Size-dependent predation on the salt-marsh snail *Cerithidea californica* Haldeman

Wayne P. Sousa

Department of Integrative Biology, University of California at Berkeley, Berkeley, California, USA

Abstract: Predation by crabs and shorebirds on the salt-marsh snail *Cerithidea californica* Haldeman was investigated with laboratory feeding experiments, a field mark–recapture study, and by examining shorebird regurgitation pellets. In Bolinas Lagoon, the field site of the study, the primary predators of *Cerithidea* are the grapsid crab *Pachygrapsus crassipes* Rathbun and the willet *Catoptrophorus semipalmatus* Gmelin. In the laboratory, male *Pachygrapsus* of three different size classes were offered snails of six different shell lengths. The average and maximum sizes of consumed snails increased and the proportion of snails in the smallest size class that were eaten declined, with increasing crab size. In a separate comparison of male and female crabs, males ate larger snails on average than did females of equal size. Shell sculpture in the form of varices appeared to reduce the rate of successful attack by crabs, but crabs circumvented this defense in several ways.

Rates of predation by a natural population of *Pachygrapsus* on marked and released *Cerithidea* were measured over a 10-wk period in summer. The local crab population consumed marked snails of a wide range of sizes. Larger snails suffered lower rates of predation, however, there was no evidence of an absolutely invulnerable snail size. There was no difference in the rates of predation on snails that were parasitized by larval trematodes and those that were uninfected. Rates of predation on marked snails varied widely, and in a density-independent manner, among the 10 snail subpopulations into which they had been released. The density of crabs living in the immediate vicinity of a snail subpopulation was the best predictor of local variation in predation rates.

The sizes of *Cerithidea* preyed upon by willets were determined by measuring shells in willet regurgitation pellets. This shorebird consumes much smaller snails on average than does the local crab population. Considering the broad diet of willets and experimental results of others, it appears that predation by shorebirds can sometimes depress the density of small *Cerithidea*, but its impact is highly variable in space and time and apparently density-independent. Living snails were found in several willet regurgitation pellets, suggesting that transport in the crop/gizzard of a bird is a potential mechanism of *Cerithidea* dispersal within and among coastal lagoons.

Key words: Horn snail; Larval trematode; Lined shore crab; Salt marsh; Size-dependent predation; Willet

INTRODUCTION

Size-dependent predation strongly influences the structure and dynamics of a wide variety of natural populations and communities (e.g., Brooks & Dodson, 1965; Dayton, 1971; Sprules, 1972; Connell, 1975; Murdoch & Oaten, 1975; Hall et al., 1976;

Correspondence address: W.P. Sousa, Department of Integrative Biology, University of California at Berkeley, Berkeley, CA 94720, USA.

Paine, 1976; Porter, 1977; Zaret, 1980; Lubchenco & Gaines, 1981; Brown et al., 1986; Wootton, 1992). In many cases, large size (sometimes achieved by the presence of spines, shields, or other elaborations of the exoskeleton) or morphological correlates of large size (e.g., thicker exoskeletons) afford the prey a refuge from predation. This refuge may be one of absolute invulnerability due to mechanical limitations of the predator, but often it is relative in nature: a predator may be capable of consuming larger prey individuals than it does, but elects not to do so because the energy intake per unit time spent handling such prey is lower than for smaller prey individuals (Elner & Hughes, 1978; Hughes, 1980; Pyke, 1984). In such cases, larger prey individuals would experience a relatively lower risk of predation than smaller ones. This relationship could be reversed if the largest prey individuals prove to be the most profitable in terms of yield per handling time.

In nature, an individual prey's risk of being eaten will also depend on the size-structure of the predator population, since larger predators can handle and consume larger prey (e.g. Elner & Hughes, 1978; Griffiths & Seiderer, 1980; Seed, 1980; Hughes & Seed, 1981; Arnold, 1984; Boulding, 1984; Lawton & Hughes, 1985; Palmer, 1985, 1990; Sanchez-Salazar et al., 1987; Robles et al., 1990). As a number of these studies have demonstrated, the size of prey that is most energetically profitable to feed on increases with the size of the predator (Hughes, 1980). In addition, rates of predation on smaller prey individuals may decline with increasing predator size because large predators lack the mechanical dexterity to handle small prey efficiently.

A predator's mode of feeding may also influence the sizes of prey that it can successfully consume. Vermeij (1978), generalizing from studies of predation on shelled marine gastropods, suggested that species of predators that extract the soft parts of the prey externally and do not ingest the hard parts (e.g., all crustaceans, most molluscs, sharks, rays, some fishes, sea turtles, sea otters, and some birds) are less constrained by large prey size than are species that consume prey relatively whole including the hard parts (e.g., some fishes, most shorebirds, and ducks). Notable exceptions include predators such as sea anemones and some starfish whose unique modes of feeding allow them to ingest quite large prey whole.

This study investigated patterns and rates of predation by crabs and shorebirds on the salt-marsh mesogastropod *Cerithidea californica* Haldeman in a coastal lagoon in northern California, USA. It addressed the following questions: (1) How do the relative sizes of predator and prey, and the sex of the predator, affect rates of predation by crabs on *Cerithidea*?; (2) Does shell sculpture, in the form of a thickened aperture lip or varix, deter crab predation?; (3) What is the impact of predation by crabs on *Cerithidea* populations in nature?; and (4) Do crabs, which extract the soft parts of snails externally, take larger individuals than shorebirds, which consume snails whole?

Study Organisms

PREY

C. californica is the only large native salt-marsh gastropod in California. Details of its distribution and life history are presented elsewhere (see references in Sousa, 1983). *Cerithidea* can grow to a maximum shell length of ≈45 mm, but the largest size found in any given population varies considerably (Race, 1981; W. P. Sousa, pers. obs.). Its shell has a tall spire, low but well-defined axial ribs, and faint spiral ribs. Shells > ≈20 mm often possess one to several thickened varices, which do not reflect annual growth increments (McCloy, 1979; W. P. Sousa, pers. obs.). *Cerithidea* is slow-moving and exhibits no obvious escape behaviors other than retracting far into its shell, usually past the most recently formed varix, if one is present. Healthy snails burrow beneath the surface of the mud during late fall and winter months in all locations with the exception of San Francisco Bay (Race, 1981), and may thereby reduce the risk of predation by dense populations of migratory shorebirds, as well as the harmful effects of winter weather. Crab predators are largely inactive during winter months (Quammen, 1980; W. P. Sousa, pers. obs.), so it is unlikely that the seasonal burrowing behavior of snails has evolved as a defense against their attacks.

PREDATORS

The grapsid crab *Pachygrapsus crassipes* Randall is probably the only significant crustacean predator on postjuvenile *Cerithidea* in Bolinas Lagoon, the site of this study. It is a medium-sized crab, males reaching ≈43 mm and females ≈37 mm carapace width in the study area. *Pachygrapsus* lives in a wide variety of hard-substratum and soft-sediment intertidal habitats. It is distributed along the Pacific coast of North America, from Charleston, Oregon to central Baja California, Mexico, including the Gulf of California (Morris et al., 1980). In salt marshes, it occupies burrows along the banks of channels or under a canopy of halophytes, most commonly *Salicornia virginica* L. or *Spartina foliosa* Trinius.

