The role of highly mobile crab predators in the intertidal zonation of their gastropod prey

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Abstract

We experimentally compared the effect of four species of highly mobile predatory crabs on their herbivorous gastropod prey. On northeastern Pacific shores the intertidal distributions of the gastropods, *Littorina sitkana* (Philippi) and *L. scutulata* (Gould), overlap broadly with those of two species of mid-shore crabs, *Hemigrapsus nudus* (Dana) and *H. oregonensis*, but do not extend below the upper limit of two species of low-shore crabs, *Lophopanopeus bellus* (Stimpson) and juvenile *Cancer productus* (Randall), or into the subtidal zone where adult *C. productus* are abundant. We hypothesized that these gastropods are absent from the low shore despite potentially higher growth and reproductive rates because of the high risk of predation from low-shore and subtidal crabs. To test whether the risk of predation was higher in the low intertidal zone, we tethered 640 adult *Littorina sitkana* at two tidal levels on four beaches varying in crab abundance. Predation rates varied from 2% to 77% per high tide period. At three of the sites the risk of predation was significantly higher at the lower than at the higher tide level. At the fourth site where *Cancer productus* found shelter under large boulders in the mid-tidal zone, the risk of predation was the same at both tidal levels. Field measurements of per capita consumption rates for the different crab species, test fishing with crab rings, field observations and analysis of the broken shell fragments of the snails showed that predation was primarily by large, subtidal *C. productus* that moved up into the intertidal to feed. These highly mobile predators aggregate to exploit patches of high prey density in ephemerally favorable habitats, consequently the change in the risk of predation with increasing tidal height is less predictable in both time and space than that for slow moving, low-shore predators.

Keywords: Cancer; Crab; *Hemigrapsus*; Intertidal zonation; *Littorina*; *Lophopanopeus*; Mobile predators; Predation; Refuge

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1. Introduction

The zonation of organisms along altitudinal, latitudinal or intertidal gradients is a reflection of their responses to both physical and biological factors (Merriam, 1894; Connell, 1961a; Whittaker, 1975). Intertidal communities have served as model systems in which to study zonation experimentally for two reasons (Connell, 1961a Connell, 1961b, 1972; Paine, 1966; Dayton, 1971, Dayton, 1975; Lubchenco, 1980). First, the physical gradients between the marine and the terrestrial environment conveniently occurs within a few meters (Gotelli, 1993). Second, many organisms that inhabit intertidal communities are slow moving or sessile and are easily transplanted or removed (Connell, 1972).

The widely held paradigm of intertidal zonation for temperate rocky shores is that marine organisms are limited by physical factors (e.g. temperature and desiccation stress) from above and by biological factors (e.g. competition and predation) from below (reviewed by Connell, 1972; Foster et al., 1988). While this paradigm appears in many text books, Underwood and Denley (1984) point out that we should not assume that it can be universally applied. For example, more careful examination has shown that the upper distribution of some algae can be affected by competion with other algae (Hawkins and Hartnoll, 1985) and by consumption by the grazing flies (Robles and Cubit, 1981). Likewise, the lower distribution of organisms may not always be limited by competition and predation. Lack of recruitment of planktonic propagules could also play a role (Underwood and Denley, 1984). Given this caveat, it does appear that predation by slow moving starfish and gastropods can determine the lower limits of distribution of sessile mussels and barnacles on wave exposed rocky shores (Connell, 1961a; Paine, 1966). The upper limit of these slow moving predators is set by desiccation to which they are more sensitive than their prey (Connell, 1972). Since they move slowly, and their handling time for an individual prey item is long (Paine, 1974; Menge, 1983), these predators do not forage much above their upper limit.

Highly mobile predators, such as crabs and fishes, become more important on wave-protected rocky shores (Ebling et al., 1964; Muntz et al., 1965; Peterson, 1979; Castilla and Paine, 1987; Robles, 1987; Robles et al., 1989; Barkai and Branch, 1988). These predators can forage throughout the entire intertidal zone during one high tide (Paine and Palmer, 1978; Edwards et al., 1982; Boulding and Hay, 1984; Robles, 1987; Robles et al., 1989; Warman et al., 1993) and often require a handling time of only a few minutes, or even seconds, to consume a preferred prey item (Lawton and Hughes, 1985). Thus, the per capita consumption rate of highly mobile predators can be much greater than that of slow moving ones. Menge (1983) compared the predation intensity by starfish, drilling gastropods and shell-crushing crabs on New England shores and concluded that crabs ranked highest with one crab species, *Carcinus maenas*, having a per capita consumption rate that was 25 times that of the drilling snail, *Nucella lapillus*.

Despite their importance, highly mobile predators are difficult to manipulate experimentally and few studies have attempted to quantify their effect on intertidal zonation (Edwards et al., 1982; Castilla and Paine, 1987). Previous workers have estimated the effect of these predators by using cages to exclude them from portions of prey populations (Menge and Lubchenco, 1981; Robles, 1987). An alternative to using

cages is to study the zonation pattern of a prey species that leaves a record of predation events. For example, many predators of shelled molluscs do not ingest the shell and the pattern of shell remains can identify the predator (Zipser and Vermeij, 1978; Boulding, 1984; Lawton and Hughes, 1985).

In our study we investigate the effect of highly mobile predatory crabs on the intertidal zonation of a model prey species, the common shelled gastropod, *Littorina sitkana*. This species was chosen because it exhibits unpredictable intertidal distribution patterns and possesses direct development. We observed that on some shores *L. sitkana* is abundant throughout the intertidal zone, whereas on others it is restricted to damp cave-like refuges in the high intertidal and supratidal zones. We suspected that variability of predator abundance is responsible for this pattern. Since *L. sitkana* lacks a free-swimming larval stage (Behrens, 1972; Behrens Yamada, 1989, 1992; Buckland-Nicks et al., 1973), and the adult snails disperse little (Boulding and Van Alstyne, 1993), the demography of populations is highly dependent on local ecological processes such as predation intensity (Behrens Yamada, 1977a, 1989). We hypothesize that the risk of predation from crabs is higher below the lower limit of *L. sitkana* than it is above this limit. We test this hypothesis by documenting the vertical distribution patterns of crabs in relation to snails on three beaches and by setting out tethered snails at two tidal levels. We predict that snails tethered below their lower limit would suffer higher rates of predation from crabs than those tethered above it. We identifed the predator responsible for the increased predation rates at the lower tidal level, through test fishing and by interpreting the shell breakage patterns of the tethered snails.

2. Materials and methods

2.1. Study sites

All field experiments were carried out on wave-protected shores at or near the University of Washington Friday Harbor Laboratories on San Juan Island (48°33′N, 123°01′W). The Cantilever Pier site, a funnel-shaped beach enclosed by vertical walls and sloping benches, is the most wave exposed. The substratum ranges from large gravel to boulders. The Lab 6 site is a gently sloping beach of intermediate wave exposure. The substratum ranges from gravel and sand interspersed with boulders in the low intertidal zone to clean gravel and small rocks in the high intertidal zone. The most sheltered site, Roche Harbor, also consists of a gently sloping beach. Mud and diatoms cover the fine gravel substratum and boulders in the low intertidal while basaltic bedrock forms the upper intertidal zone. A northern exposure and fresh water seepages keep Roche Harbor damper than the other two sites. The intertidal zone at all three sites ranges from − 0.9 m to 2.7 m (U.S. datum).

2.2. Description of predators and prey

Five species of shell-breaking crabs occur on the rocky and gravel shores on San Juan Island, WA, as well as on other wave protected shores of the Northeastern Pacific. The

ubiquitous shore crabs (Brachyura:Grapsidae), *Hemigrapsus nudus* (Dana) and *Hemigrapsus oregonensis* (Dana), inhabit the mid-tidal zone while *Lophopanopeus bellus* (Stimpson) (Brachyura:Xanthidae) and *Cancer oregonensis* (Dana) (Brachyura:Cancridae), live in the low intertidal zone (Kozloff, 1983 Table 1). Juvenile *Cancer productus* (Randall) (< 90 mm carapace width) are found in the intertidal zone at low tide while larger subtidal individuals move into the intertidal at high tide to forage (Boulding, personal observation, Robles et al., 1989; Walker and Behrens Yamada, 1993). *Hemigrapsus* spp., *Lophopanopeus bellus* and *Cancer oregonensis* are relatively small as adults, rarely exceeding 40 mm in carapace width, whereas *C. productus* attain a carapace width of over 180 mm (Table 1). The two *Hemigrapsus* species are generalist omnivores (Knudsen, 1964; Behrens Yamada, 1977a) and have claws with occlusal margins lined with serrations as well as a scoop that scrapes encrusting organisms off rocks. The other three species *Lophopanopeus bellus, Cancer oregonensis* and *C. productus*, possess claws with blunt molar teeth (Behrens Yamada and Boulding, in prep.). Stomach analyses and field observations suggest that these crabs are opportunistic foragers that routinely feed on shelled prey such as barnacles, mussels, clams, oysters and other crabs (Knudsen, 1964; Bernard, 1979; Boulding and Hay, 1984; Palmer, 1985; Robles et al., 1989; Behrens Yamada et al., 1993; Walker and Behrens Yamada, 1993). Feeding experiments were conducted on all the crab species except *Hemigrapsus oregonensis*, since the two *Hemigrapsus* species have a similar diet (Knudsen, 1964; Behrens Yamada, 1977a, Boulding, unpublished observation).

