, 1996). In species with such recruitment facilitation, the potential for an indirect effect of predators on settlement exists, mediated via the effect of predators on already settled individuals. If predators reduce the density of the conspecifics providing the cue for settlement, then settlement will be reduced. This indirect effect was found in bluebanded gobies at Catalina Island (Steele, 1997a). Using two separate approaches, one graphical and one statistical, Steele determined that the indirect reduction in recruitment was relatively small, only about 7% of the direct effect of predators on recruitment (fig. 16-7). However, in cases where recruitment facilitation is particularly strong and predatory effects on population density large, this indirect pathway for predator effects on the rate of settlement could be quite important.

Studies on the effects of predators on recruitment of marine fishes of California have generally found that predators reduce recruitment of their prey, though some studies failed to detect any effect. This range of effects, from negative to none, is typical of marine fishes in other areas. For example, Levin et al. (1997) and Petrik et al. (1999) studied the effects of predators on recruitment of two species of estuarine fish in Texas. They found a negative effect of predators on recruitment of one species, but not the other. The system in which the effects of predators on marine fish recruitment have been studied in the most detail is coral reefs, and the findings have generally been similar, though with a couple of interesting twists. Like the studies in California, the most common finding on coral reefs is that predators reduce recruitment of their prey (e.g., Shulman et al., 1983; Doherty and Sale, 1985; Carr and Hixon, 1995; Beets 1997; Steele and Forrester, 2002b; Webster, 2002; Almany, 2003). An interesting effect that has occasionally been found in coral-reef fishes, however, is a positive effect of predators on recruitment (Steele et al., 1998; Almany, 2003). In the case of a tropical goby, Steele and colleagues (1998) suggested that the predators manipulated were not the key predators of the target species, and that, in fact, the large predators manipulated actually reduced the abundance of the primary, small predators of the goby, indirectly enhancing its recruitment. Almany (2003) suggested that the positive effect of predators that he found on recruitment of a small wrasse was due to two factors: first, the wrasse is a cleaner fish and therefore is subject to little predation and, second, reefs with large predators provided a better source of food for the wrasse (greater numbers of ectoparasites) than was present on reefs without predators. In summary, studies on the effects of predators on California's fishes have found results that are generally consistent with those from other systems, usually finding negative effects of predators on recruitment.

Mortality

Predation has been implicated as a significant, if not the primary, source of mortality in populations of marine fishes (Bailey and Houde, 1989; Hixon, 1991; Sogard, 1997), despite a conspicuous lack of direct evidence in most systems. Explicit observations and experiments to determine the impact of predation on fish populations have been restricted mainly to nearshore fishes, especially those that occupy temperate and tropical reefs and have small home ranges. This situation is understandable considering the logistical difficulties in observing predation events in nature, in measuring the ecological impact of these events, and in manipulating mobile piscivores and their prey.

Predation has long been implicated as an important process in the near shore habitats of California by the strong relationships between fish abundance and the abundance of shelter-providing habitats (Limbaugh, 1955; Quast, 1968; Miller and Geibel, 1973; Feder et al., 1974; Ebeling and Bray, 1976; Coyer, 1979; Hobson et al., 1981; Hobson and Chess, 1986). These relationships, however, do not conclusively demonstrate that predation is an important ecological process because they can be generated by behavioral choices (habitat preferences) of the prey in the absence of predation (Steele, 1999). An example of the importance of shelter-providing habitat is provided by Ebeling and Laur (1985). They used an experimental and observational approach to demonstrate the importance of understory kelp (*Pterygophora californica* and *Laminaria farlowii*) to young-of-year of surfperches (Embiotocidae) of five species. In the observational portion of their study, they found that the abundance of young surfperch tracked the percentage cover of the macroalgae. To demonstrate the causal nature of the relationship, they conducted an experiment in which blades of *P. californica* were removed along a 5-m band while another similar area of *P. californica* was left as an unmanipulated control. The abundance of young surfperches declined significantly in the area where blades were removed but not in the control, whereas the abundance of adult surfperches did not differ between treatments. Ebeling and Laur attributed the decrease in abundance of young surfperches mainly to predation by the kelp bass.

Direct tests of the impact of predation on California's marine fishes were not made until the 1980's. As noted earlier, Behrents (1987) conducted one of the first field experiments to directly manipulate the presence of predators to test their effects on the rates of mortality and recruitment of the bluebanded goby. She manipulated both the presence of predators (mainly kelp bass) with cages and the abundance of shelter holes on artificial habitats. In addition to effects on recruitment, Behrents found that mortality was higher in the presence of predators. The strength of the effect of predators (which unfortunately could not be distinguished from a cage artifact) depended upon the size of the gobies and the abundance of shelter. Steele (1996) later tested for cage artifacts on bluebanded and blackeye gobies by placing small reefs with 3 treatments (complete cages, partial cages, and no cages) inside a large enclosure that kept all predators away from them. With this design, potential artifacts of cages were tested directly without being confounded with effects of predators. The unfortunate finding of this study was that bluebanded goby survival (though not recruitment: Steele, 1997a, 1999) was affected by cage artifacts. Hence, it is difficult to interpret the results of Behrents' study.

Further investigation led Steele to design partial cages, which allowed predators access to gobies, but that did not differ from complete cages in their effects. Comparing partially caged and fully caged treatments allowed the effects of predators to be measured unambiguously. With this technique, Steele measured the impact of predation on bluebanded and blackeye gobies, and he assessed the relative importance of predation vs. intra- and interspecific competition. Predation on bluebanded gobies was severe (about twice as many gobies died on reefs exposed to predators as on reefs free of predators) and the intensity of predation varied spatially (Steele, 1998). Moreover, the relative importance of predation was very high for bluebanded gobies, which suffered little, if at all, from intra- and interspecific competition. By contrast, blackeye gobies were not affected significantly by predation, and intraspecific competition had relatively more important effects.