Pachygrapsus has a diverse diet. On rocky shores, it appears to be primarily herbivorous, feeding on diatoms and green algae (Hiatt, 1948; Sousa, 1979; Robles & Cubit, 1981; Robles, 1982), however, dead animal matter and living limpets, coiled gastropods, hermit crabs, isopods, sea urchins, and even dipterans are occasionally taken (Morris et al., 1980; Lindberg, 1985). In salt marshes, as on exposed shores, *Pachygrapsus* feeds on diatoms and green algae (Hiatt, 1948; Quammen, 1980; W. P. Sousa, pers. obs.), but also consumes oligochaete and polychaete worms (Quammen, 1980), crustaceans (Willason, 1981; W. P. Sousa, pers. obs.), dead animal matter, especially fish (Quammen, 1980), and *Cerithidea* (McCloy, 1979; this study). Undoubtedly, this list of food items is not exhaustive.

Pachygrapsus exhibits marked sexual dimorphism, both in carapace dimensions,

females being on average narrower and shorter than males (Hiatt, 1948), and more importantly for this study, in cheliped size. The chelae of an individual crab are monomorphic (i.e., approximately equal in size and shape), but the chelae of male crabs are larger, heavier, have a greater mechanical advantage (Warner & Jones, 1976; Vermeij, 1977; Elner, 1978), and exert a greater crushing force than chelae of female crabs of equal carapace width (Lee. 1981; also see Brown et al., 1979). In either sex, the larger the crab, the greater the crushing force it can exert (also see Boulding, 1984).

Hemigrapsus oregonensis Dana is another common grapsid crab of west coast salt marshes. It is considerably smaller than *Pachygrapsus*, reaching a maximum carapace width of ≈ 25 mm in the study area. In preliminary laboratory feeding trials, in which *Cerithidea* ranging from 3 to 30 mm in length were offered, *Hemigrapsus* consumed only snails ≤ 5 mm in length (W. P. Sousa, unpubl. data). The main food of *Hemigrapsus* appears to be diatoms and green algae (Morris et al., 1980). It is probably not a significant predator on postjuvenile *Cerithidea* in nature.

The willet *Catoptrophorus semipalmatus* Gmelin was the only species whose diet was found to include *Cerithidea* in a study of the feeding biology of eight common shorebirds of Bolinas Lagoon conducted between June 1973 and February 1974 by the Point Reyes Bird Observatory. ≈ 20% of the 74 willet regurgitation pellets included in the published analyses contained *Cerithidea* (Page & Stenzel, 1975; Stenzel et al., 1976). The snail was absent from dietary samples of black-bellied plover, short-billed dowitcher, dunlin, long-billed curlew, marbled godwit, western sandpipers, and least sandpipers. Quammen (1980) studied the food habits of dowitchers, dunlin, avocets, and western sandpipers on mud/sand flats in Mugu Lagoon and Upper Newport Bay. *Cerithidea* is common at both of these southern California sites, particularly in muddier areas (MacDonald, 1969a,b; Onuf, 1987). No *Cerithidea* were found in the stomachs or fecal samples of dowitchers, dunlin, or avocets. Snails were found in the stomach of one out of 14 western sandpipers from Mugu Lagoon, and in two out of 12 stomachs of the same species from Upper Newport Bay. As noted above, none of the 73 dietary samples collected by Page & Stenzel (1975) from western sandpipers in Bolinas Lagoon contained *Cerithidea*. Thus, present data strongly indicate that the willet is the primary avian predator of *Cerithidea*.

Like the crabs that prey on *Cerithidea*, the willet is a generalist predator. It feeds on a variety of gastropods, pelecypods, polychaetes, dipterans, and crustaceans (Page & Stenzel, 1975; Stenzel et al., 1976; Quammen, 1980). Willets feed both on exposed shores and on protected mud flats and salt marshes.

Detailed analyses of the stomach contents of estuarine bony and elasmobranch fishes at several sites in California indicate that such fishes rarely, if ever, feed on *Cerithidea* Adams (1970) found no gastropods in the stomachs of five species of bony tide flat fishes in Bolinas Lagoon. Only a small number of opisthobranchs (*Acteocina* spp. Gould and *Bulla gouldiana* Pilsbry) were found in two of seven bony fish species examined from Mugu Lagoon (Quammen, 1980; Onuf, 1987). No snails were found in the guts of shovelnose guitarfish, the most abundant elasmobranch at the latter site

(Onuf, 1987). Dense populations of *Cerithidea* inhabit the upper tidal flats and salt marshes at both these sites. No gastropods were found in stomachs of four common species of elasmobranch fishes collected from Elkhorn Slough (Talent, 1982) or of bat rays from Tomales Bay (Karl & Obrebski, 1976), even though the introduced potamid snail *Batillaria attramentaria* Sowerby is abundant on mud flats in both these estuaries (W. P. Sousa, pers. obs.). *Batillaria* is very similar in size, morphology, and microhabitat use to *Cerithidea*. In sum, fishes do not appear to be significant predators on *Cerithidea*, and consequently were not considered in this study.

STUDY SITES

Snails and crabs used in laboratory studies of crab predation were collected from populations at the Pine Gulch Creek study site (Sousa, 1983; hereafter PGC) in Bolinas Lagoon, located ≈ 24 km northwest of San Francisco, California. At this site, snails are distributed as a series of subpopulations occupying shallow (5–15 cm deep) depressions (hereafter called pans) in the surface of the mud flat that hold standing water at low tide. The inhabited pans range in size from slightly < 1 to 20 m^2, and are located along the lower margin of the *Spartina/Salicornia*-dominated marsh. Snails rarely, if ever, move from one pan to another at this site (W. P. Sousa, unpubl. data). Mark–recapture studies of snail growth and survival were conducted in a number of these pans (Sousa, 1983). Willet regurgitation pellets were collected from several sites within Bolinas Lagoon (see Methods for details).

METHODS

LABORATORY STUDIES OF CRAB PREDATION

16 crabs (13 males and three females) ranging in size from 21 to 38 mm in carapace width (hereafter c.w.) were collected on 30 October 1980 from burrows at the Pine Gulch Creek study site. They were held individually overnight in covered plastic boxes (length × width × height: $30 \times 16 \times 9$ cm) containing ≈ 1 cm of seawater. The next day, 60 *Cerithidea*, 10 each of six different shell lengths (5, 10, 15, 20, 25, and 30 ± 1 mm), were introduced into each box. The snails were not screened for the presence of larval trematode parasites (as was done in the field study described below).

Crabs were allowed to feed on the original allotment of 60 snails without replacement for 22 days. On Days 1 (1 November), 3, 5, 12, and 22, the numbers of snails in each size class that had been eaten since the last observation date were tallied. In addition, broken shells and shell fragments were collected from each box and examined to determine the manner in which the soft parts had been extracted. The experiments were run at room temperature (21 °C) with natural lighting from a south-facing

window. The water in all boxes was replaced with freshly aerated seawater every other day.