Table 1
Comparison of the four crab species used in field experiments 1–3 to determine prey consumption rate

|	Hemigrapsus nudus	Lophopanopeus bellus	Cancer oregonensis	Cancer productus
Shore level (U.S. tables)	mid intertidal; 0 to 1.8 m	subtidal to −0.2 m	subtidal to −0.2 m	juveniles intertidal to 1.3 m; subtidal adults invade intertidal during high tide
Habitat*	semi-protected rocky shore	quiet bays	semi-protected to quiet bays	semi-protected to quiet bays
Substratum*	under rocks on gravel bottom	burrowed in sand under rocks	under rocks, wedged in crevices	juveniles buried in sand under boulders on mud-gravel bottom
Max. carapace width* (CW) (mm) in nature	56	34	47	180
Carapace width (mm) of crabs in field experiments 1–3	17–27	19–25	26	24–49
Live weight (g)	4–7	4.5–7.5	4–6.5	4–17
Dimensions (mm) of 5 g crab				
Carapace width	22.1	21.9	26.0	33.5
Propodus height	7.7	9.0	8.5	6.9
Mid-dactyl chelal gape	3.7	5.5	4.4	3.8

* Data from Morris et al. (1980).
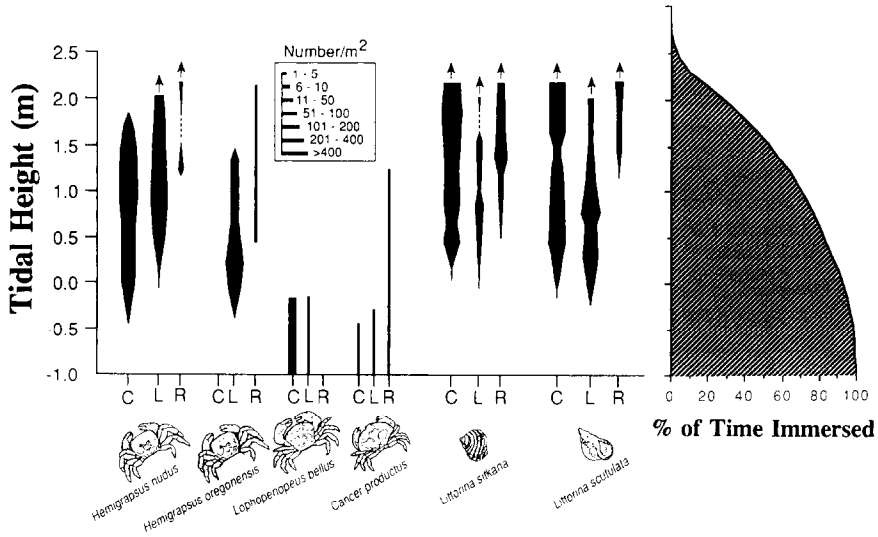
Fig. 1. Intertidal ranges and mean abundance of shell-breaking crabs and littorinid snails in relation to tidal immersion on three San Juan Island, Washington beaches. Cantilever Pier is represented by C; Lab 6 by L; Roche Harbor by R. The Cantilever Pier site is most wave-exposed while Roche Harbor is most sheltered. Note that the abundance categories are represented on a logarithmic scale. The number of quadrats per level was usually four. Arrows indicate that the upper limits for a species were not determined. Tidal height is taken from U.S. tables in which 0 m is defined as mean lower low water.

These crabs differ greatly in carapace shape (Fig. 1). To enable comparison, we used wet biomass as a measure of crab size. Carapace and claw measurements were taken as described in Lawton and Elner (1985). In general, *Cancer productus* has a greater carapace width (CW) for its biomass than the other four species (Table 1).

The grazing snail, *Littorina sitkana* (Philippi) (Prosobranchia: Littorinidae), together with its congener, *L. scutulata*, is the most abundant intertidal prey organisms on San Juan Island, WA, each species attaining densities exceeding $400/m^2$. The geographic distribution of *L. sitkana* ranges from the Bering Sea to southern Oregon (Keen, 1937; Behrens Yamada, 1977a,b, 1992). Its shell is moderately thick-walled and spherical, often with heavy spiral ridges (Boulding et al., 1993). Females lay gelatinous egg masses on rocks, in crevices or on algae and eggs hatch directly into juvenile snails (Behrens, 1972; Behrens Yamada, 1989, 1992; Buckland-Nicks et al., 1973). Shell length was measured as described in Behrens Yamada (1989).

2.3. Intertidal zonation of crabs and snails

Intertidal transects were taken at low tide on all three beaches by stretching a tape measure between the low and high tide level. Twelve bench marks were evenly marked off along the tape by tying fluorescent surveyor's tape to rocks. The corresponding tidal level for the bench marks at Cantilever Pier and at Lab 6 were obtained from the tide gauge at the Friday Harbor Laboratories pier. Bench marks at the Roche Harbor site

were estimated using a surveyor's level and the recorded low tide mark as a reference point. The abundance of *L. sitkana* and *L. scutulata* greater than 1 mm in shell length and that of all crabs greater than 3 mm in carapace width was recorded within 50 cm × 50 cm quadrats. At least two, and usually four quadrats were taken at each tidal level. We used eight quadrats per tide level for rare species such as juvenile *Cancer productus* at Cantilever Pier and *Littorina* spp. and *Hemigrapsus* spp. at Roche Harbor. In addition to taking the transects, we turned over a minimum of 20 boulders at each site and measured the carapace width of all the crabs that were using the boulders for shelter. Although our transects were taken at low tide and thus provide good estimates of the abundance of permanent residents in the intertidal zone, such as *Hemigrapsus nudus, H. oregonensis, Lophopanopeus bellus* and juvenile *Cancer productus*, they cannot provide abundance estimates of transient species, such as adult *C. productus*.

2.4. Predation risk at different tidal heights

Since most marine predators forage only when submerged, we calculated the relative predation risk at each tidal level. Tidal data for the Friday Harbor tidal station for the year 1990 were obtained from NOAA. The data consisted of actual tidal height readings, in ft, taken at the Friday Harbor Laboratories Pier at 6-min intervals. The frequency of immersion for each 0.5 ft interval was calculated and plotted in conjunction with the transect data (Fig. 1).

2.5. Ranking of per-capita prey consumption

Long-term field feeding experiments were set up inside cages at the 0.6 m tidal level at Lab 6 Beach in order to obtain relative feeding rates for similar-sized crabs of the four species. Field cages (50 × 30 × 10 cm) were sewn from 4 mm plastic mesh with Velcro[TM] fasteners for easy opening and closing. All cages contained a cement building block (6 × 19.5 × 39 cm) with three 2 × 9 cm 'tunnels'. The algal growth on the surfaces of the blocks provided food for the snails while the three 'tunnels' provided shelter for both crabs and snails.

The prey species, *Littorina sitkana*, was sorted into size categories using a series of soil test sieves. Size categories varied slightly between experiments but generally fell into the shell length categories: small (5–8 mm), medium (7–10 mm) and large (10–13 mm). To color code the prey size classes, snails were stuck, aperture down, to double-sided carpet tape on sheets of cardboard. The shells of each size class were spray painted a different color to allow for the assignment of shell fragments to the correct size class. No mortalities or behavior changes resulted from the marking procedure.

Similar-sized crabs consisting of juvenile *Cancer productus* and adult crabs of the other three species were introduced into field cages (Tables 1 and 2). Since female *Hemigrapsus* spp. possess small claws and feed primarly on algae (authors' unpublished observation), only male crabs with all appendages intact were used in the experiments. Once inside the cages, crabs sheltered under the cement block or inside the tunnels. The two *Cancer* species and *Lophopanopeus bellus* immediately began preying on the snails.

The experimental design for each of the three field cage experiments was similar

Table 2
Design of field cage experiments for comparing prey consumption rate by four crab species at the 0.6 m tidal level

	Experiment		
	1	2	3
Date	Apr. 7–	Sept 4–	Apr. 9–
	Jun. 16/88	Nov. 23/88	Jun. 14/89
Duration (days)	70	80	66
Hemigrapsus nudus		3(2)	10(1)
Lophopanopeus bellus		3(2)	5(1)
Cancer oregonensis	2(1)		
Cancer productus	2(1)	3(2)	5(1)
Controls	4	4	5

Numbers in crab rows indicate number of replicate cages followed in parentheses by number of crabs per cage at beginning of experiment

(Tables 2 and 3). Typically, 30 small, 30 medium and 30 large *Littorina sitkana* were introduced into a cage, followed 3 days later by one or two male crabs of a given species. Cages were monitored once or twice during an experiment to check for crab survival, to collect shell fragments, to patch ripped cages and to terminate a trial if over 70% of the snails had been eaten. Crabs sometimes died while molting. If this occurred within the first week of the experiment, that crab was replaced; if it occurred later, the trial was terminated.