Density-dependent Predation and Population Regulation

Density dependence has been a major focus of recent research on marine fishes (reviewed by Hixon and Webster, 2002). In reef fishes, this recent interest was largely motivated by a desire to test the recruitment limitation hypothesis (Doherty, 1981; Victor, 1983), which specifically excludes the possibility of post-settlement density-dependent mortality (Doherty, 1983; Doherty and Fowler, 1994), and instead posits that patterns of abundance in demersal fish populations are set primarily by variable settlement. A more refined viewpoint seeks to determine the relative influence of density-independent versus density-dependent processes (since they are not mutually exclusive) (e.g., Schmitt and Holbrook, 1999). Despite the recent interest in density dependence by reef fish biologists, the study of density dependence has a long and rich history in general ecology (reviewed in Hixon et al., 2002) and fisheries biology (e.g., Ricker, 1954; Beverton and Holt, 1957). This is no surprise, because population regulation, essential for the persistence of populations, can only occur if one or more demographic rate is density-dependent (Murdoch, 1994). By a variety of mechanisms (discussed below), predators can cause the density dependence necessary for population regulation. Nevertheless, field experimental tests for predator-induced density dependence in marine fishes are only now becoming common (Hixon and Carr, 1997; Steele, 1997a; Forrester and Steele, 2000; Anderson, 2001; Carr et al., 2002; Webster, 2002; Holbrook and Schmitt, 2002). Tests for density-dependent predation have been made with three species of California's marine fishes. We discuss these studies after a brief description of the mechanisms by which predators can cause density-dependent mortality of their prey.

Predators can cause density-dependent mortality of their prey via four general responses to prey density: the functional response, the aggregative response, the developmental response, and the numerical response (Holling, 1959; Murdoch, 1970, 1971, 1994; Murdoch and Oaten, 1975). These four types of responses are not mutually exclusive. Briefly, the functional response is a behavioral response of individual predators to prey density, and it is measured as the number of prey killed per predator as a function of prey density (Solomon, 1949; Holling, 1959). Three basic forms of the functional response have been described, Types I, II, and III, but only the Type III response can cause density-dependent prey mortality, and it does this only over a limited range of relatively low prey densities (Holling, 1959). The aggregative response is also driven by predator behavior, and it relates the number (or time spent by) predators in an area to the density of prey there (Hassell, 1966; Hassell and May, 1974). If a strong positive relationship exists between the two variables, prey mortality may be density-dependent. The developmental response relates the somatic growth rate of predators to the density of their prey (Murdoch, 1971). If better-fed predators (ones that live in areas with dense prey populations) grow more, and as a consequence of their increased size require and eat more prey, then this too can cause density-dependent predation. Finally, the numerical response, like the aggregative response, relates the density of predators to the density of their prey, with strong positive relationships potentially causing density-dependent predation. The numerical response, however, differs from the aggregative response in the mechanism that causes predator numbers to increase with prey density: greater predator densities at high prey densities are generated by increased predator survival and/or reproductive output, not by attraction to dense prey patches. Very few field studies on marine fishes have evaluated any of these four classes of predator responses to prey densities.

Anderson (2001) is the only published study of which we are aware that both tested for predator-induced density-dependent mortality with a field experiment and evaluated the mechanisms (predator responses) responsible for any density-dependent mortality. He studied the kelp perch, *Brachyistius frenatus*, and tested whether predatory kelp bass exhibited density-dependent functional and/or aggregative responses to prey fish density. First, in laboratory mesocosms, he evaluated the functional response of kelp bass by manipulating the density of juvenile kelp perch and quantifying the rates of predation at each density. He also concurrently manipulated the amount of shelter-providing habitat (giant kelp, *Macrocystis pyrifera*). The availability of shelter influenced the shape of the functional response, causing it to range from density-independent