A 10-wk mark–recapture study of snail growth at the Pine Gulch Creek study site during the summer of 1981 (Sousa, 1983) also yielded data on the intensity and patterns of crab predation. ≈ 100 snails ranging from 10 to 37 mm in length were collected from each of 10 subpopulations during the last week of June. The snails were screened in the laboratory for the presence of mature infections of redial or sporocyst trematode larvae by inducing cercarial larvae to shed (see Sousa, 1983, for details). Immature infections of rediae or sporocysts that do not release cercariae are not detectable by this technique (Curtis & Hubbard, 1990; W. P. Sousa, unpubl. data), nor are infections by metacercarial stages. Each snail was individually marked and measured (length to the nearest 0.05 mm), and then returned to its respective pan on 19 July. The tagged sample in each pan at the start of the study was composed of 20% 10–16 mm, 40% 16.05–23 mm, and 40% > 23-mm snails. Each snail was marked with a numbered, color-coded floating tag, attached to the shell by a short length of monofilament. See Sousa (1983) for details of methods.

As a means of assessing the impact of crab predators on gastropod populations, this marking technique has two major advantages over the more common approach of placing a mark directly on a snail's shell. First, because the tag floats, it is more visible to the investigator than is a mark on the shell, which usually becomes overgrown by algae or covered with sediment as the snail crawls. Consequently, the rates of recovery of marked individuals were relatively high in this study, averaging 66.4%. Secondly, a tag affixed by a clear strand of monofilament does not alter the appearance of the snail to nearly the same degree as does a mark made directly on the shell. Therefore, a visual predator is less likely to be differentially attracted to, or repelled by, a snail marked with a floating tag. The marked snails in this study were readily attacked and consumed by crabs.

On the other hand, one artifact attendant to the use of floating tags is that they often become entangled with algal mats and salt marsh plants, thereby restricting the movements of marked snails to varying degrees. Since *Cerithidea* is very slow-moving relative to *Pachygrapsus*, and exhibits no obvious escape behavior other than to retract into its shell, this artifact probably does not substantially increase a snail's vulnerability to attack. Tagged snails fed normally, and those that were not preyed upon showed good growth over the 10-wk-period (Sousa, 1983), despite any restriction in movement that may have occurred.

Several times during the 10 wk of the study, the pans into which marked snails had been released were carefully searched for tags that remained attached to the shells of dead snails or shell fragments. Rates of predation reported herein were calculated as the number of tagged, empty, crab-damaged shells and shell fragments found during

these searches divided by the total number of tagged snails (living and dead) that were recovered. Often, the only portion of the shell remaining was several shards of shell stuck to a piece of dried glue at the end of the monofilament line. Such tags were sometimes found tangled in the *Salicornia* at the edges of pans. Undoubtedly, some were carried away at high tide, so the rates of predation reported herein are underestimates. This conclusion is further supported by the fact that pans with the highest estimated rates of predation had the lowest tag recovery rates ($r = -0.65$, $p = 0.04$, $n = 10$).

As noted above, *Pachygrapsus* is the only known crushing predator of > 5 mm-long *Cerithidea* in the study marshes. Since the shells of consumed, marked snails were damaged in identical ways to snails eaten in the laboratory feeding trials, I attribute all field mortality of marked snails involving shell breakage to *Pachygrapsus*.

The mean density of snails living in each of the pans into which marked snails were released was estimated with replicated 225-cm^2 scoop cores taken in August 1981, as described in Sousa (1990).

PREY SELECTION BY WILLETS IN THE FIELD

To determine the size classes of *Cerithidea* that are selected as prey by willets, I measured the dimensions of shells recovered from pellets that the birds regurgitate as they forage or roost in the marsh. Willets swallow molluscs and small crustaceans such as amphipods whole, while larger decapod crustaceans are often shaken apart, the appendages either eaten before the carapace, or not at all (Stenzel et al., 1976; W. P. Sousa, pers. obs.). Digestion is accomplished by grinding the hard-shelled prey items against one another (sometimes aided by the presence of sand) in the muscular gizzard. Periodically, a bolus of shells, shell fragments, and carapace parts are regurgitated. These regurgitation pellets provide a record of recent feeding activity on hard-bodied prey. The pellets examined in this study came from two sources. L. Stenzel, Point Reyes Bird Observatory, kindly allowed me to examine all 126 willet regurgitation pellets collected throughout Bolinas Lagoon during the course of the observatory's 1973–74 study of shorebird diets described earlier (Page & Stenzel, 1975; Stenzel et al., 1976). 19 of these pellets (15.1%), collected between 7 August 1973 and 26 Jan 1974, contained *Cerithidea* shells or fragments thereof. All pellets were collected fresh from roost sites immediately after flocks of willets had been flushed away by observers, so we can be confident that they were correctly identified as being produced by this particular shorebird.

Additional pellets containing *Cerithidea* were collected from the Bolinas Lagoon mud flat on four dates: four pellets on 6 April 1980, one pellet on 7 November 1981, three pellets on 21 September 1985, and one pellet on 18 October 1986. In all cases, the pellets had been deposited since the last high tide and in areas where I had seen flocks of willets foraging and roosting just prior to collecting them; on the April date, several willets flushed from the site of collection as I approached.

Not all the shells found in regurgitation pellets are complete enough to provide an accurate, direct measurement of shell length. Usually, the apex and varying amounts of the lip have been broken off as the shells are ground together in the bird's gizzard. In many cases, however, the ultimate whorl is sufficiently undamaged to allow an accurate measurement of its diameter. From this measurement, I was able to estimate shell length from the following regression equation of shell length on width from intact, living animals: log shell length (apex to aperture lip) = 1.25 log maximum shell width + 0.22 ($n = 854$, $r = 0.97$, $p < 0.001$). There did not appear to be an obvious bias in the sizes of measurable, intact snails within a pellet.

RESULTS

LABORATORY STUDIES OF CRAB PREDATION

The pooled cumulative percents of snails of different size consumed over the 22-day period by the three size classes of male crabs are plotted in Fig. 1. Not all size-classes of snails were eaten by all three sizes of crabs, so variances in predation rates were structurally heteroscedastic among the cells of the design. Therefore, the experiment could not be analysed as a replicated factorial ANOVA. Instead, I analysed the cumulative counts pooled over replicate crabs for the final sampling date (Day 22) as a multidimensional contingency table (Fienberg, 1970). The three factors were crab size (three levels), snail size (six levels), and survival (killed vs. not killed).