At termination of an experiment, we recorded the number of live snails and empty, crushed and peeled shells in each size category. Intact but empty shells are produced when a snail dies of causes other than crab predation. Crushed shells are produced by shell-breaking crabs when the snails are small enough to fit inside the gape of the crab's claw but can also be produced by fish predators and by moving rocks. Peeled shells, consisting of an intact columella with whorl remnants (Zipser and Vermeij, 1978), are produced by shell-breaking crabs when a gastropod shell is too large to fit inside the claw gape. Crabs peel shells by using one claw to progressively break back the lip of the shell aperture (Lawton and Hughes, 1985). Peeled shells are diagnostic of crab predation because no other predators, including shell crushing fishes such as pile perch (*Damalich-thys vacca*), nor crushing by rocks, produce such a pattern (S. Norton, personal communication and authors' unpublished observations).

Peeled shells were usually retained inside the cages but the fragments from crushed shells tended to fall through the cage mesh. This resulted in a high proportion of missing snails inside crab cages. Control cages without crabs, in contrast, exhibited a maximum of only two and usually no missing snails (Table 3). We recovered some painted shell fragments from crushed shells in the sediment below the crab treatment cages. The hypothesis that the presence of crabs did not affect snail survival was tested for each crab species in each experiment using χ^2-tests.

Daily per-capita consumption rate was calculated for each crab in field experiments 1 to 3 by assuming that peeled shells, crushed shells and missing snails were eaten by the crabs. The biomass of consumed snails was estimated from the regression: dry biomass

Table 3
Fate of snails in field experiments 1 to 3 caged with four species of intertidal crabs

Crab species	Carapace width (mm)	Experiment No.	No. of crabs/cage	Duration (days)	Small					Medium					Large				
					L	P	C	E	M	L	P	C	E	M	L	P	C	E	M
Control		1	0	70	79	0	1	9	1	82	0	2	6	0	85	0	0	5	0
		2	0	70	27	0	0	2		27	0	0	3	0	27	0	0	3	0
		2	0	80	56	0	1	1	2	58	0	1	1	0	42	0	2	16	0
		2	0	20	29	0	0	0	0	30	0	0	0	0	28	0	0	2	0
		3	0	66	147	0	0	0	3	148	0	0	0	2	147	0	0	3	0
Grand total					338	0	2	13	7	345	0	3	10	2	329	0	2	29	0
Hemigrapsus nudus	23–27	2	2	80	82	0	0	7	1	87	3	0	0	0	77	0	0	12	1
	17–25	3	1	66	227	1	1	4	7	233	1	0	4	2	233	2	0	2	3
Grand total					309	1	1	11	8	320	4	0	4	2	310	2	0	14	4
Lophopanopeus bellus	19–25	2	2	80	31	11	0	7	44*	38	45	2	6	6*	24	47	0	14	12*
	19–25	3	1	31	26	1	0	0	3	26	4	0	0	0	28	2	0	0	0
		3	1	66	21	6	0	2	1	28	1	0	0	1	28	2	0	0	0
Grand total					80	18	0	9	48	92	50	2	6	7	80	51	0	14	12
Cancer oregonensis	25–26	1	1	70	30	12	0	3	15	29	19	0	5	7	25	28	0	6	1
Cancer productus	24–26	1	1	70	34	16	1	3	6	27	26	1	3	3	38	18	0	2	2
	42–48	2	2	20	19	37	0	2	32	14	72	0	0	4	6	75	0	8	1
	24–49	3	1	66	46	26	0	3	15	35	51	0	1	3	30	58	0	0	2
		3	1	<34	25	5	0	0	0	21	6	0	0	3	20	10	0	0	0
Grand total					124	84	1	8	53	97	155	1	4	13	94	161	0	10	5

Live (L), peeled (P), crushed (C), empty (E) and missing (M) snail shells.
No significant difference in the survival of snails was found between control and Hemigrapsus nudus cages. In contrast, the other three crabs significantly reduced the survival of snails ($\chi^2 > 20$, $df = 1$, $p < 0.001$). Asterisk indicates that ripped cage was salvaged by patching hole and by replacing missing snails

(mg) = 4.57 + 17.7 × shell length (cm)^3; ($p < 0.001$; $R^2 = 0.954$) (adapted from Menge, 1972).

2.6. Role of site, tide level and size of snail on predation rate

2.6.1. Procedure

Both fish and subtidal crabs forage in the intertidal during high tides (Boulding and Hay, 1984; Robles et al., 1989). The impact of these mobile predators on *Littorina sitkana* populations was assessed by tethering snails at two tidal levels: 0 m and 1.3 m during the August 21–24, 1991 tidal sequence. This tidal sequence, between spring and neap tides, was chosen because it mimics the average annual exposure time at each tidal level (Fig. 1). Tethered snails were set up at the three original sites, Cantilever Pier, Lab 6 and Roche Harbor, plus a fourth site below the Friday Harbor Laboratories Pier. We picked the fourth site because a previous study revealed that many adult *Cancer productus* were foraging at this site (Walker and Behrens Yamada, 1993).

Five-meter lengths of lead line from a fishing net were stretched out along the 0 m and 1.3 m tidal levels at all four sites. Extra-large adult *Littorina sitkana* (14.6–17.3 mm in length) and medium–large *L. sitkana* (9.2–11.8 mm) were fastened at the apex to pieces of 20 cm long 1 kg test monofilament using marine epoxy glue. Forty extra-large and 40 medium–large 'leashed' snails were alternately tied along each of the eight lead lines on August 21, 1991.

The fate of snails on the lead lines was monitored after each of three consecutive higher high tides and the number of live, peeled, crushed and missing snails noted. Logistic regression analysis was carried out to test for the role of site, tide level and snail size on predation rate (Nelder and Wedderburn, 1972). Similar tethering experiments to test for tide level effects were done at irregular intervals between August 1989 and February 1991. Between 25 and 50 adult *L. sitkana* (9.5–14 mm) were tethered to lead lines at various tidal levels. For each separate experiment and at each site we used χ^2-tests to compare the number of snails predated at each tidal level.

Shell breakage patterns give us clues to the size of the crab predator responsible. For example, from laboratory experiments we know that medium–large and extra-large *L. sitkana* can be crushed by *Cancer productus* larger than 90 mm and 138 mm CW respectively. Smaller crabs open these snails by peeling. We tested whether size of the crabs preying on the tethered snails varied between sites and tide levels. We used logit analysis on the proportion of predated snails that were peeled, with site, tide level and snail size as fixed variables. If smaller crabs are preying at the upper tidal level, we would expect more snails to be peeled than crushed. Cantilever Pier was not included in this analysis because tethered snails at this site experienced a very low predation rate.

The attack pattern on tethered snails was examined for spatial and temporal variability. The lead line at the 1.3 m level at Lab 6 was tested for randomness of attack because it was the only one experiencing an intermediate predation rate. The lead line was divided into eight equal sections of 10 snails each and the number of snails 'hit' in each section was recorded for all 3 days. Hits were defined as crushed and peeled shells as well as missing snails and live snails with 'chipped lips'. A chipped lip is evidence of an unsuccessful predation act (Raffaelli, 1978) in which a crab was interrupted during

the peeling process. The data from tethered snail trials between August 1989 and February 1991 were examined for patterns of temporal variation in predation rates.

2.6.2. Interpretation

Tethering artifacts probably did not affect the relative rates of predation between sites and tide levels. Tethered scallops have been found to be eaten by crabs at the same rate as untethered ones (Barbeau and Scheibling, 1994), and we observed similar predation rates on tethered and untethered snails at Roche Harbor (Needham and Behrens Yamada, in prep.). Crabs are able to move much faster than *Littorina sitkana*, so tethering is unlikely to affect the rate at which they capture snails. Tethered snails did not engage in attention-attracting behaviors in an attempt to escape the tether such as have been reported for more mobile prey (Peterson and Black, 1994). They hid in cobble and even copulated with non-tethered snails.

While peeled shells are diagnostic of crab predation (Lawton and Hughes, 1985), crushed shells can be produced by rolling rocks and fishes as well as large crabs (authors' *unpublished data*). Since all our sites were wave-protected, rolling rocks can be ruled out as a major factor. Mollusc-crushing fish species are rarer and less specialized in the northeastern Pacific intertidal than in tropical regions (Palmer, 1980; Choat, 1982). The pile perch, *Damalichthys vacca*, is a local species with pharyngeal teeth adapted for crushing mollusks (Brett, 1979). Although this fish is known to be a significant predator on *Littorina sitkana* at other wave-protected sites (McCormack, 1982), pile perch were never observed while SCUBA diving near the Cantilever Pier, Lab 6 or the Lab Pier sites (S. Norton, personal communication). The cockscomb gunnel, *Anoplarchus* spp., observed under boulders at the Lab 6 and at Roche Harbor did not possess a sufficiently large mouth to accept even an 8 mm long *Littorina sitkana* (authors' unpublished data).

Our scoring technique was conservative in that it underestimates the true rate of crab predation. Predation on tethered snails was assumed only when shells showed the diagnostic 'peel' pattern or were crushed with the apex still attached to the epoxy. Severed monofilament lines and epoxy without shell remnants were scored as 'missing' and not included in the analysis. Missing snails most likely were carried off or crushed to fine shell gravel by large crabs because we observed a correlation between the number of missing snails and number of crushed shells ($p = 0.02$).