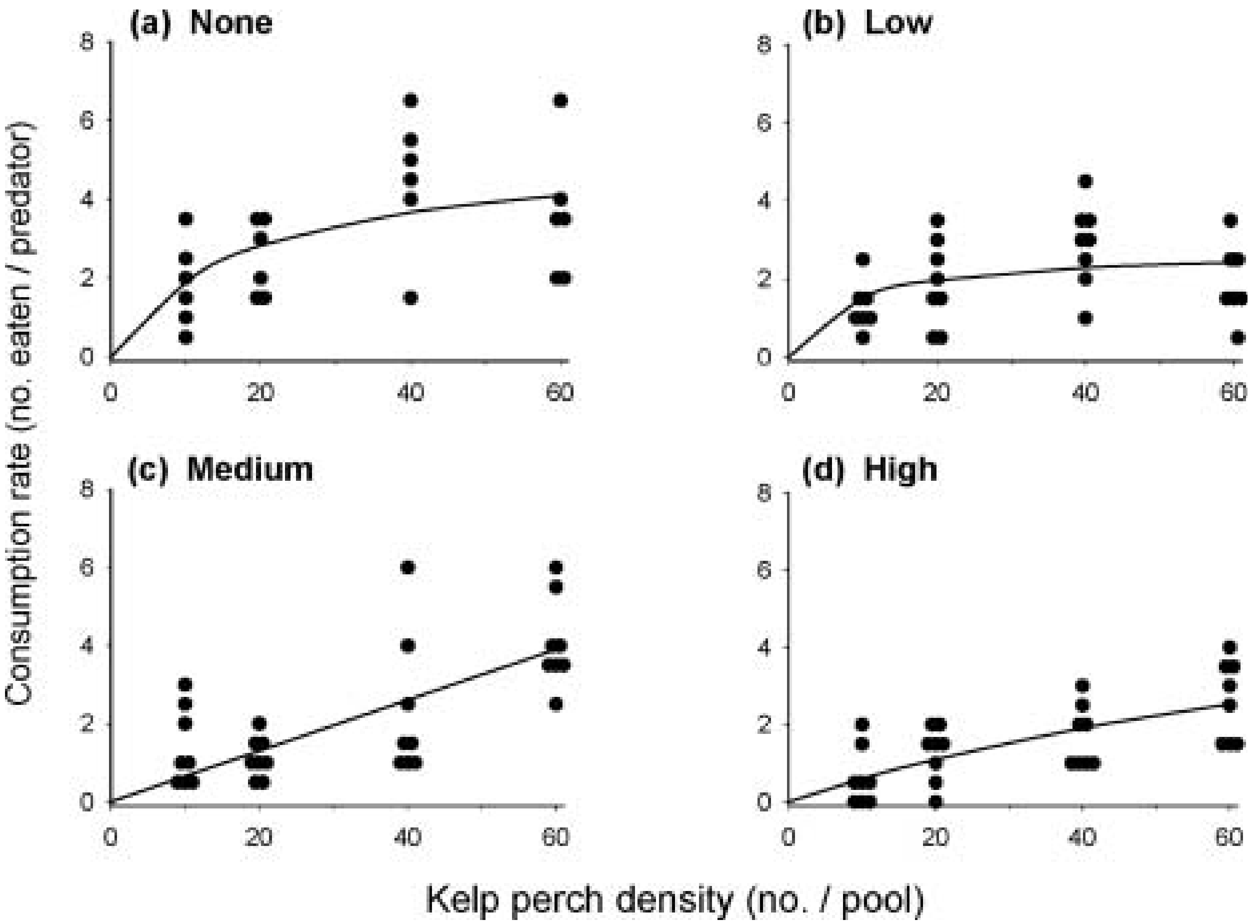


FIGURE 16-8 Relationship between the density of kelp perch (no. individuals per pool) and the functional response (number of prey eaten per predator over 15 hours) under conditions of (1) none, (b) low, (c) medium, and (d) high levels of habitat structure (giant kelp, *Macrocystis pyrifera*) (from Anderson 2001 with permission from the Ecological Society of America).

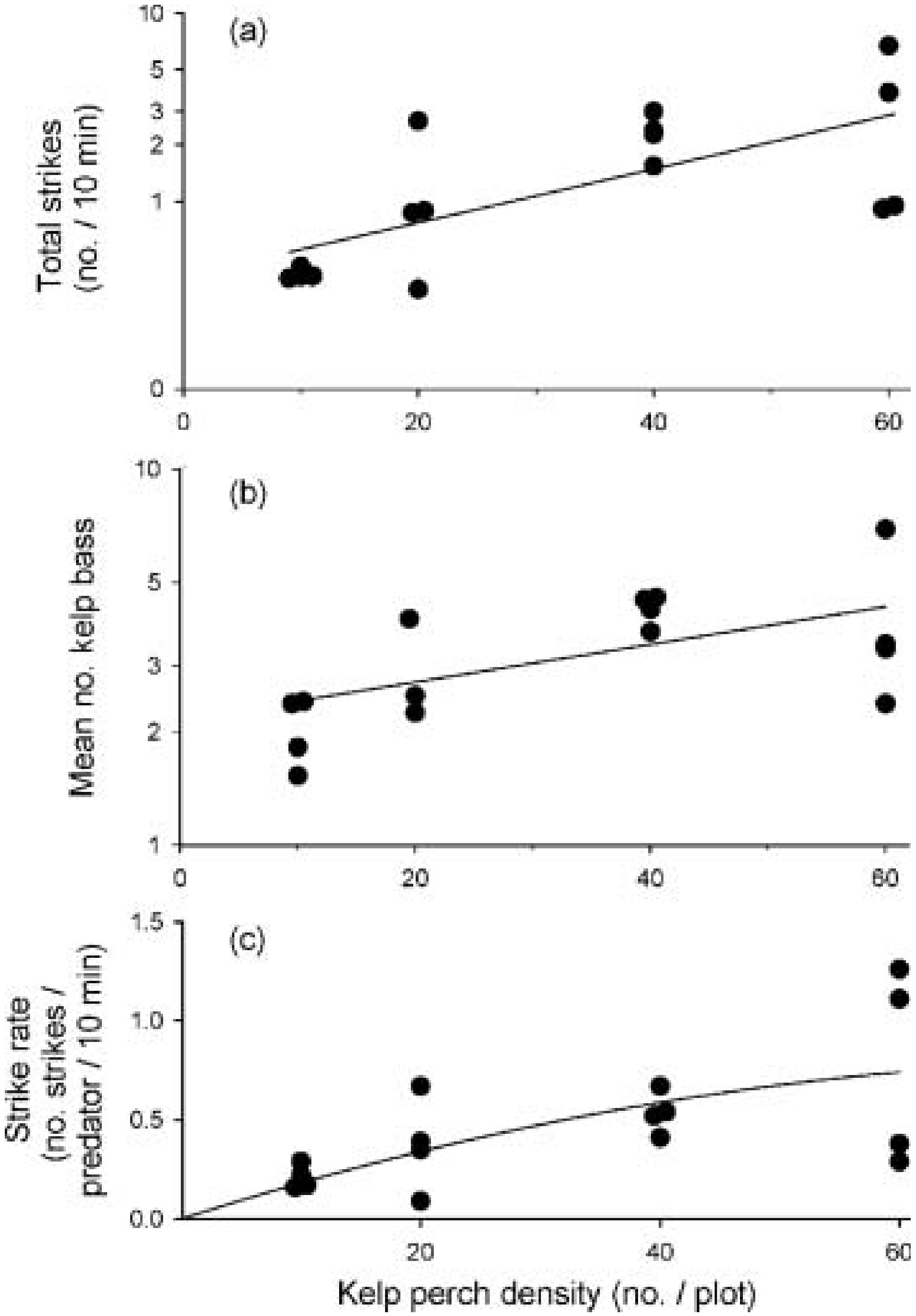
to inversely density-dependent, indicating a Type I or Type II functional response, respectively, depending upon the quantity of kelp (fig. 16-8).