Rates of predation were strongly affected by the interactive influences of crab and snail size (G statistic associated with deletion of the three-way interaction, crab size × snail size × survival, from the full model = 184.68, df = 10, $p < 0.001$). This interaction is clearly visible in Fig. 1. Small crabs only consumed snails ≤ 15 mm, exhibiting a strong initial preference for 5-mm snails, and adding progressively larger snails to the diet as the supply of 5-mm individuals was depleted. All snails consumed by medium-sized crabs were ≤ 20 mm, with the exception of a single 30-mm individual consumed between Days 12 and 22. In contrast to small crabs, medium crabs ate a higher proportion of 10-mm than 5-mm snails. Medium crabs consumed more than twice as many 15-mm snails as small crabs, and $> 20\%$ of the 20-mm snails, a size class that appears to be invulnerable to small crabs. Large crabs consumed all six size classes of snails, but only a few in the 5-mm and 30-mm classes. They preyed most heavily, and with about equal frequency, on 10-, 15-, and 20-mm snails. They also took a substantial number of 25-mm snails, a size class eaten by neither of the two smaller size classes of male crabs. In summary, the average and maximum sizes of consumed snails increased with crab size. In contrast, the proportion of snails in the smallest size class that were eaten declined with increasing crab size. Probably owing to their proportionately larger, more powerful chelae, male crabs consumed larger snails on average than female crabs of equal c.w. width (Table I).
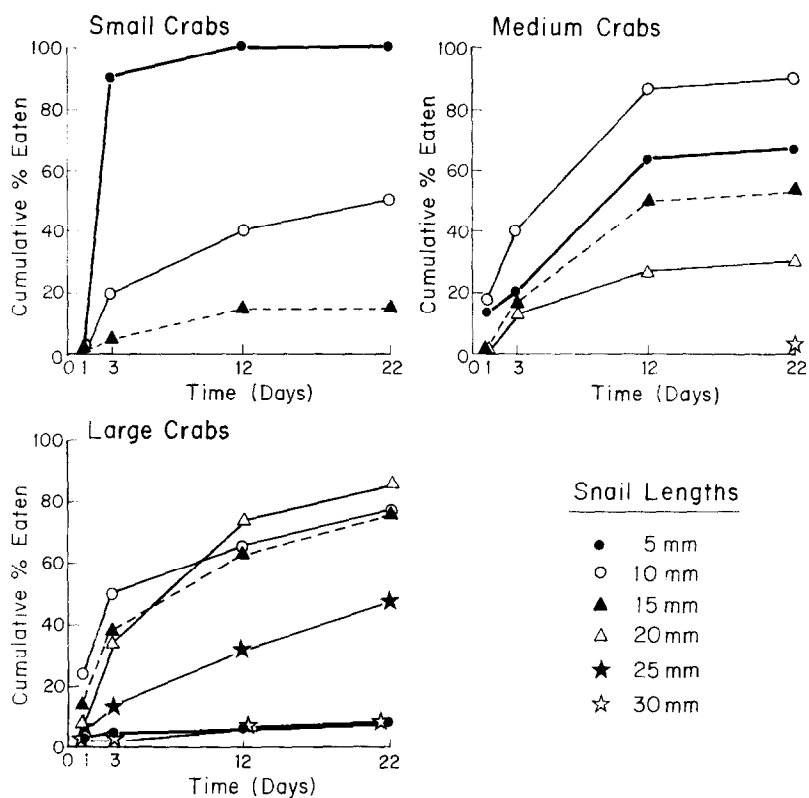
Fig. 1. Mean cumulative percentages of six length classes of *C. californica* consumed by male *P. crassipes* of different c.w. values over a 22-day period in the laboratory. 10 snails of each length class were offered on Day 0 to each of two small (21–27 mm c.w.), three medium (32–33 mm c.w.), and five large (36–38 mm c.w.) crabs.

TABLE I

Cumulative numbers of snails of different lengths consumed over a 22-day period by female and male crabs of the same c.w.

Trial	Crab c.w. (mm)	Crab sex	Snail length (mm)						G^*	df	p
			5	10	15	20	25	30			
1	27	♀	10	2	0	0	0	0	3.8	1	0.051
		♂	10	8	2	0	0	0			
2	33	♀	10	7	1	0	0	0	7.3	2	0.026
		♂	9	10	9	2	0	0			
3	37	♀	5	8	3	3	0	0	20.5	4	<0.001
		♂	0	4	7	7	6	1			

* Where necessary, adjacent size classes were pooled to insure expected values ≥ 1.

FIELD STUDY OF CRAB PREDATION

Natural crab populations consumed a wide size range of the marked–released snails, including several individuals > 30 mm in length (Fig. 2). The mean length of consumed snails ($\bar{x} = 21.0$, SD $= 6.1$) was slightly, but significantly ($t = 2.2$, df $= 1$, $p = 0.028$), smaller than that of snails that were not preyed upon ($\bar{x} = 22.5$, SD $= 5.7$), suggesting that larger snails in the released sample were at slightly lower risk of predation than smaller snails. This trend, albeit variable, is evident in the plot of percent eaten vs. snail length in Fig. 2.

Parasitism by larval trematodes (i.e., rediae or sporocysts) had no apparent effect on a snail's risk of predation by crabs. Snails that were shedding cercariae at the time of release ($n = 169$) suffered 13.0% mortality from crab attacks, while 13.9% of non-shedding snails ($n = 439$) were killed by crabs ($G = 0.08$, $p = 0.774$). Since some non-shedding snails carried immature larval parasites at the time of release and others could have acquired infections in the field, I also compared the proportions of infected and uninfected snails that suffered crab predation, using the infection rate in surviving non-shedding snails as an estimate of the prevalence of infection in non-shedding snails that had been consumed by crabs. When rates of parasitism were estimated in this manner, 13.5% of infected snails ($n = 303$) were eaten by crabs as compared to 13.8% of uninfected snails ($n = 305$). Again, there was no evidence that the risk of predation by crabs is different for infected vs. uninfected snails ($G = 0.01$, $p = 0.932$).

Rates of predation varied significantly among the pans into which marked snails were released (Fig. 3; $G = 79.69$, $p < 0.001$), ranging from 1.6 to 55.1% (total number of snails, living and dead, recovered per pan ranged from 44 to 87). These rates were not
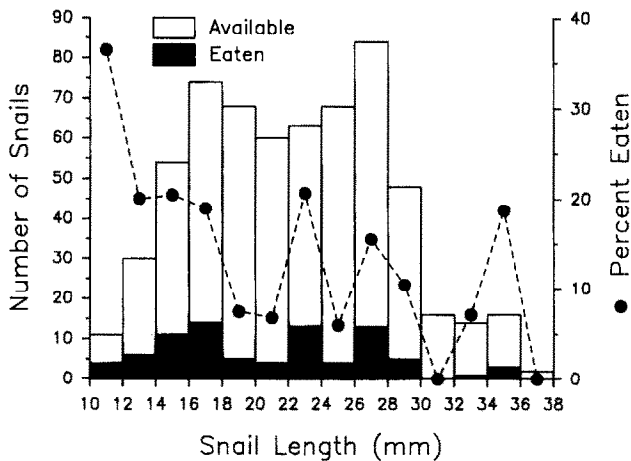