2.7. Linking of predation rate to Cancer productus abundance

Standard crab rings (85 cm diameter), designed for sports fishing, were used to estimate the relative abundance of foraging subtidal *Cancer productus* at the four study sites between August 24 and 27, 1991. Fresh salmon heads were obtained from a local fish cannery, divided into standard bait packages of 5 heads per plastic bag and frozen. One baited crab ring was set out during high tide at the 0 m level at each of the four sites using a row boat. Rings were checked every 30 min for 2 h and the CW and sex of all caught crabs noted. This procedure was repeated once at the three laboratory sites and twice at Roche Harbor. To prevent crabs from being caught more than once, they were released over 100 m away from their capture site.

3. Results

3.1. Intertidal zonation of crabs and snails

Five species of shell-breaking crabs and two species of *Littorina* were found in the transects (Fig. 1). Other predators on *Littorina* spp., such as starfish and whelks and other grazers, such as limpets, were very rare. The density of both species of *Littorina* spp. was greatest at Cantilever Pier, with *L. sitkana* exceeding $400/m^2$. At Cantilever Pier and at Lab 6, both species of *Littorina* extended down to the 0 m level. This was not the case at Roche Harbor. Littorinid snails were extremely rare at Roche Harbor below the 1.3 m level ($< 3/m^2$) and all of those we found at this level were less than 5 mm in shell length. Significant aggregations of adult *L. sitkana* ($> 400/m^2$), however, were found at Roche Harbor near fresh water seepages and other damp refuges above the 2.5 m tidal level. These aggregations were above the mean high tide level and thus do not appear in Fig. 1.

The two *Hemigrapsus* species coexist with the two species of *Littorina* throughout the lower–mid to high intertidal zone (Fig. 1). The abundance of these crabs seemed to be correlated with the presence of gravel and rock shelter. Cantilever Pier thus had the highest density with up to 300 *Hemigrapsus* spp. per m^2 whereas the maximum density of *Hemigrapsus* spp. at Roche Harbor was only 18 $/m^2$ (Fig. 1). About 90% of the *H. nudus* ($N = 286$) and 86% of the *H. oregonensis* ($N = 570$) in our transects were less than 15 mm in CW, while the largest were 23 mm.

The other three crab species, *Lophopanopeus bellus*, *Cancer oregonensis* and juvenile *C. productus*, were primarily found below the 0 m mark, although at Roche Harbor juvenile *C. productus* extended up to the 1.3 m level (Fig. 1). Only one *C. oregonensis* was recovered at Cantilever Pier. It thus appears that *C. oregonensis* is not a major intertidal predator. The abundance of *Lophopanopeus bellus* was greatest at Cantilever Pier, intermediate at Lab 6 Beach and not found in our transect at Roche Harbor (Fig. 1). Juvenile *Cancer productus* did not exceed $5/m^2$ at any of the three sites and were mostly found under boulders. About 1.3 *C. productus* per boulder were recovered at Lab 6 and at Roche Harbor. Only one *C. productus* was recovered in the Cantilever Pier transect despite the presence of boulders. *Lophopanopeus bellus* at Cantilever and Lab 6 averaged 18 mm CW. *Cancer productus* at Lab 6 averaged 37 CW. The boulder survey at Roche Harbor yielded *C. productus* of 55 mm average and 78 mm maximum CW. Larger individuals of *C. productus* are usually not found in the intertidal at low tide unless they are molting.

3.2. Predation risk at different tidal levels

The tidal immersion time for different tidal heights at Friday Harbor follows a sigmoid curve with an inflection point in the high tidal zone (Fig. 1). At the 0 m level, organisms are submerged 93% of the time while at the 1.3 m level, 59%. Between the 0 and 1 m level, immersion time decreases gradually from 93% to 70% but between 1.5 m and 2.5 m, it decreased rapidly from 52% to only 2% immersion. Although prey are vulnerable to highly mobile marine predators at all tidal levels, their risk of predation
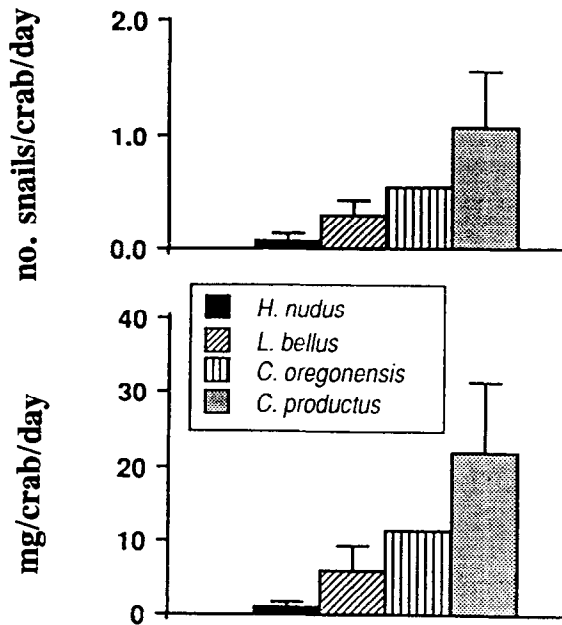
Fig. 2. Field consumption rates by predatory crabs on three size groups of *Littorina sitkana* (mean and 95% confidence interval) in field experiments 1–3. Consumption rates are given in number of snails and biomass (mg dry weight) eaten per crab per day. All crabs had similar wet biomass of 5–7 g.

becomes progressively less above the 1.5 m tidal level. Since sites above the 2.5 m level are immersed less than 2% of the time, they represent a spatial refuge from marine predators.

3.3. Ranking of per-capita prey consumption

The survival of *Littorina sitkana* in all the *Lophopanopeus bellus, Cancer oregonensis* and *C. productus* cages was significantly lower than that in control cages (Table 3; $\chi^2 > 20$, $df = 1$, $p < .001$). Since the number of empty shells were similar in crab and snail-only control cages, most of the mortality in crab cages was due to direct predation. No significant difference in snail survival was observed between *Hemigrapsus nudus* and control cages, suggesting that *L. sitkana* is not an important food item for this species when alternative food such as algae is available.

Crabs varied greatly within species and between species in terms of per-capita prey consumption (Fig. 2 Table 3). While all four crab species ate the small, medium and large size-classes of *Littorina sitkana*, the per-capita consumption rates of the three low shore crabs were significantly greater than those of *Hemigrapsus nudus*. In field experiments, *H. nudus* averaged 0.06 snails per day, *Lophopanopeus bellus*, 0.3, *C. oregonensis*, 0.5 and *Cancer productus*, 1.1 per day. The same trend was observed when consumption rate was measured in biomass. Juveniles of *C. productus* are more

Table 4
Analysis of Deviance Summary and estimation of probabilities of observing as large a deviance due to chance for tide level, size and site effects on predation rate of tethered *Littorina sitkana*. Logistic analysis was carried out on the logit or log of proportion live to predated snails per day

Factor	df	Deviance	P
Level	1	3.97	0.0463
Size	1	115.90	<0.0001
Sites	3	298.70	<0.0001
Level × Size	1	2.03	0.1542
Size × Site	3	2.28	0.5167
Level × Site	3	12.54	0.0057
Level × Roche Harbor	1	10.38	0.0013
Level × Other 3 Sites	2	2.16	0.3391
Size × Level × Site	3	3.80	0.2841
Residual	32	40.95	0.1334

voracious predators than *Lophopanopeus bellus* and *Cancer oregonensis* of similar size, possibly because they have a greater energy requirement for growth than adults of the other two species.

In contrast to the three low shore crab species, *Hemigrapsus nudus* was noticeably reluctant to eat *Littorina sitkana*. Only half of the *Hemigrapsus nudus* in field experiments 2 and 3 ate any snails (Table 3).

3.4. Role of site, tide level and size of snail on predation rate

The logistic regression analysis on the proportion of dead to live snails per day showed that site, tidal level and snail size significantly affected the predation rate on tethered *Littorina sitkana* (Table 4). On all 3 days, the ranking of the predation rates for the four sites was consistent: Cantilever Pier < Lab 6 and Roche Harbor < Lab Pier (Fig. 3). At the 0 m level, predation rate at Cantilever Pier was less than 8% per day while at the Lab Pier it was over 70% per day.

Predation was more intense at the 0 m level than at the 1.3 m level at Cantilever Pier, Lab 6 and Lab Pier. Roche Harbor differed from the other three sites in exhibiting similar predation risks at both levels (Table 4 Fig. 3). The results from our previous tethering experiment between August 1989 and February 1991 exhibited the same pattern (Table 5). About half of the seven trials at Lab 6 yielded significantly higher predation rates at the lower tidal level. In contrast, none of the three trials at Roche Harbor did (Table 5). At all four sites, extra-large snails experienced a higher mortality rate than medium–large snails (Fig. 3 Table 4).