Subsequently, in a field experiment manipulating the number of juvenile kelp perch on plots of giant kelp, Anderson quantified the strike rate (number of capture attempts) of kelp bass as a proxy for the functional response. During two-hour trials conducted at dusk, when kelp bass forage actively, he also recorded the average number of kelp bass present on each plot to assess whether kelp bass exhibited an aggregative response to areas of higher prey concentration. In contrast to the laboratory experiments, mortality during the field experiment was density-dependent (fig. 16-9). Such predator-induced density dependence could have occurred either if there was a different functional response in the field than in the lab (a Type III response instead of Types I or II found in the lab), or if there was a Type II functional response combined with an aggregative response (Hassell, 1978). Anderson found that there was a strong aggregative response by kelp bass, and suggested that this behavior combined with a Type II functional response was the most likely cause of the observed density-dependent predation. He recommended that both the functional and aggregative responses be evaluated to gain a sound mechanistic understanding of patterns of predator-induced mortality over short time scales.

Without focusing on the mechanisms, Steele and colleagues evaluated the possibility of density-dependent predation in the bluebanded goby and the blackeye goby (Steele, 1997a, 1997b, 1998; Forrester and Steele, 2000). As noted earlier, Steele's (1997a) study suggested that predation on recently settled recruits of both species was density-dependent because predatory reductions in recruit density were greatest in areas that received the highest natural recruitment of gobies and lowest in areas that received the fewest recruits. This suggestion was supported for bluebanded gobies by Steele's (1998) study, which found that high-density populations tended to suffer higher mortality than low-density populations if they were exposed to predators, but not if predators were kept away. In this study, there was no evidence of an aggregative response by predators to bluebanded goby density, indicating that a Type III functional response was most likely the cause of density-dependent predation. The finding of density-independent mortality in the absence of predators in both bluebanded and blackeye gobies (Steele, 1998), coupled with the finding of strong density-dependent mortality of both species when exposed to predators (Steele, 1997b), gave strong, but not irrefutable, support for the notion that predators were causing density-dependent mortality in both species.

These findings motivated an explicit test for predator-induced density-dependent mortality in bluebanded and blackeye gobies (Forrester and Steele, 2000). In this study, prey (goby) densities were manipulated across the natural range (using 8 different densities) and crossed with the absence or presence of predators, by excluding (by cages) or allowing predators (mainly kelp

FIGURE 16-9 Relationship between the density of kelp perch and (a) the total number of strikes by kelp bass at kelp perch, standardized to a 10-min interval, (b) the mean number of kelp bass recorded on field plots, and (c) the calculated per-predator strike rate (from Anderson, 2001 with permission from the Ecological Society of America).



bass) access to the small artificial reefs inhabited by the gobies. This experiment revealed that predators were indeed the cause of density-dependent mortality in bluebanded gobies, i.e., mortality of this species was density-dependent in the presence of predators but density-independent on predator-free patch reefs. By contrast, mortality of blackeye gobies was independent of density regardless of whether predators were present or not, contrary to earlier results (Steele1997b). Forrester and Steele concluded that these inconsistent results for blackeye gobies indicate that the conditions that cause population regulation must vary temporally or ontogenetically.

Density-dependence can occur in two different forms: temporal or spatial. Temporal density dependence occurs when a single population experiences higher mortality rates when it is dense than when it is sparse. Spatial density dependence occurs when mortality rates of populations distributed across space are greater in dense populations than in sparse populations. The two forms of density dependence are not mutually exclusive, but also, the presence of one does not ensure the presence of the other (Stewart-Oaten and Murdoch, 1990).

The work of Anderson, Steele, and colleagues dealt with spatial density dependence (although comparison among some of their studies suggests that temporal density dependence may occur). We are aware of only one field study in California that addresses temporal density dependence. Hobson and colleagues (2001) conducted an 11-yr study in Mendocino County that explored temporal (interannual) variation in predation on young young-of-year (YOY) rockfishes (*Sebastes* spp.). The authors found that YOY rockfishes were more prevalent in the guts of three predators (black rockfish, *Sebastes melanops*; blue rockfish, *Sebastes mystinus*; kelp greenling, *Hexagrammos decagrammus*) during years when YOY were abundant. This finding implies that predation on YOY rockfishes was temporally density-dependent, and Hobson et al. suggested that this form of predation dampens interannual variation in year-class size of young, nearshore rockfishes.

Overall, studies on density-dependent predation in California's marine fishes have found results that are generally consistent with the findings of studies on coral-reef fishes (reviewed by Hixon and Webster, 2002). Predation appears to be a common cause of density-dependent mortality and we speculate that shelter limitation may be a common cause of density-dependent predation (Anderson, 2001; Holbrook and Schmitt, 2002; Forrester and Steele, 2004).

Distributional Patterns of Prey and Predators: Importance of Habitat Structural Complexity

Patterns of Covariation Between Predators and Prey

A number of conflicting factors influence the distributional patterns of prey and their predators. Successful predators will be located near their prey, at least when they are actively hunting, and this should generate a positive correlation between predator and prey densities. Depletion of prey by their predators, however, should generate a negative correlation between predators and prey. Moreover, to maximize their fitness, prey should avoid their predators, and this too should generate a negative correlation between prey and predator densities. The patterns generated in nature will depend on (1) the relative mobility of predators and prey, (2) the relative rates of consumption by predators vs. recruitment of prey, and (3) the scale at which the pattern is measured. Because relative mobility and rates of consumption vs. recruitment will vary from system to system, it is difficult to predict how predators and prey should be distributed relative to one another.

Anderson (1994), Carr (1994), and Steele (unpublished) have explored the relationship between reef-fish prey and predators (kelp bass) at Santa Catalina Island. In Carr's study, young-of-year kelp bass, which are extremely susceptible to being eaten by older cannibals, were the prey. Carr (1994) found no consistent relationship between the densities of predators and prey, in some years finding positive relationships, in others negative relationships, and in yet others, no relationship. Anderson (1994) found that both juvenile and adult densities of kelp perch were negatively related to kelp bass density. Steele found that bluebanded goby densities were not significantly correlated with the density of their predators ($r = 0.16$, $P = 0.50$, $n = 21$), but blackeye goby densities were positively correlated with predator density ($r = 0.68$, $P = 0.0007$, $n = 21$). So, perhaps not surprisingly, no consistent relationship between predator and prey densities emerges from the few studies to examine this relationship in California's fishes.