Fig. 2. Numbers and percentages of *C. californica* of different lengths eaten by *P. crassipes* during the 10-wk mark–recapture study of snail growth and survival. Data are pooled over the 10 snail subpopulations into which marked snails were released.
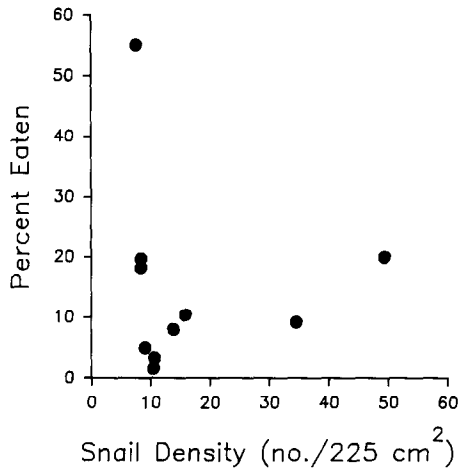
Fig. 3. Percentage of marked *C. californica* eaten by *P. crassipes* during the 10-wk mark–recapture study plotted against snail density for each of the 10 snail subpopulations into which marked snails were released.

correlated with the density of snails living in the pan during the period of release (with proportion killed arcsine-transformed and density log-transformed, $r = -0.11$, $p = 0.769$, $n = 10$). Instead, the local density of *Pachygrapsus* appeared to better explain variation in predation rates among snail subpopulations than did snail density. It was not possible to determine crab density directly without destroying the habitat, but the four pans with the highest predation rates had the highest densities of active, large crab burrows within 1 m of their edges (W. P. Sousa, unpubl. data). This variation in the density of crab burrows probably reflects some difference in the suitability of the local environment or sediment for the construction or maintenance of burrows.

METHODS OF CRAB ATTACK

In both the laboratory and field, crabs employed several means of extracting snails from their shells. Predation on snails < 10 mm was only examined in the laboratory trials. All 5-mm snails killed by crabs were crushed, most frequently at the aperture end of the shell. In the lab and field, crabs attacked snails > 10 mm mainly by peeling the shell back from the aperture. Such attacks were not always successful. Sometimes the crab simply ceased its attack, presumably to search for easier prey. In other cases, particularly with snails > 20 mm, peeling was stopped by the presence of a thickened aperture lip or by a varix farther back on the shell. While such structural features appeared to reduce the chance of successful attack, they did not provide absolute protection. Large snails possessing one or both of these features still suffered moderate rates of predation because medium to large crabs circumvented these defenses in two ways. Most commonly, the crab simply cut the shell in two by holding it perpendicular to the long axis of the chela and applying pressure to a suture line between
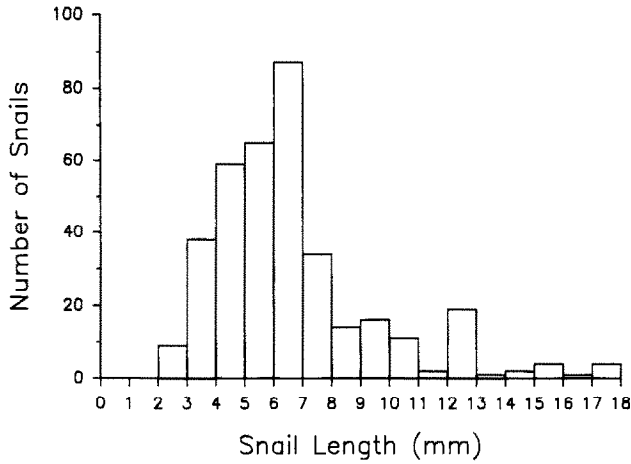
Fig. 4. Length distribution of 366 measurable *C. californica* shells found in willet regurgitation pellets.

adjacent whorls. Snails as large as 30 mm were killed in this manner. Alternatively, crabs would break a hole in a whorl behind the thickened shell lip or varix and continue peeling from that point until the snail could be extracted. This method was effective against snails as large as 36 mm, particularly if the shell was eroded or partially dissolved by exposure to acidic sediments (W. P. Sousa, pers. obs.).

FIELD STUDY OF WILLET PREDATION

Willets consume considerably smaller snails on average than do crabs (Fig. 4). The largest shell found in a regurgitation pellet was 17 mm, but the median length of snails
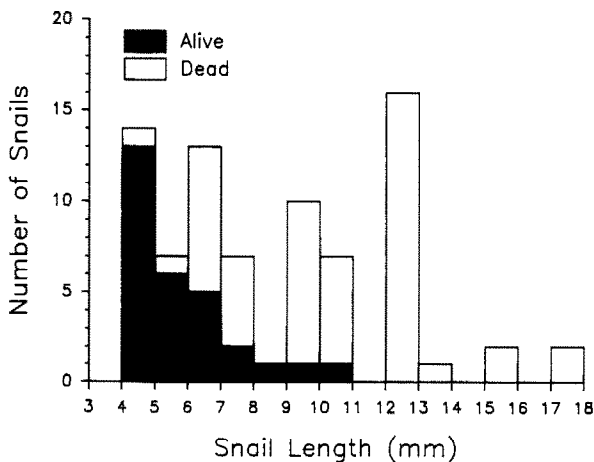

Fig. 5. Length distributions of living and dead *C. californica* found in four willet regurgitation pellets collected on 6 April 1980.

in each of the 25 pellets that contained measurable *Cerithidea* was much smaller, ranging from 4 to 7 mm.

Surprisingly, a number of living snails were found in the four pellets collected in April 1980. When the pellets were returned to the laboratory and placed in dishes of seawater, a total of 29 snails (36.2% of the 80 measurable snails in the pellets) emerged from their shells and began to actively crawl about. The average length of these surviving snails was considerably smaller than that of the dead snails in the pellets (Fig. 5). Due to their small size, they apparently remained in the interstices between the larger shells in the bolus and were not crushed as the larger shells were ground against each other; the opercula of the small snails were sealed tightly enough to exclude harmful gastric juice.

DISCUSSION

These studies clearly demonstrate that the risk of predation faced by an individual *Cerithidea* depends not only on its size, but on the size, sex, and species of predator that attacks it. As noted in the introduction, a number of other laboratory studies have demonstrated similar size-related patterns of predation on marine gastropod and pelecypod prey by crabs and lobsters. Generally, the minimum, average and maximum sizes of prey individuals that a predator consumes increase with the predator's size (Hughes, 1980). All three of these patterns were observed in the laboratory study of *Pachygrapsus* predation on *Cerithidea*. In the same studies, male *Pachygrapsus* consumed larger snails than did female crabs of equal c.w., as Elner (1980) found for male and female *Carcinus maenas* L. feeding on mussels. In both crab species, males have proportionately larger, more powerful chelae than females. Exceptions to these size- and sex-related predation rates include crabs that have not fully regenerated previously autotomized chelae. As a result, such individuals have proportionately smaller, weaker chelae and are less efficient at opening (or are unable to open) large prey as compared to crabs that have not suffered the loss of a chela (Elner, 1980). Broken or worn chelae can similarly compromise a crab's ability to handle prey (Juanes & Hartwick, 1990).