The attack patterns on the tethered snails reflect the size structure of their predators. Of the extra-large snails that were killed, 40% were peeled and 60% were crushed outright. We know that only large *Cancer productus* of carapace width > 138 mm can crush snails that large. Of the medium–large snails, 11% were peeled and 89% were crushed. Since crabs of carapace width < 90 mm peel medium–large snails, we conclude that over 90% of all the snails were killed by subtidal adult *C. productus* > 90 mm in carapace width.
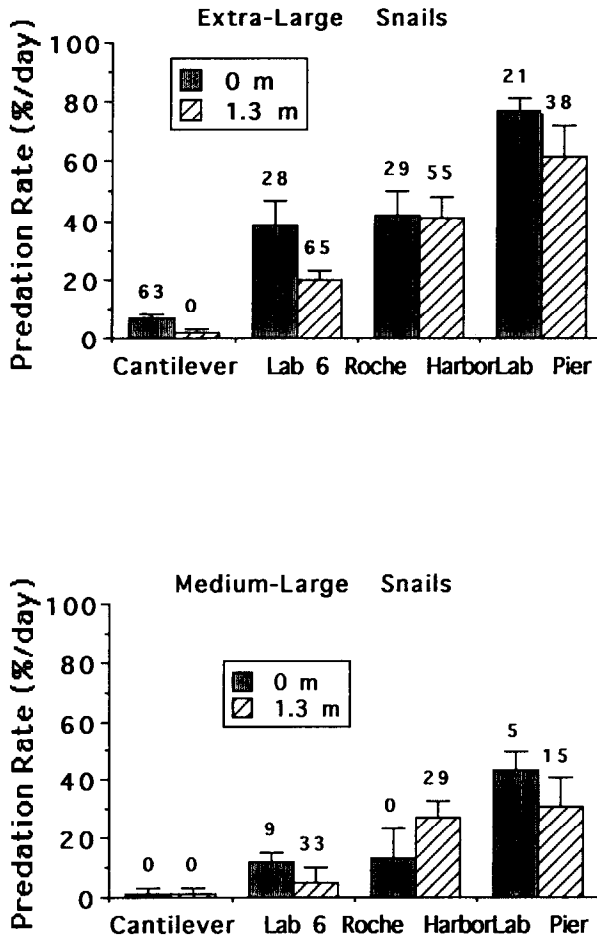
Fig. 3. Relative predation rate (% per day, mean and maximum) on *Littorina sitkana* tethered at four sites and two tidal levels (0 and 1.3 m) over 3 consecutive days. Percent predation per day was calculated by dividing the number of peeled and crushed snails by the total live and damaged shells recovered and multiplied by 100. Figures above bars represent the percent of predated snails that were opened by using the peeling technique.

Logistic regression analysis on the proportion of the predated snails that were peeled was significant for tidal level, size and site (Table 6 Fig. 3). A significantly higher percentage of *Littorina sitkana* were peeled at the 1.3 m level than at the 0 m level (Table 6 Fig. 3). This was true for both size classes of snails at all three sites that experienced significant predation (Fig. 3). Of the extra-large snails that were predated, 46% were peeled at the 1.3 m level and 27% at the 0 m level. Percent peeled for medium–large snails was 23% at the 1.3 m level and only 5% at the 0 m level. We thus conclude that crabs feeding at the 1.3 m tidal level were significantly smaller than those feeding at the 0 m tidal level and that 95% of the snails at the 0 m level were killed by crabs > 90 mm in carapace width. A significantly lower proportion of extra-large snails

were peeled at the Lab Pier than at the other two sites, indicating that this site harbored significantly more larger crabs (Fig. 3).

While the ranking of relative predation rates among the sites remained consistent (Table 5), we observed great spatial and temporal variability in the attack pattern of tethered snails. Predation rate at the 0 m level at Lab 6 varied from 3% to 47% per day (Table 5). On sequential trials, predation rate at the 1.2 m level increased from 10% to 59% from June 25 to 26 1990, but did not increase from August 21 to 22, 1990 (Table 5). The attack pattern along the 1.3 m lead line at Lab 6 did not conform to a Poisson distribution, indicating that snails were attacked in a clumped rather than a random fashion (Table 7).

3.5. Linking of predation rate to Cancer productus abundance

Crab fishing with standardized bait (five salmon heads per ring) yielded adult C. productus of both sexes, ranging in carapace width from 95 to 140 mm at all four sites. No other species of crab was caught. Cantilever Pier had the lowest abundance with < 2 crabs per h, while the Lab Pier had the highest with > 16 crabs per h. A significant positive correlation was found between predation rate on tethered snails at the 0 m tidal level and the relative abundance of subtidal, adult C. productus at the same site a few days later (Fig. 4).
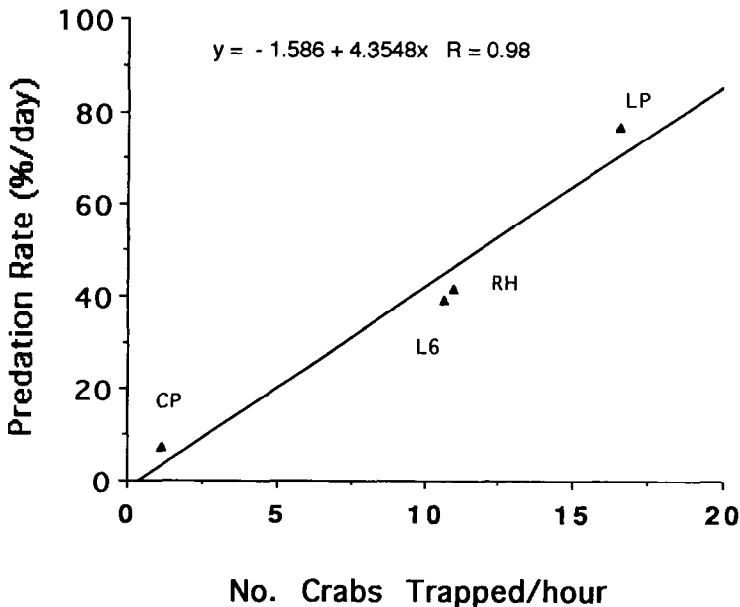

Fig. 4. Regression of relative predation rate (% per day) on *Littorina sitkana* tethered at the 0 m tidal level and relative abundance of *Cancer productus* (No. trapped per hour at high tide) at the same tidal level a few days later. Sites are indicated: CP = Cantilever Pier, L6 = Lab 6, RH = Roche Harbor and LP = Lab Pier. The regression was significant at $p < 0.02$.

Table 5
Comparison of crab predation rate at different tidal levels on three shores

Site	Date	Days	Tidal level (m)	Live	Peeled	Crushed	Missing	% Eaten[a]	p
Canti-	6/23/90	1	0.0	27	2	1	0	10	
lever		1	0.6	30	0	0	0	0	*
Pier		1	1.2	30	0	0	0	0	
	2/09/91	1	0.0	34	4	1	1	13	
		1	0.6	39	1	0	0	3	*
		1	1.2	39	0	0	0	0	
Lab 6	8/25/89	5	0.0	19	0	4	5	17	N.S.
		5	0.6	22	0	5	2	19	
	1/25/90	2	−0.3	37	6	1	31	19	
		2	0.6	64	0	0	17	0	<0.005
		2	1.2	88	1	1	8	1	
	6/25/90	1	0.0	24	4	1	1	17	
		1	0.6	21	0	6	3	22	N.S.
		1	1.2	28	0	3	0	10	
	6/26/90	1	0.0	18	2	5	4	28	
		1	0.6	19	4	4	2	30	N.S.
		1	1.2	11	9	7	0	59	
	8/21/90	1	0.3	20	10	8	3	47	<0.01
		1	0.9	33	2	3	2	13	
	8/22/90	1	0.3	26	5	7	2	32	<0.025
		1	0.9	36	0	3	1	8	
	2/09/91	1	0.0	36	0	1	3	3	
		1	0.6	40	0	0	0	0	*
		1	1.2	39	0	0	0	0	
Roche	8/27/89	2	0.0	25	0	5	6	17	N.S.
Harbor		2	0.6	26	0	5	4	16	
	3/19/90	4	0.3	59	8	20	11	32	
		4	0.6	40	9	9	4	31	N.S.
		4	1.2	37	11	8	4	33	
	6/25/90	1	0.0	10	6	1	8	41	N.S.
		1	1.4	20	2	1	2	13	

The fate of medium to large tethered *Littorina sitkana* (9–14 mm) was scored as live, peeled, crushed and missing. No distinction was made between peeled and crushed shells prior to 1990, when both peeled and crushed shells were scored as crushed. Missing snails were not included in mortality or in calculating expected frequencies for the one-way x^2. p values are from x^2 tests that mortality rates were equal for the different tidal levels.* Indicates that too few snails were crushed to permit a x^2-test.[a] % Eaten = number peeled + number crushed divided by total recovered.