Variable relationships between predator and prey density are not unique to California's marine fishes. Work on coral-reef fishes has documented similar variability. For example, Hixon and Beets (1989, 1993) found either a negative or no relation between prey and predator density, depending on which way they measured prey density. In contrast, both Beukers and Jones (1997) and Stewart and Jones (2001) found a positive relationship between prey and predator density. In Beukers and Jones' study, the densities of both prey and predators were positively correlated with the same habitat attribute (coral cover), and this may have driven the positive predator-prey correlation, whereas in Hixon and Beets' studies, habitat quality was standardized on artificial reefs. Hence, it appears that similar habitat needs of predators and prey may drive positive correlations between prey and predator densities. Predators and prey may have similar habitat needs if the predators are prey of even larger species and they use structurally complex habitats in the same way their prey do, as refugia. Alternatively, predators may use such areas as ambush sites for hunting their prey. In any event, structurally complex habitats play very important roles in mediating the predator-prey interaction, and these are discussed next.

Interactive Effects of Predators and Habitat Structure

Structurally complex habitats can provide both food and shelter from predators, although decoupling the relative value of each of these resources is no simple task (Jones, 1984, DeMartini and Roberts, 1990). On the temperate reefs that provide much of the habitat for nearshore fishes in California and other temperate areas, structurally complex habitats are typically comprised of stands of macroalgae and rocky reefs, which provide a variety of interstices, crevices, caves, and undercuts. Several researchers have documented positive relationships between the recruitment and abundance of reef fishes and the abundance of macroalgae (Larson and DeMartini, 1984; Moreno and Jara, 1984; Ebeling and Laur, 1985; Choat and Ayling, 1987; Carr, 1989, 1991, 1994; DeMartini and Roberts, 1990; Holbrook et al., 1990; Levin, 1991, 1993; Anderson, 1994; Levin and Hay, 1996, 2002), and, as noted earlier, predation is often implicated as a cause of these relationships because these structurally complex habitats are believed to provide suitable refuges from predation.

Despite the prevalent notion that predators drive these habitat-abundance relationships, relatively few field experiments have tested the importance of structurally complex habitats in generating patterns of recruitment and fish abundance. Behrents (1987) manipulated the density and size of shelters for the bluebanded goby by inserting different numbers and sizes of test tubes into foam buoys that were anchored near the seafloor. All of her artificial goby habitats were exposed to predators. She found that habitats providing many shelter holes received higher recruitment than those with few holes did. She attributed enhanced recruitment on habitats with extra holes to the provision of extra shelter from predators. More recently, Hartney (formerly Behrents) and Grorud (2002) examined the importance sea urchins (*Centrostephanus coronatus*) as shelter for bluebanded gobies. Adult gobies are strongly associated with these urchins and field manipulations indicated that the abundance of bluebanded gobies was causally linked to the presence of urchins. Moreover, urchin presence strongly enhanced recruitment and survival of gobies. Hartney and Grorud also used artificial urchin models to mimic the physical structure provided by live urchins, but they found that these models afforded only about half the protection of live urchins. Either the models did not adequately represent the structural complexity of live urchins or other attributes (e.g., behavior) of urchins enhance goby survival. Without concurrently manipulating the presence of predators, however, one cannot be certain that the increased recruitment and survival that Hartney (Behrents) and Grorud found in habitats

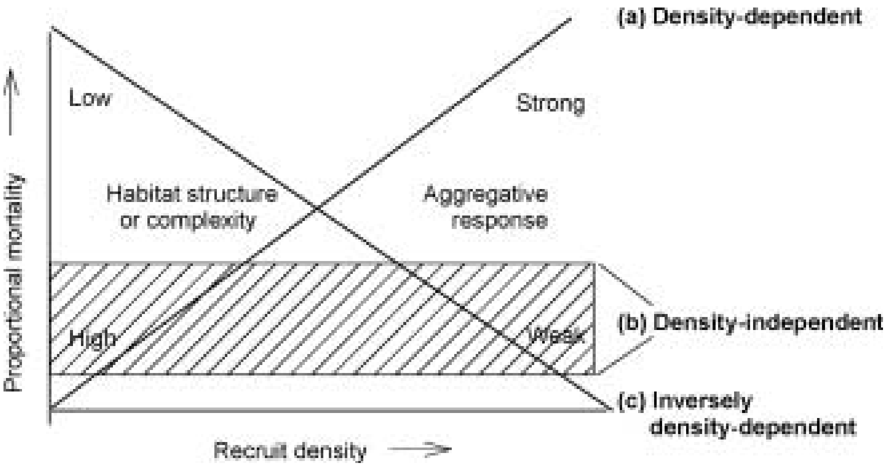


FIGURE 16-10 Conceptual model of differential patterns of mortality for local populations of kelp perch based on the degree of habitat structure (amount of habitat) or structural complexity (habitat attributes) at lower densities of kelp perch and the strength of an aggregative response by kelp bass at higher densities of kelp perch: a) density-dependent mortality with high habitat structure or complexity and a strong aggregative response, b) inverse density-dependent mortality with low habitat structure or complexity and a weak aggregative response, and c) density-independent mortality (hatched region) caused by medium to high levels of habitat structure or complexity and a relatively weak aggregative response (from Anderson 2001 with permission of the Ecological Society of America).

with abundant shelter was caused by predation. The positive effect of shelter could instead be generated by (1) settlement preferences, (2) post-settlement migration to areas with abundant helter, or (3) positive effects of shelter-providing habitat on post-settlement survival that are unrelated to predation (e.g., protection from abiotic disturbances).