The population of *Pachygrapsus* at the Pine Gulch Creek site consumed marked snails of a wide range of sizes. Larger snails were at slightly lower risk, but there was no evidence of what could be called an absolutely invulnerable size class. Unfortunately, it was not possible to determine, without extensive excavation, the size structure of the crab population surrounding the pans into which the snails were released. Such a procedure would have destroyed the marsh and negatively impacted the subpopulations of snails that were the subjects of a long-term demographic study (Sousa, 1990).

Whether or not a snail was host to trematode rediae or sporocysts did not affect its risk of predation by crabs. This is not particularly surprising since *Cerithidea* exhibits no obvious escape or defensive behaviors other than to retract into its shell. Host behavioral modifications by parasites have been shown to increase rates of predation

in a number of other systems (Holmes & Bethel, 1972; Moore, 1983, 1984; Sousa & Grosholz, 1991). In some instances, predation by a definitive host species on an infected intermediate host comprises the mechanism of transmission in the complex life cycles of helminth parasites. Specific modifications of intermediate host behavior by the larval parasite can render that host more vulnerable to predators and thereby increase the rate of transmission. However, this scenario does not apply to the crab–snail interaction, because birds, not crabs, are the definitive hosts for the trematodes that infect *Cerithidea*. No transmission occurs when the redial and sporocyst larvae that infect the snail are consumed by a crab; these parasite stages are simply digested.

Mortality due to *Pachygrapsus* predation was spatially density-independent; variation in rates of predation among snail subpopulations was positively correlated with the local abundance of crabs, as estimated by the density of active burrows. In contrast, Boulding & Hay (1984) found that the rate of predation on marked, experimentally planted clams (*Protothaca staminea* Conrad) by three species of cancrid crabs (*Cancer productus* Randall, *C. gracilis* Dana, and *C. magister* Dana), increased with clam density. While it is premature to generalize from one field study each of predation rates by these two crabs, there are at least two fundamental differences in the biology of *Pachygrapsus* and *Cancer* that may explain why the former species did not cause density-dependent mortality of its mollusc prey while the latter species did. First, as an omnivore with a very diverse diet, *Pachygrapsus*, may have little reason to search out or spend disproportionate time feeding in habitat patches that support denser subpopulations of *Cerithidea*. On the other hand, *Cancer* spp. are carnivores that feed heavily on clams, and are therefore more likely to seek out dense patches of clams and spend more time feeding in them (Boulding & Hay, 1984). Secondly, *Cancer* crabs forage over relatively large areas of the low intertidal and subtidal, often moving > 50 m in a day (Boulding & Hay, 1984). Although no direct measurements of *Pachygrapsus* foraging movements have been made, the finding that crab predation rates on *Cerithidea* were highest in pans that were immediately surrounded by dense concentrations of burrows suggests that foraging crabs do not move far from protective cover. Similarly, in Goleta Slough near Santa Barbara, California, McCloy (1979) found that *Pachygrapsus* exerted heavy predation pressure on *Cerithidea* populations only in an area adjacent to a stretch of riprap that had been deposited along the banks of a marsh creek. This area supported the highest densities of *Pachygrapsus*. Since *Pachygrapsus* forages in the upper intertidal, and not uncommonly in the daytime, it is at considerable risk of predation by shorebirds (Stenzel et al., 1976; W. P. Sousa, pers. obs.). When encountered in the open, *Pachygrapsus* rapidly retreat to the nearest available shelter. With this restriction on the distance over which individual crabs can safely forage, *Pachygrapsus* is unlikely to cause density-dependent mortality among the snail populations of upper intertidal pans.

Shell sculpture in the form of varices seems to reduce the rate of successful attack by crabs, but a rigorous demonstration of their defensive function would require enumeration of unsuccessful as well as successful attacks (e.g., Palmer, 1990). Such in-

formation was not collected in this study. Crabs displayed several means of circum-
venting the protection afforded by varices against a peeling attack.

Willets fed on considerably smaller *Cerithidea* than did *Pachygrapsus*. This observa-
tion is consistent with the conclusion of Vermeij (1978) that predators that ingest prey
whole cannot consume prey items as large as those taken by predators that crush the
prey's exoskeleton then extract the soft parts. *Cerithidea* $> \approx 17$ mm have apparently
attained a refuge in size from willet predation. Because little, if any, body tissue remains
in the shells of snails recovered from regurgitation pellets, I was unable to evaluate the
influence of parasitism by larval trematodes on the risk of predation by willets. Most
snails of the sizes consumed by willets are not infected by redial or sporocyst larvae
(Sousa, 1983). However, metacercarial stages of two of the trematode species that
infect Bolinas snail populations are sometimes present in the tissues of small snails
(W. P. Sousa, unpubl. data). For the same reasons as discussed above in the context
of crab predation, such infections are unlikely to alter the vulnerability of snails to willet
predation.

The impact of willet predation on the density of small snails was not measured in
this study, however, McCloy (1979) experimentally assessed levels of shorebird pre-
dation on small *Cerithidea* (< 10 mm) on a mud flat in the Sweetwater River Estuary
near San Diego, California. He created 12 shallow 0.25-m^2 pools on the mud flat, and
placed 50 small *Cerithidea* in each. Half the pools were covered with a wire mesh cage
to exclude birds, and half were left open. The number of snails remaining after foraging
birds, including willets and sanderlings, had followed the tidally receding waterline
through the area occupied by the experimental pools was counted. This experiment was
repeated on seven different days. In only one of these trials was there a statistically
significant decline in snail numbers in the open pools as compared to the pools from
which birds had been excluded. McCloy concluded that while predation by shorebirds
can depress the density of small *Cerithidea*, "this effect is patchy in time and space, and
apparently independent of the density of *Cerithidea*". This result is not entirely unex-
pected. As described earlier, willets have a very diverse diet of which *Cerithidea* is only
a minor component (Page & Stenzel, 1975; Stenzel et al., 1976), and individual birds
forage over a wide variety of lagoonal and open coast habitats. Therefore, it is doubtful
that willets concentrate their feeding efforts in denser subpopulations of snails.

Even when feeding on a preferred prey species, or one that comprises a substantial
portion of the diet, shorebirds do not consistently cause spatially density-dependent
mortality of soft-sediment prey. Goss-Custard (1977) found that redshank *Tringa
totanus* L. feeding on the amphipod *Corophium volutator* Pallas caused density-
dependent mortality of the crustacean on one transect within an estuary in northeast
Scotland, but not on a second. Across the estuary as a whole, he predicted that red-
shank would cause density-dependent mortality over the middle ranges of amphipod
density, but that mortality due to redshank predation would be inversely density-
dependent at high amphipod densities. Sutherland (1982) showed that predation of
cockles *Cerastoderma edule* L. by oystercatchers *Haematopus ostralegus* L. was density-

independent or inversely density-dependent over much of the range of natural prey densities within the intertidal of a sandy bay in Wales. Only at very low prey densities, were rates of oystercatcher predation on cockles positively density-dependent. The results of the studies reported here and those of McCloy (1979) indicate that fluctuations in the numbers of snails within local *Cerithidea* populations are unlikely to be regulated in a density-dependent manner by crab or shorebird predation.