4. Discussion

4.1. Causes of zonation

The interaction of physical and biological factors is a common theme of biotic zonation patterns in both terrestrial and marine environments. Prey are often excluded from a physically benign part of their potential habitat by the foraging activities of a

Table 6

Analysis of deviance summary and estimates of probabilities of observing as large a deviation due to chance for tide level, size and site effects on proportion of predated *Littorina sitkana* that were peeled

Factor	df	Deviance	p
Level	1	28.63	<0.0001
Size	1	26.85	<0.0001
Sites	2	10.24	0.0060
Level × Size	1	0.84	0.3605
Size × Site	2.	0.10	0.9517
Level × Site	2	2.07	0.3554
Size × Level × Site	3	2.26	0.3225
Residual	24	30.52	0.1680

Logistic Regression was carried out on the logit or log of proportion of peeled snail shells to total peeled and crushed shells. Cantilever Pier was omitted from the analysis due to low predation rates.

predator. When a predator is physiologically restricted from fully exploiting the harsher habitats, one finds peak prey and predator abundances in different biotic zones. For example, ants and other insects are rare inside ant-lion zones (Gotelli, 1993), and certain mangroves and sage brush species are rare in zones where seed predators are common (Smith et al., 1989; Louda, 1982). Similar patterns emerge in intertidal communities. For example, the lower limit of the mussel zone is set by the upper limit at which starfish are capable of foraging within one high tide (Paine, 1966, 1974). While the effect of slow moving intertidal predators such as starfish and drilling snails on the zonation of their prey is well understood (Paine, 1966, 1974; Connell, 1961a), the effect of highly mobile crabs is not. Our experiments show that the intertidal zonation of the gastropod, *Littorina sitkana*, is affected by highly mobile crabs from the subtidal zone and that the effect of the crabs varies in time and space.

The crabs that prey on *L. sitkana* can be divided into three groups based on the upper limit of their distribution when the tide is out: (1) mid-shore crabs *(Hemigrapsus nudus*

Table 7

Testing for randomness in the attack patterns of snails tethered along the leadline at the 1.3 m level at Lab 6 over three consecutive high tides (August 21–24, 1991). The frequency of snails 'hit' per section of lead line was compared with that of a Poisson distribution

Number of L. sitkana 'hit' per section of lead line	Observed frequency	Number of 'hits' per category	Poisson frequency		χ^2 contribution
0	6	0	4.533		0.475
1	3	3	7.556		2.747
2	11	22	6.296		3.515
3	2 ⎫	6	3.498 ⎫		
4	1 ⎬ 4	4	1.457 ⎬ 5.44		0.381
5	1 ⎭	5	0.486 ⎭		
Total	24	40	23.83		$\chi^2 = 7.118*$

* $P < 0.05$

and *H. oregonensis*), (2) low shore crabs (*Lophopanopeus bellus, Cancer oregonensis* and juvenile *C. productus*), and (3) subtidal crabs (adult *Cancer productus*). The upper limit of the mid-shore crabs is higher than that of the low shore and subtidal crabs because of their greater physiological tolerance of emersion stress. *Hemigrapsus* spp. osmoregulate (Dehnel and Carefoot, 1965), and fully compensate for emersion-induced acidosis (Burnett and McMahon, 1987), and even forage at low tide (E.G. Boulding, personal observation). In contrast, juvenile *Cancer productus* are sensitive to low oxygen tensions and to acidosis of their body fluids during aerial exposure. Adult *C. productus* are even more sensitive than the juveniles (DeFur and McMahon, 1984a,b).

The physiological tolerances of the three groups of crabs to emersion stress is inversely correlated to the rate at which they consume adult *Littorina sitkana* (shell length > 5 mm). In our field cages, *Hemigrapsus nudus* consumed substantially fewer snails (0.06 snail per day) than the low shore crabs: *Lophopanopeus bellus* (0.3 snails per day), *Cancer oregonensis* (0.5 snails per day) and juvenile *C. productus* (1.1 snails per day) of equal body mass (4–7 g). The subtidal adult *C. productus* are much larger (> 150 g) and consume over 60 times as many snails (C. Needham, unpublished data) than the smaller mid-shore and low shore crabs.

The intertidal distribution of *Littorina sitkana* and *L. scutulata* overlap widely with the mid-shore crabs of the genus *Hemigrapsus*. Despite their high abundance (up to 300 crabs per m^2), these mid-shore crabs do not exclude the snails from the mid-intertidal zone on the wave protected beaches of San Juan Island. While very large, male *H. nudus* (> 30 mm CW) are capable of efficiently crushing adult *Littorina sitkana* outright (S. Behrens Yamada and E.G. Boulding, in prep.), and can be significant predators on adult and juvenile snails at wave-exposed sites on the outer coast (Boulding and Van Alstyne, 1993), the largest *Hemigrapsus nudus*, we used in our field cages (17–27 mm CW) consumed adult *Littorina sitkana* at a very low rate (< 0.1 per day). Since the median size of the *Hemigrapsus* spp. in our study sites is < 15 mm in CW, much smaller than those in our cages, their impact would be even less. Further field and laboratory experiments with smaller *H. nudus* (14–17 mm CW) and smaller *Littorina sitkana* (2–6 mm) yielded even lower predation rates (authors' unpublished data). Thus, the coexistence between *Littorina* spp. and *Hemigrapsus* spp. is possible on the wave-protected beaches of San Juan Island because these crabs are inefficient predators on adult snails and prefer alternative prey (S. Behrens Yamada, unpublished data).

At low tide, the distribution of the low shore and subtidal crabs (*Lophopanopeus bellus, Cancer oregonensis* and juvenile and adult *C. productus*) do not overlap with that of *Littorina* spp. which suggests that predation by any or all of these crabs could be responsible for setting the lower limit of these snails. The density of *Cancer oregonensis* was the lowest, *Lophopanopeus bellus* intermediate and juvenile *Cancer productus* the highest, suggesting that the latter was the most important predator. The upper distribution of the low shore crabs is below the 0 m tidal level at Cantilever Pier and Lab 6 but not at Roche Harbor where juvenile *C. productus* reach a tide level of 1.3 m. This upward shift in the upper distribution of this low shore crab coincides with an upward shift in the lower distribution of *Littorina* spp., again suggesting that crab predation may set the lower distribution of their prey.

4.2. Assessing predation risk at different tidal levels

Four lines of evidence suggest that subtidal adult *Cancer productus* were responsible for killing most of the tethered snails. First, *C. productus* > 90 mm but < 138 mm in carapace width are the only predators on these shores that can crush medium–large (9.2–11.8 mm) *Littorina sitkana* outright, but must peel extra-large (14.6–17.3 mm) *L. sitkana*. Second, significantly more extra-large than medium–large *L. sitkana* were killed at all four sites. This pattern is consistent with the feeding preference of large adult *Cancer productus* (Behrens Yamada and Navarrete, in prep.). Third, peeled and crushed shells were produced after we directly observed large *C. productus* attacking tethered snails below the Friday Harbor Lab Pier (Walker and Behrens Yamada, 1993). Fourth, test fishing at the 0 m tidal level at the four sites yielded a positive correlation between *C. productus* abundance and predation rate on tethered snails. Taken together, this evidence strongly indicates that large subtidal *C. productus* are the dominant predators on *Littorina sitkana* on these wave-sheltered beaches.

Our direct measurement of total predation rates on tethered *L. sitkana* suggest that risk of predation decreases up the shore with decreasing immersion time. Our data from the tethering experiment in August 1991 showed that the risk of predation was significantly less at the higher tidal level (1.3 m) than at the lower tidal level (0.0 m) at three of the four sites. Thus, the risk of predation was generally greater in the low intertidal (0 m) which was submerged 93% of the time, than in the mid-intertidal (1.3 m) which was submerged 59% of the time. This is the same general pattern that has been shown for slow moving intertidal predators (e.g., Connell, 1961a; Paine, 1966). Departures from this general pattern can be explained by local shifts in the desiccation gradient and by the aggregation response of mobile predators.

Roche Harbor differed from the other three sites in exhibiting similar predation rates at the low and mid-tide level in all the trials between 1989 and 1991. As mentioned earlier, this site is unusual in that fresh water seepage, combined with boulders embedded in a fine gravel and mud substratum provide damp refuges at low tide for large juvenile *Cancer productus* up to the 1.3 m tidal level. We believe that these unusually damp conditions at this site cause an upward shift in the desiccation gradient. Snails at the 1.3 m tidal level thus have no refuge from these low shore crabs. If we had positioned the lead lines well above the 1.3 m level, we predict that we would have detected decreasing predation pressure with increasing tidal height. At Roche Harbor, *Littorina sitkana* thrive in damp crevices above the 2.5 m level. Since this level is inundated by the tide only 2% of the time, it provides a spatial refuge from *Cancer productus*.

In contrast to slow moving predators that have well-defined foraging zones, highly mobile predators are capable of exploiting patches of high prey abundance even in ephemerally favorable habitats such as the mid and high intertidal zone. Adult *C. productus* can easily forage up to the upper intertidal zone and return to the subtidal during one high tide period, perhaps carrying prey with them (Boulding and Hay, 1984). Prey scarcity in the lower, most accessible zone may drive mobile predators such as *C. productus* to move rapidly to better feeding grounds in the higher tidal zones as soon as

these zones are covered by the tide (Robles et al., 1989 and Navarrete, personal communication). On two subsequent days in June 1990, the predation rate on tethered snails in the mid-zone at Lab 6 increased from 10% per day to 59% per day. This pattern may suggest that some crabs 'learn' to return to food sources in the mid-tidal zone and that their feeding activities attract others. The clumped attack patterns on snails along the lead lines also supports the view that crabs aggregate to feed. *C. productus* have well-developed, amino-acid sensitive chemoreceptors (Case, 1964), and thus are attracted to chemicals exuding from live and damaged prey. Clams in high density patches experienced a significantly higher mortality rate from *C. productus* than clams in low density patches (Boulding and Hay, 1984). Field observations from the Lab Pier suggest that once prey in a high density patch is attacked by one crab, the increased chemical signal from the damaged prey rapidly attracts more crabs (Walker and Behrens Yamada, 1993). Since *C. productus* aggregate to forage in areas of high prey abundance (Boulding and Hay, 1984), including such ephemerally favorable habitats as the mid and high intertidal (Robles et al., 1989), their effect on their prey is less predictable in both space and time than that of slower moving predators.