To evaluate the hypothesis that abundance-shelter relationships are driven solely by predation, Steele (1999) manipulated both the abundance of shelter (the density of rocks, which provide shelter) and the presence of predators for bluebanded and blackeye gobies to assess effects on abundance via recruitment and survival of these species. In the presence of predators, both species exhibited the expected pattern of enhanced recruitment and survival on artificial reefs with abundant shelter relative to those with sparse shelter. In blackeye gobies, as expected if the shelter-related patterns of recruitment and survival were driven by predation, there was no effect of shelter abundance on recruitment and survival when predators were absent, but there was a positive effect of shelter in presence of predators. In bluebanded gobies, however, even in the absence of predators, recruitment and survival increased with increasing abundance of shelter. This result demonstrated that shelter-related patterns of abundance were not driven solely by predation, although it did play an important role, even for bluebanded gobies, in which exposure to predators exaggerated the effects of shelter abundance. Overall, shelter availability did modify the impact of predation, but Steele suggested that other factors such as settlement preferences or use of purported shelter for purposes other than escaping predation might contribute to the positive relationships between fish abundance and habitat availability.

In his studies on density-dependent predation in kelp perch, Anderson (2001) manipulated both the density of juvenile kelp perch and the biomass of giant kelp, which provided shelter from predatory kelp bass. Large laboratory mesocosms were employed in which the amount of giant kelp was varied across a range of biomass. Anderson found that the pattern of mortality changed from inversely density-dependent (greater proportional mortality at lower densities) under conditions of no or low amounts of kelp, to density-independent at medium and high amounts of kelp. He suggested that the amount of kelp (four adult plants per plot) used in his field experiments caused increased survival at lower densities because there was necessarily greater per capita refuge availability at lower perch densities. Anderson further suggested that the pattern of predator-induced mortality (inversely density-dependent, density-independent, or density-dependent) experienced by kelp perch at varying densities would depend upon the amount of habitat or its structural complexity at low densities of kelp perch and upon the strength of an aggregative response by predators (fig. 16-10).

Community Structure

Predation has been shown to influence community or assemblage structure in a variety of ways (reviewed in Sih et al., 1985; Hixon, 1986), but how it affects the structure of temperate reef fish communities remains virtually unexplored. Perhaps the most influential model of how predators affect community structure is Paine's (1966) keystone predation hypothesis, which was developed from work on intertidal invertebrates. In this model, predation serves to maintain species diversity by disproportionately reducing the density of the competitively dominant prey species, to levels below those that would otherwise lead to competitive exclusion of inferior competitors. Nonselective predators may also help maintain species diversity if their predation causes intermediate levels of disturbance, which keep communities in a nonequilibrial state in which competitive exclusion is not possible. This situation is a special case of the more general intermediate disturbance hypothesis proposed by Connell (1978). Rather than maintain or promote species diversity, predators may cause species diversity to decline if they are 1) opportunistic and do not focus their attention on the dominant competitors (Hixon, 1986; Hixon and Beets, 1989, 1993) or 2) prefer prey species that are poor competitors (Lubchenco, 1978). In case 1, rare species may be lost from communities when they are consumed, leading to lower overall diversity (Hixon, 1991) and this has been found in studies of coral-reef fishes (Hixon and Beets, 1989, 1993; Caley, 1993; Eggleston et al., 1997). It is difficult to predict what sort of effect predators may have on the community diversity of California's reef fishes because the answer will depend on the preferences of the predators and the nature of competitive interactions between prey fishes.

We suspect that predation on marine fishes of California has the same effect on diversity as seen in studies on coral reefs: it will reduce species diversity. In part, this is because piscivorous predators tend to be generalists regardless of whether they are found in temperate or tropical systems, and hence, they are unlikely to disproportionately affect competitively dominant prey species. Moreover, while there are many important exceptions (e.g., Hixon, 1980; Larson, 1980; Schmitt and Holbrook, 1990), the notion of competitive dominants may have little meaning for marine fishes since interspecific competition among prey fish species is generally not strong (reviewed in Jones, 1991). Therefore competition may be unlikely to lead to competitive exclusion, which leaves little potential role for predators as mediators of competition. The notion that predation in California will serve to decrease fish community diversity is supported by the observation that generally the greatest diversity of fishes is found where structural refuge is abundant (Ebeling et al., 1980a, 1980b; Larson and DeMartini, 1984; Bodkin, 1986, 1988; Ebeling and Laur, 1988; Carr, 1989; DeMartini and Roberts, 1990; Holbrook et al., 1990), although exceptions have been found (Stephens et al., 1984;, Patton et al., 1985). Of course, these relationships between structural refuge and fish diversity may not be driven by predation (as noted earlier in this chapter), but it is likely that predation plays some role in generating these patterns and it should be weakest in areas with abundant refuge.

In addition to affecting fish assemblage structure by altering diversity, predators may play an important role in generating predictable patterns of relative abundance and distribution. This role of predators also has been little explored. Recent work on coral-reef-fish assemblages by Almany (2003) has shown that that reefs with predators have predictably different patterns of relative abundance of prey species due to differential susceptibility to predation. Other work in the tropics (e.g., Carr and Hixon, 1995; Webster, 2002) has shown differential risk of predation for different prey species. As mentioned earlier, at Santa Catalina Island, Steele (1996, 1997a, 1998) found that bluebanded and blackeye gobies differed substantially in their risk of predation, with bluebanded gobies suffering greater rates of predation than blackeye gobies. Field and lab studies demonstrated that relative risk of predation varied as a function of habitat type: in sandy areas with sparse rocky cover, bluebanded gobies suffered greater mortality than blackeye gobies, but in areas with abundant rocky cover, blackeye gobies suffered greater predation (Fig. 16-11a). These habitat-related changes in the relative risk of predation may help explain the distributions of the two species in the field: blackeye gobies were most abundant and bluebanded gobies least abundant at the reef-sand interface, where rocky cover was relatively sparse, but the reverse pattern was true in predominantly rocky sections of the reef where there was high cover (Fig. 11b). Presumably, the differences in risk of predation faced by the two species are related to their coloration and behavior. The light, sand-colored blackeye goby moves little and is very cryptic when resting on sand, but when resting on dark-colored rocky background is quite obvious. The brilliantly colored, crimson and electric-blue-striped bluebanded goby, which moves more frequently, is very easily detected where sand is abundant and rocks are sparse, but is more difficult to detect on a dark-colored rock background, where it rapidly retreats to abundant small crevices when predators are near. Because of natural differences in color patterns, morphology, and behaviors of prey species, it is likely that different species will suffer different rates of predation, which are habitat specific. Hence, it is likely that predators play a major role in creating and maintaining the habitat-specific patterns of relative abundance of fish in nature. This role of predators and their other effects on fish community structure are poorly known, especially in temperate systems, and merit greater attention in the future.