The discovery of living snails within some willet regurgitation pellets indicates that if a snail's shell remains intact, a tightly fitting operculum can act as an effective barrier against bird digestive enzymes. The same is true for some species of gastropods that are consumed by the marine cottid fish *Asemichthys taylori* Gilbert then defecated alive (Norton, 1988). Similarly, some species of juvenile freshwater molluscs can be ingested by waterfowl and regurgitated from the crop in a viable condition (Mackie, 1979). Depending on the length of time that *Cerithidea* remain in the crop/gizzard of willets and the patterns of bird movement, living snails may be dispersed within or among coastal lagoons. Since *Cerithidea* has no planktonic larval stage and adult dispersal is limited, transport in the digestive tracts of birds may be an intermittent, but important, mechanism of habitat colonization and gene flow.

REFERENCES

Adams, K.M., 1970. A Bolinas Lagoon tide flat community (juvenile fish and phycophilous crustacea). Masters thesis, San Francisco State College, San Francisco, California, 79 pp.

Arnold, W.S., 1984. The effects of prey size, predator size, and sediment composition on the rate of predation by the blue crab, *Callinectes sapidus* Rathbun, on the hard clam, *Mercenaria mercenaria* (Linné). *J. Exp. Mar. Biol. Ecol.*, Vol. 80, pp. 207–219.

Boulding, E.G., 1984. Crab-resistant features of shells of burrowing bivalves: decreasing vulnerability by increasing handling time. *J. Exp. Mar. Biol. Ecol.*, Vol. 76, pp. 201–223.

Boulding, E.G. & T.K. Hay, 1984. Crab response to prey density can result in density-dependent mortality of clams. *Can. J. Fish. Aquat. Sci.*, Vol. 41, pp. 521–525.

Brooks, J. L. & S. J. Dodson, 1965. Predation, body size and composition of plankton. *Science*, Vol. 150, pp. 28–35.

Brown, J. H., D. W. Davidson, J. C. Munger & R. S. Inouye, 1986. Experimental community ecology: the desert granivore system. In, *Community ecology*, edited by J. Diamond & T. J. Case, Harper and Row Publishers, New York, pp. 41–61.

Brown, S. C., S. R. Cassuto & R. W. Loos, 1979. Biomechanics of chelipeds in some decapod crustaceans. *J. Zool. London*, Vol. 188, pp. 143–159.

Connell, J. H., 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. In, *Ecology and evolution of communities*, edited by M. L. Cody & J. M. Diamond, Harvard University Press, Cambridge, Massachusetts, pp. 460–490.

Curtis, L. A. & K. M. Hubbard, 1990. Trematode infections in a gastropod host misrepresented by observing cercariae. *J. Exp. Mar. Biol. Ecol.*, Vol. 143, pp. 131–137.

Dayton, P. K., 1971. Competition, disturbance and community organization: the provision and subsequent utilization of space in a rocky intertidal environment. *Ecol. Monogr.*, Vol. 41, pp. 351–389.

Elner, R. W., 1978. The mechanics of predation by the shore crab, *Carcinus maenas* (L.), on the edible mussel, *Mytilus edulis* L. *Oecologia (Berlin)*, Vol. 36, pp. 333–344.

Elner, R. W., 1980. The influence of temperature, sex and chela size in the foraging strategy of the shore crab, *Carcinus maenas* (L.). *Mar. Behav. Physiol.*, Vol. 7, pp. 15–24.

Elner, R. W. & R. N. Hughes, 1978. Energy maximization in the diet of the shore crab, *Carcinus maenas*. *J. Anim. Ecol.*, Vol. 47, pp. 103–116.

Fienberg, S. E., 1970. The analysis of multidimensional contingency tables. *Ecology*, Vol. 51, pp. 419–433.

Goss-Custard, J. D., 1977. Predator responses and prey mortality in redshank, *Tringa totanus* (L.), and a preferred prey, *Corophium volutator* (Pallas). *J. Anim. Ecol.*, Vol. 46, pp. 21–35.

Griffiths, C. L. & J. L. Seiderer, 1980. Rock-lobsters and mussels — limitations and preferences in a predator–prey interaction. *J. Exp. Mar. Biol. Ecol.*, Vol. 44, pp. 95–109.

Hall, D. J., S. T. Threlkheld, C. W. Burns & P. H. Crowley, 1976. The size-efficiency hypothesis and the size structure of zooplankton communities. *Annu. Rev. Ecol. Syst.*, Vol. 7, pp. 177–208.

Hiatt, R. W., 1948. Biology of the lined shore crab, *Pachygrapsus crassipes* Randall. *Pac. Sci.*, Vol. 2, pp. 134–213.

Holmes, J. C. & W. M. Bethel, 1972. Modification of intermediate host behavior by parasites. In, *Behavioural aspects of parasite transmission*, edited by E. U. Canning & C. A. Wright, Academic Press, London, pp. 123–149.

Hughes, R. N., 1980. Optimal foraging theory in the marine context. *Oceanogr. Mar. Biol. Annu. Rev.*, Vol. 18, pp. 423–481.

Hughes, R. N. & R. Seed, 1981. Size selection of mussels by the blue crab *Callinectes sapidus*: energy maximizer or time minimizer? *Mar. Ecol. Prog. Ser.*, Vol. 6, pp. 83–89.

Juanes, F. & E. B. Hartwick, 1990. Prey size selection in Dungeness crabs: the effect of claw damage. *Ecology*, Vol. 71, pp. 744–758.

Karl, S. & S. Obrebski, 1976. The feeding biology of the bat ray, *Myliobatis californica*, in Tomales Bay, California. In, *Fish food habits studies, 1st. Pac. Northwest Tech. Workshop Proc. WSG-WO 77–2*, edited by C. A. Simenstad & S. J. Lipovsky, Washington Sea Grant, Division of Marine Resources, University of Washington, Seattle, Washington, pp. 181–186.

Lawton, P. & R. N. Hughes, 1985. Foraging behaviour of the crab *Cancer pagurus* feeding on the gastropods *Nucella lapillus* and *Littorina littorea*: comparisons with optimal foraging theory. *Mar. Ecol. Prog. Ser.*, Vol. 27, pp. 143–154.

Lee, J., 1981. Morphology and forces in the chelae of the lined shore crab, *Pachygrapsus crassipes*. Unpublished undergraduate honors thesis, University of California, Berkeley, California, 39 pp.

Lindberg, D. R., 1965. Crab predation on intertidal populations of the urchin *Strongylocentrotus purpuratus*. *Bull. South. Calif. Acad. Sci.*, Vol. 84, pp. 109–111.

Lubchenco, J. & S.D. Gaines, 1981. A unified approach to marine plant–herbivore interactions. I. Populations and communities. *Annu. Rev. Ecol. Syst.*, Vol. 12, pp. 405–437.

MacDonald, K.B., 1969a. Quantitative studies of salt marsh mollusc faunas from the North American Pacific coast. *Ecol. Monogr.* Vol. 39, pp. 33–60.