4.3. Intertidal distribution and abundance of Littorina sitkana

Littorina sitkana may be absent from the lower intertidal either because mortality from predators is higher there and/or they select higher intertidal habitats when predators are present. *L. littorea* is known to adjust its vertical distribution by responding to gravity, light, surface tension (Newell, 1979) and to water-borne chemical cues exuding from damaged conspecifics (Hadlock, 1980). When *L. sitkana* were exposed to *Cancer productus* feeding on conspecific snails, they exhibited strong escape behavior by migrating up the shore (Needham and Behrens Yamada, in prep.). This behavior has a definite survival advantage on beaches with a high *C. productus* abundance such as Roche Harbor. By releasing marked *Littorina sitkana* at the 1.5 m tidal level at this site and retrieving them after one tidal cycle, we demonstrated that a high proportion of those snails that failed to migrate up the shore were retrieved as crushed and peeled shells (Needham and Behrens Yamada, in prep.). Similar upward migrations to water-borne stimuli from crushed conspecifics and predatory crabs have been observed for *Nucella lapillus* (Vadas et al., 1994). While escape behavior from predators plays a role in determining the intertidal distribution of *Littorina sitkana*, the relative importance of this factor compared to predator-caused mortality was not determined.

It appears that the current lower limit of *L. sitkana* on San Juan Island beaches represents a trade-off between the increased risk of predation at lower levels and the reduced fecundity higher on the shore. Another snail, *Tegula funebralis*, migrates to a lower intertidal zone upon reaching a size of 12 mm; the risk of predation from starfish increases in the low intertidal but the fecundity of snails that fail to migrate down is substantially lower (Paine, 1969). In the absence of predators, *Littorina sitkana* with its direct development, has the potential to populate the whole intertidal zone (Behrens, 1972; Behrens Yamada, 1992). Indeed, growth rate, fecundity and juvenile survival in littorines increase with longer submergence time (Boulding, 1990; Behrens Yamada and Mansour, 1987; McQuaid, 1983). When *L. sitkana* were caged at the 0.7 m level at Lab

6 Beach, they exhibited excellent survival, growth and reproduction (Behrens Yamada, 1989). If the risk of predation was uniformly low throughout the intertidal, one would expect high densities of large *L. sitkana* lower on the shore. Circumstantial evidence confirming this prediction was found on an oyster lease south of Courtney, British Columbia (49°40'N, 124°54'W) where crab and starfish predators were controlled. On the lease, high densities of *L. sitkana* and their egg masses were found in the lower intertidal zone (Behrens Yamada, unpublished observation). In contrast, at Roche Harbor where both intertidal juvenile and subtidal adult *Cancer productus* are abundant higher on the shore than at the other three sites, *Littorina sitkana* are common only in damp refuges above the 2.5 m level.

Differences in the rate of predation by subtidal *Cancer productus* appears to be responsible for differences in the abundance in *Littorina sitkana* among the different protected sites. The risk of predation at all four sites for adult *L. sitkana* was correlated with the abundance of subtidal *Cancer productus*. The ranks of the risk of predation at the three sites for which we have data were the same as the ranks of the natural abundances of *L. sitkana*.

4.4. Predator invasions and the biogeography of Littorina sitkana

We predict that the invasion of the upper intertidal zone by a more efficient predatory crab would result in the local extinction of *L. sitkana*. Unlike species with planktonic dispersal, direct developers, like *L. sitkana*, can maintain viable populations only in those habitats in which all life stages can persist (Behrens, 1972). The southern limit of the geographical distribution of *L. sitkana* coincides with the northern limit of another shell-breaking crab, the grapsid *Pachygrapsus crassipes* (Behrens Yamada, 1977a). *P. crassipes* has claws modified for crushing hard-shelled prey (Brown et al., 1979; Lindberg, 1985; S. Behrens Yamada, unpublished data), and is physiologically adapted to live in the upper intertidal (Burnett and McMahon, 1987).

We may soon be able to test the above prediction with the introduction of the European green crab, *Carcinus maenas*, to Central California. This species appeared in San Francisco Bay in 1989 and within 4 years has spread 200 km north to Bodega Bay (Grosholz and Ruiz, 1995). This fast growing and rapidly dispersing species is a physiological and ecological generalist and is expected to have a major impact on intertidal communities from Alaska to Baja California. Its impact on poorly-dispersing direct developers, such as *Littorina sitkana*, could be especially devastating.

References

Barbeau, M.A. and R.E. Scheibling, 1994. Procedural effect of prey tethering experiments: predation of juvenile scallops by crabs and sea stars. *Mar. Ecol. Progr. Ser.*, Vol. 111, pp. 305–310.

Barkai, A. and G.M. Branch, 1988. The influence of predation and substrata complexity on recruitment to settlement plates: a test of the theory of alternative states. *J. Exp. Mar. Biol. Ecol.*, Vol. 124, pp. 215–237.

Behrens, S., 1972. The role of wave impact and desiccation on the distribution of *Littorina sitkana* (Philippi, 1845). *Veliger*, Vol. 15, pp. 129–132.

Behrens Yamada, S., 1977a. Geographic range limitation of the intertidal gastropods *Littorina sitkana* and *L. planaxis*. *Mar. Biol.*, Vol. 39, pp. 61–65.

Behrens Yamada, S., 1977b. Range extension in *Littorina sitkana* (Philippi, 1845) and range contraction in *L. planaxis* (Philippi, 1847). *Veliger*, Vol. 19, p. 368.

Behrens Yamada, S., 1989. Are direct developers more locally adapted than planktonic developers? *Mar. Biol.*, Vol. 103, pp. 403–411.

Behrens Yamada, S., 1992. Niche relationships in Northeastern Pacific Littorines. In, *Proceedings of the Third International Symposium on Littorinid Biology* edited by J. Grahame, P.J. Mill and D.G. Reid. The Malacological Society of London, UK, pp. 281–291.

Behrens Yamada, S. and R.A. Mansour, 1987. Growth inhibition of native *Littorina saxatilis* by introduced *L. littorea*. *J. Exp. Mar. Biol. Ecol.*, Vol. 105, pp. 187–196.

Behrens Yamada, S., S.H. Metcalf and B.C. Baldwin, 1993. Predation by the crab, *Cancer oregonensis*, inside oyster trays. *J. Shellfish Res.*, Vol. 12, pp. 89–92.

Bernard, F.R., 1979. The food of Hecate Strait crabs, August 1977. Manuscript Report, *Fish. and Mar. Ser. Canada*, Vol. 1464, pp. 1–23.

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

Boulding, E.G., 1990. Systematics, ecology and ecological genetics of some northeastern Pacific *Littorina*. Ph.D thesis, Department of Zoology, University of Washington, Seattle, Washington, 239 pp.

Boulding, E.G. and K. Van Alstyne, 1993. Mechanisms resulting in differential survival and growth of two species of *Littorina* on wave exposed and on protected shores. *J. Exp. Mar. Biol. Ecol.*, Vol. 169, pp. 139–166.

Boulding, E.G. and 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.

Boulding, E.G., J. Buckland-Nicks and K.L. Van Alstyne, 1993. Morphological and allozyme variation in *Littorina sitkana* and related Littorina species from the Northeastern Pacific. *Veliger*, Vol 36, pp. 43–68.

Brett, J.R., 1979. Some morphological and behavioral adaptations of pile perch (*Rhacochilus vacca*) feeding on mussels (*Mytilus edulis*). *Can. J. Zool.*, Vol. 57, pp. 658–664.

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

Buckland-Nicks, J., F.S. Chia and S. Behrens, 1973. Oviposition and development of two intertidal snails, *Littorina sitkana* and *Littorina scutulata. Can. J. Zool.,* Vol. 51, pp. 359–365.

Burnett, L.E. and B.R. McMahon, 1987. Gas exchange, hemolymph acid-base status and the role of branchial water stores during air exposure in three littoral crab species. *Physiol. Zool.,* Vol. 60, pp. 27–36.

Case, J., 1964. Properties of the dactyl chemoreceptors of *Cancer antennarius* Stimpson and *C. productus* Randall. *Biol. Bull.,* Vol. 127, pp. 428–446.

Castilla, J.C. and R.T. Paine, 1987. Predation and community organization on eastern Pacific, temperate zone, rocky intertidal shores. *Revista Chilena de Historia Natural,* Vol. 60, pp. 131–151.

Choat, J.H., 1982. Fish feeding and the structure of benthic communities in temperate waters. *Ann. Rev. Ecol. Syst.,* Vol. 13, pp. 423–449.