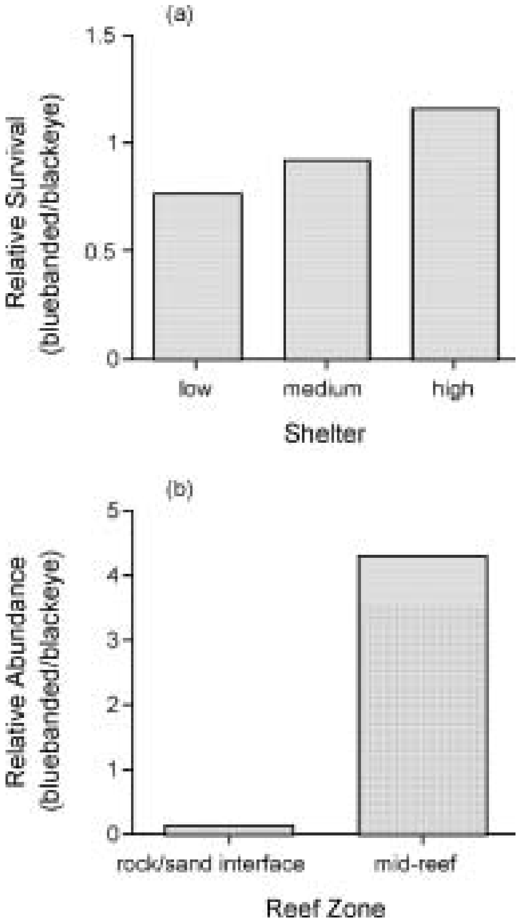


FIGURE 16-11 The potential influence of predation on patterns of distribution of two reef fishes. a) The survival of the bluebanded goby relative to that of the blackeye goby increases as shelter (rock rubble) becomes more abundant. b) Bluebanded gobies are relatively rare at the rock/sand interface of reefs where shelter is sparse, but are abundant relative to blackeye gobies in the mid-reef zone where rocky cover is abundant. Absolute abundance in each zone was divided by the overall mean for each species and then these standardized species abundances were used to calculate the ratio shown. (Unpublished data from Steele.)

Regional and Geographic Comparisons: Generalities in the Effects of Predators?

Given that relatively few studies have explored the ecological effects of predation on marine fishes, it is difficult to determine whether there are generalities to be found. But, overall, regardless of the system, predators seem to play some important role in the local ecology. Although there are cases in nearly every system in which research has failed to detect significant effects of predators for some prey species, there are almost always counter-examples in the same community. Hence, at the community or assemblage level, it seems likely in that in virtually every system predators will have some important impacts.

Although most findings of studies on predation in temperate and tropical systems are similar, one aspect of tropical systems seems likely to cause the effects of predators to differ somewhat from temperate systems. Tropical systems, particularly coral reefs, harbor much more diverse assemblages of fishes than do temperate reefs. This extra diversity generates a greater variety of possible interactions, particularly indirect interactions, mediated through intermediary species. For example, in temperate systems, there tends to be one or a few dominant predator species, e.g., the kelp bass in southern California, whereas in tropical systems there are many more species, e.g., many different species of groupers, snappers, jacks, lizardfish, moray eels, etc. This sets up the possibility of complex interactions among predators, which may be synergistic (Hixon and Carr, 1997), additive, or inhibitory. When they are inhibitory, enhancing the abundance of one predator species may actually enhance survival of the prey species (Steele et al., 1998). Moreover, if the many different species in tropical systems have different responses to prey density (functional, aggregative, developmental, or numerical), then fluctuations in the relative abundance of the different members of the predator assemblage may cause the combined effect of the assemblage to vary substantially over time or in space. Furthermore, greater diversity of prey species in tropical systems than temperate systems may also generate more complexity in the effects of predators and interactions among prey species. For example, Webster and Almany (2002) recently demonstrated an indirectly mutualistic relationship between different prey species on the Great Barrier Reef. A number of species benefited (increased recruitment and survival) from enhanced abundance of one prey taxa, cardinalfishes. The authors argue that cardinalfishes were the preferred prey and, hence, were targeted by predators where abundant, to the extent that other prey species were ignored. In such complex systems, there may be greater opportunities prey switching, which may generate a density-dependent, Type III functional response. Regardless of the potential differences between temperate and tropical systems, the available evidence suggests that predators will play important roles in the ecology of many marine fishes.

Topics for Future Research

Research on the ecological effects of predators on marine fishes is still in its early phases. Consequently, there is a wide variety of topics that beg for study. Here we outline some of the topics that we think are most worthy of attention, but note that just about any field study that explores the effects of predators on some aspect of prey behavior or demography will make a meaningful contribution to the still sparse literature on the effects of predators on marine fishes.