MacDonald, K.B., 1969b. Molluscan faunas of Pacific coast salt marshes and tidal creeks. *Veliger*, Vol. 11, pp. 399–405.

Mackie, G.L., 1979. Dispersal mechanisms in Sphaeriidae (Mollusca:Bivalvia). *Bull. Am. Malacol. Union*, Vol. 1979, pp. 17–21.

McCloy, M.J., 1979. Population regulation in the deposit-feeding mesogastropod *Cerithidea californica* as it occurs in a San Diego salt marsh habitat. Masters thesis, California State University, San Diego, California. 101 pp.

Moore, J., 1983. Responses of an avian predator and its isopod prey to an acanthocephalan parasite. *Ecology*, Vol. 64, pp. 1000–1015.

Moore, J., 1984. Parasites and altered host behavior. *Sci. Am.*, Vol. 250, pp. 108–115.

Morris, R.H., D.P. Abbott & E.C. Haderlie, 1980. *Intertidal invertebrates of California*. Stanford University Press, Stanford, California, 690 pp.

Murdoch, W.W. & A. Oaten, 1975. Predation and population stability. *Adv. Ecol. Res.*, Vol. 9, pp. 1–131.

Norton, S.F., 1988. Role of the gastropod shell and operculum in inhibiting predation by fishes. *Science*, Vol. 241, pp. 92–94.

Onuf, C.P., 1987. The ecology of Mugu Lagoon, California: an estuarine profile. *U.S. Fish Wildl. Serv. Biol. Rep.*, No. 85(7.15), 122 pp.

Page, G. & L. Stenzel, 1975. Aspects of the ecology of shorebirds on Bolinas Lagoon. Unpublished report for the Department of Parks and Recreation, County of Marin, California, 89 pp.

Paine, R.T., 1976. Size-limited predation: an observational and experimental approach with the *Mytilus–Pisaster* interaction. *Ecology*, Vol. 57, pp. 858–873.

Palmer, A.R., 1985. Adaptive value of shell variation in *Thais lamellosa*: effect of thick shells on vulnerability to and preference by crabs. *Veliger*, Vol. 27, pp. 349–356.

Palmer, A.R., 1990. Predator size, prey size, and the scaling of vulnerability: hatchling gastropods vs. barnacles. *Ecology*, Vol. 71, pp. 759–775.

Porter, K.G., 1977. The plant–animal interface in freshwater ecosystems. *Am. Sci.*, Vol. 65, pp. 159–170.

Pyke, G.H., 1984. Optimal foraging theory: a critical review. *Annu. Rev. Ecol. Syst.*, Vol. 15, pp. 523–575.

Quammen, M.L., 1980. The impact of predation by shorebirds, benthic feeding fish and a crab on the shallow living invertebrates in intertidal mud flats of two southern California lagoons. Ph.D. dissertation, University of California, Irvine, California, 131 pp.

Race, M.W., 1981. Field ecology and natural history of *Cerithidea californica* (Gastropoda:Prosobranchia) in San Francisco Bay. *Veliger*, Vol. 24, pp. 18–27.

Robles, C., 1982. Disturbance and predation in an assemblage of herbivorous diptera and algae on rocky shores. *Oecologia (Berlin)*, Vol. 54, pp. 23–31.

Robles, C.D. & J. Cubit, 1981. Influence of biotic factors in an upper intertidal community: dipteran larvae grazing on algae. *Ecology*, Vol. 62, pp. 1536–1547.

Robles, C., D. Sweetnam & J. Eminike, 1990. Lobster predation on mussels: shore-level differences in prey vulnerability and predator preference. *Ecology*, Vol. 71, pp. 1564–1577.

Sanchez-Salazar, M.E., C.L. Griffiths & R. Seed, 1987. The effect of size and temperature on the predation of cockles *Cerastoderma edule* (L.) by the shore crab *Carcinus maenas* (L.). *J. Exp. Mar. Biol. Ecol.*, Vol. 111, pp. 181–193.

Seed, R., 1980. Predator–prey relationships between the mud crab *Panopeus herbstii*, the blue crab, *Callinectes sapidus* and the Atlantic ribbed mussel *Geukensia* (= *Modiolus*) *demissa*. *Estuarine Coastal Mar. Sci.*, Vol. 11, pp. 445–458.

Sousa, W.P., 1979. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. *Ecol. Monogr.*, Vol. 49, pp. 227–254.

Sousa, W. P., 1983. Host life history and the effect of parasitic castration on growth: a field study of *Cerithidea californica* Haldeman (Gastropoda:Prosobranchia) and its trematode parasites. *J. Exp. Mar. Biol. Ecol.,* Vol. 73, pp. 273–296.

Sousa, W. P., 1990. Spatial scale and the processes structuring a guild of larval trematode parasites. In, *Parasite communities: patterns and processes,* edited by G. W. Esch et al., Chapman and Hall, London, pp. 41–67.

Sousa, W. P. & E. D. Grosholz, 1991. The influence of habitat structure on the transmission of parasites. In, *Habitat structure: the physical arrangement of objects in space,* edited by S. S. Bell et al., Chapman and Hall, London, pp. 300–324.

Sprules, W. G., 1972. Effects of size-selective predation and food competition on high-altitude zooplankton communities. *Ecology,* Vol. 53, pp. 375–386.

Stenzel, L. E., H. R. Huber & G. W. Page, 1976. Feeding behavior and diet of the long-billed curlew and willet. *Wilson Bull.,* Vol. 88, pp. 314–332.

Sutherland, W. J., 1982. Spatial variation in the predation of cockles by oystercatchers at Traeth Melynog, Anglesey. II. The patterns of mortality. *J. Anim. Ecol.,* Vol. 51, pp. 491–500.

Talent, L. G., 1982. Food habits of the gray smoothhound, *Mustelus californicus,* the brown smoothhound, *Mustelus henlei,* the shovelnose guitarfish, *Rhinobatos productus,* and the bat ray, *Mylobatis californica,* in Elkhorn Slough, California. *Calif. Fish Game,* Vol. 68, pp. 224–234.

Vermeij, G. J., 1977. Patterns in crab claw size: the geography of crushing. *Syst. Zool.,* Vol. 26, pp. 138–151.

Vermeij, G. J., 1978. *Biogeography and adaptation.* Harvard University Press, Cambridge, Massachusetts, 332 pp.

Warner, G. F. & A. R. Jones, 1976. Leverage and muscle type in crab chelae (Crustacea:Brachyura). *J. Zool. London,* Vol. 180, pp. 57–68.

Willason, S. W., 1981. Factors influencing the distribution and coexistence of *Pachygrapsus crassipes* and *Hemigrapsus oregonensis* (Decapoda:Grapsidae) in a California salt marsh. *Mar. Biol.,* Vol. 64, pp. 125–133.

Wootton, J. T., 1992. Indirect effects, prey susceptibility, and habitat selection: impacts of birds on limpets and algae. *Ecology,* Vol. 73, pp. 981–991.

Zaret, T. M., 1980. *Predation and freshwater communities.* Yale University Press, New Haven, Connecticut, 187 pp.