Connell, J.H., 1961a. Effect of competition predation by *Thais lapillus* and other factors on the distribution of the barnacle *Balanus balanoides. Ecol. Monogr.,* Vol. 31, pp. 61–104.

Connell, J.H., 1961b. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus. Ecology,* Vol. 42, pp. 710–723.

Connell, J.H., 1972. Community interaction on marine rocky intertidal shores. *Ann. Rev. Ecol. Syst.,* Vol. 3, pp. 169–192.

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

Dayton, P.K., 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. *Ecol. Monogr.* Vol. 45, pp. 137–159.

DeFur, P. and B.R. McMahon, 1984a. Physiological compensation to short-term air exposure in red rock crabs, *Cancer productus* Randall, from littoral and sublittoral habitats. I. Oxygen uptake and transport. *Physiol. Zool.,* Vol. 57, pp. 137–150.

DeFur, P. and B.R. McMahon, 1984b. Physiological compensation to short-term air exposure in red rock crabs, *Cancer productus* Randall, from littoral and sublittoral habitats. II. Acid-base balance. *Physiol. Zool.,* Vol. 57, pp. 151–160.

Dehnel, P.A. and T.H. Carefoot, 1965. Ion regulation in two species of intertidal crabs. *Comp. Biochem. Physiol.,* Vol. 15, pp. 377–397.

Ebling, F.J., J.A. Kitching, L. Muntz and C.M. Taylor, 1964. The ecology of Lough Ine. XIII. Experimental observations on the destruction of *Mytilus edulis* and *Nucella lapillus* by crabs. *J. Anim. Ecol.,* Vol. 33, pp. 73–82.

Edwards, D.C., D.O. Conover and F. Sutter, 1982. Mobile predators and the structure of marine intertidal communities. *Ecology,* Vol. 63, pp. 1175–1180.

Foster, M.S., A.P. DeVogelaere, C. Harrold, J.S. Pearse and A.B. Thum, 1988. Causes of spatial and temporal patterns in rocky intertidal communities in central and northern California. *Mem. Calif. Acad. Sci.,* No. 9. 45 pp.

Gotelli, J.N., 1993. Ant lion zones: causes of high-density predator aggregations. *Ecology,* Vol. 74, pp. 226–237.

Grosholz, E.D. and G.M. Ruiz, 1995. The spread and potential impact of the recently introduced European green crab, *Carcinus maenas,* in central California. *Mar. Biol.* Vol. 122, pp. 239–247.

Hadlock, R.P., 1980. Alarm response of the intertidal snail *Littorina littorea* to predation by the crab *Carcinus maenas. Biol. Bull.,* Vol. 159, pp. 269–279.

Hawkins, S.J. and R.G. Hartnoll, 1985. Factors determining the upper limits of intertidal canopy-forming algae. *Mar. Ecol. Prog. Ser.,* Vol. 20, pp. 265–271.

Keen, A.M., 1937. An abridged check list and bibliography of West North American marine mollusca. Stanford University Press, Stanford, California, USA. 87 pp.

Knudsen, J.W., 1964. Observations of the reproductive cycles and ecology of the common Brachyura and crab-like Anomura of Puget Sound, WA. *Pacific Sci.,* Vol. 18, pp. 3–33.

Kozloff, E.N., 1983. *Seashore life of the northern Pacific coast.* An illustrated guide to Northern California, Oregon, Washington and British Columbia. University of Washington Press, Seattle, USA. 370 pp.

Lawton, P. and R.W. Elner, 1985. Feeding in relation to morphometrics within the genus *Cancer*: evolutionary and ecological considerations. Proceedings of the Symposium on Dungeness Crab Biology and Management. *Alaska Sea Grant Report,* Vol. 85–3, pp. 357–379.

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

Lindberg, R., 1985. Crab predation on intertidal populations of the urchin *Strongylocentrotus purpuratus. Bull. S. Calif. Acad. Sci.*, Vol. 84, pp. 109–111.

Louda, S.M., 1982. Distribution ecology: variation in plant recruitment over a gradient in relation to insect seed predation. *Ecol. Monogr.*, Vol. 52, pp. 25–41.

Lubchenco, J., 1980. Algal zonation in the New England rocky intertidal community: an experimental analysis. *Ecology*, Vol. 61, pp. 333–344.

McCormack, S.M.D., 1982. Maintenance of shore-level size gradients in an intertidal snail (*Littorina sitkana*). *Oecologia (Berlin)*, Vol. 54, pp. 177–183.

McQuaid, C.D., 1983. Population dynamics and growth of the gastropod *Oxystele variegata* (Anton) on an exposed rocky shore. *S. Afr. J. Zool.*, Vol 18, pp. 56–61.

Menge, B.A., 1972. Foraging strategy of a starfish in relation to actual prey availability and environmental predictability. *Ecol. Monogr.*, Vol 42, pp. 25–50.

Menge, B.A., 1983. Components of predation intensity in the low zone of the New England rocky intertidal region. *Oecologia (Berlin)*, Vol. 58, pp. 141–155.

Menge, B.A. and J. Lubchenco, 1981. Community organization in temperate and tropical rocky intertidal habitats: prey refuges in relation to consumer pressure gradients. *Ecol. Monogr.*, Vol. 51, pp. 429–450.

Merriam, C.H., 1894. Laws of temperature control of the geographic distribution of terrestrial animals and plants. *Nat. Geogr. Mag.*, Vol. 6, pp. 229–238.

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

Muntz, L., F.J. Ebling and J.A. Kitching, 1965. The ecology of Lough Ine XIV. Predatory activity of large crabs. *J. Anim. Ecol.*, Vol. 34, pp. 315–329.

Nelder, J.A. and R.W.M. Wedderburn, 1972. Generalized linear models. *J. Royal Stat. Soc.*, Series A, Vol. 35, pp. 370–384.

Newell, R.C., 1979. *Biology of intertidal animals*. Marine Ecological Survey Ltd., Kent. 781 pp.

Paine, R.T., 1966. Food web complexity and species diversity. *Am. Nat.*, Vol. 100, pp. 65–75.

Paine, R.T., 1969. The *Pisaster-Tegula* interaction: prey patches, predator food preference, and intertidal community structure. *Ecology*, Vol. 50, pp. 950–961.

Paine, R.T., 1974. Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia (Berlin)*, Vol. 15, pp. 93–120.

Paine, R.T. and A.R. Palmer, 1978. *Sicyases sanguineus*: a unique trophic generalist from the Chilean intertidal zone. *Copeia*, 1978, pp. 75–80.

Palmer, A.R., 1980. *A comparative and experimental study of feeding and growth in thaidid gastropods*. Dissertation. University of Washington, Seattle, Washington, USA.

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.

Peterson, C.H., 1979. The importance of predation and competition in organizing the intertidal epifaunal communities of Barnegat Inlet, New Jersey. *Oecologia (Berlin)*, Vol. 39, pp. 1–24.

Peterson, C.H. and R. Black, 1994. An experimentalist's challenge: when artifacts of intervention interact with treatments. *Mar. Ecol. Progr. Ser.*, Vol. 111, pp. 289–297.

Raffaelli, D.G., 1978. The relationship between shell injuries, shell thickness and habitat characteristics of the intertidal snail *Littorina rudis* Maton. *J. Moll. Stud.*, Vol. 44, pp. 166–170.

Robles, C., 1987. Predator foraging characteristics and prey population structure on a sheltered shore. *Ecology*, Vol. 68, pp. 1502–1514.

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

Robles, C., D. Sweetham and D. Dittman, 1989. Diel variation of intertidal foraging by *Cancer productus* in British Columbia. *J. Nat. Hist.*, Vol. 23, pp. 1041–1049.

Smith, T.J., H.T. Chan, C.C. McIvor and M.B. Robblee, 1989. Comparisons of seed predation in tropical tidal forests from three continents. *Ecology*, Vol. 70, pp. 146–151.

Underwood, A.J. and E.J. Denley, 1984. Paradigms, explanations and generalizations in models of the structure of intertidal communities on rocky shores. In, *Ecological Communities: Conceptual Issues and the Evidence*, edited by D.R. Strong, D. Simberloff, L. Abele and A.B. Thistle, Princeton University Press. pp. 151–180.

Vadas, R.L., M.T. Burrows and R.N. Hughes, 1994. Foraging strategies of dogwhelks, *Nucella Lapillus* (L): interacting effects of age, diet and chemical cues to the threat of predation. *Oecologia*, Vol. 100, pp. 439–450.

Walker, S. and S. Behrens Yamada, 1993. Implications for the gastropod fossil record of mistaken crab predation on empty mollusc shells. *Palaeontology*, Vol. 36, pp. 735–741.

Warman, C.G., D.G. Reid and E. Naylor, 1993. Variation in the tidal migratory behavior and rhythmic light-responsiveness in the shore crab *Carcinus maenas. J. Mar. Biol. Assoc. U.K.*, Vol. 73, pp. 355–364.

Whittaker, R.H., 1975. *Communities and ecosystems*. MacMillan Publ. Co., New York, New York, USA.

Zipser, E. and G.J. Vermeij, 1978. Crushing behavior of tropical and temperate crabs. *J. Exp. Mar. Bio. Ecol.*, Vol. 31, pp. 155–172.