Much of the recent research on predation in marine fishes has focused on whether predation causes density-dependent mortality and, hence, may be capable of causing or contributing to population regulation (Hixon and Carr, 1997; Steele, 1997a; Forrester and Steele, 2000; Anderson, 2001; Holbrook and Schmitt, 2002; Steele and Forrester, 2002b; Webster, 2002; reviewed by Hixon and Webster, 2002). While most of these studies have found that predators can cause density-dependent mortality, two important questions remain: (1) what are the mechanisms that cause density-dependent mortality and (2) does the density-dependence detected actually cause population regulation? Recent studies on coral-reef fishes (Holbrook and Schmitt, 2002; Forrester and Steele, 2004) provide excellent examples of how to discover the mechanisms of density-dependent predation. Gaining this sort of mechanistic understanding will be extremely valuable for predicting whether density-dependent predation will scale up spatially and whether it will cause temporally density-dependent mortality, which is required for population regulation. Studies like Anderson's (2001), which test the responses of predators (functional, aggregative, developmental, and numerical), are also particularly needed. The functional and aggregative responses may play particularly important roles in driving density dependence, but effort should not be focused on them alone. To our knowledge, there has yet to be a test of developmental or numerical responses in marine fishes, which would require long-term study. Because local populations of marine fishes are usually open (i.e., new offspring arrive via planktonic dispersal from other local populations), one of the normal mechanisms that can cause a numerical response is absent in most marine fishes: enhanced fecundity in predator populations that are well fed on dense prey populations will not increase local population density. Nevertheless, the bipartite life cycle of most marine fishes provides the opportunity for a different sort of numerical response: correlated settlement patterns between predators and prey. Given that the pelagic offspring of both prey and predators are exposed to the same oceanographic features, it seems plausible that there may be correlated patterns of settlement, which may cause density-dependent prey mortality via predation. This possibility deserves attention.

Field tests for temporally density-dependent predation are virtually non-existent, yet it is this sort of mortality that is required for population regulation. In this regard, we believe that two sorts of studies are necessary: field experimental manipulations of density at different times and long-term, large-scale monitoring efforts that evaluate whether natural patterns of mortality at spatial scales relevant to population management are density-dependent. Coupling these sorts of studies with explorations of the mechanisms of density-dependent predation would make them particularly valuable. Along these lines, given that most experimental studies, by necessity, are done at small scales, developing methods to extrapolate the findings of these studies to larger scales is a central, unresolved problem in ecology.

The interaction between predation and habitat structure is another area in need of more detailed study. As noted earlier, it is generally not known what role, if any, predation plays in establishing relationships between fish abundance and habitat availability. Factorial studies that manipulate both predators and habitat complexity are necessary to resolve this issue. A mechanistic understanding of how predation is influenced by structural complexity is needed to predict how spatial or temporal variation in habitat structure will influence prey mortality. This level of understanding may be particularly valuable because variation in habitat quality may modify the strength of density-dependent mortality (Forrester and Steele, 2004) and hence the potential for population regulation.

As noted earlier, studies of the nonlethal effects of predators on demographic rates of their prey, especially growth, are rare for marine animals in general and fish in particular. Because of the potential for nonlethal effects on growth to influence other demographic rates, further studies of these phenomena are needed. Beyond simply testing for nonlethal effects, which is valuable in and of itself, studies that evaluate the demographic consequences of nonlethal effects of predators would provide especially important insight into the effects of predators on their prey. To achieve their greatest utility, such studies should be coupled with behavioral studies that seek to understand the causes of nonlethal effects.

Predation is a process that occurs within a matrix of other ecological interactions, yet it is often studied in isolation, in single factor experiments that seek to measure just the effects of predators. While these sorts of studies are valuable and usually logistically more manageable, factorial experiments that manipulate predation along with other potentially important processes (e.g., competition) are particularly useful because they allow the relative importance of different ecological processes to be measured and they can reveal interactions among processes. Good examples of this type of study include Steele, 1997a, 1998, Carr et al., 2002, and Almany, 2003. Such studies must become more common if we hope to understand the role of predation in a broader ecological context.

Community-level effects of predation on marine fishes have seldom been explored. Given the important role of predation in structuring other marine communities (e.g., Paine, 1966; Estes et al., 1998), we view this area as a high priority for future study. Areas in need of study include cascading effects of predators, indirect effects mediated via interaction chains, and effects of predator preference on risk of predation and community composition.

Comparative studies of predation in regions that are species rich (e.g., tropics) and species poor (e.g., temperate zones) would be informative. We have noted some of the reasons to expect differences between such assemblages. Such comparisons would also be valuable in determining whether the very simple systems treated by most mathematical models of predator-prey dynamics, which often have only one predator and one prey species and rarely have more than a few species, offer insight into more complex fish communities. Are tightly linked predator-prey dynamics likely, or even possible? Are different species of prey and predators functionally equivalent so that different species can be pooled in models? Are prey regulated at the assemblage-level rather than the species level?

Size-selective predation is widely expected in fishes but little tested in the field (Sogard, 1997). Consequently its importance in the population dynamics of marine fishes is poorly understood. Most studies on this topic have been made in the lab, which may be too unrealistic an environment to extrapolate results to the field, or inferred from observational studies in the field which suffer from some serious problems that detract from their utility (Sogard, 1997). Many of the arguments for the importance of factors that influence fish growth hinge on there being significant size-dependent mortality (often viewed as being caused by predators). Currently, we know little about size-dependent patterns of mortality in nature, so such arguments are hollow. We hope to see more field studies of size-dependent predation, especially because they are not technically very challenging.

Recently, there has been considerable interest in the effects of condition (e.g., size, energy reserves) on risk of mortality in marine organisms (e.g., Booth and Hixon, 1999; Searcy and Sponaugle, 2001; Phillips, 2002). The goal of much of this work has been to link larval condition to post-settlement performance, but post-settlement condition should also affect demographic rates. In the context of predation, what especially needs to be determined is whether the relatively subtle differences in condition found in nature translate to measurable variation in risk of predation.

Last, as any reader of this chapter will notice, work on predation in California's marine fishes has mostly been done at Santa Catalina Island. If we hope to have any sense of the general importance of predation to the ecology of the marine fishes of California, studies must be made in other places. We hope this chapter helps to motivate work on predation in the less benign but more widespread subtidal habitats of California.

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