



Claw morphology, prey size selection and foraging efficiency in generalist and specialist shell-breaking crabs

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Abstract

Claw morphology, and claw-closing forces of four species of intertidal crabs from San Juan Island, Washington were compared and related these findings were related to prey size selection, shell breaking times and total handling times on their snail prey, *Littorina sitkana* Philippi. Two functional groups of crabs emerged: generalists and specialists on hard-shelled prey. The generalist, *Hemigrapsus nudus* (Dana), has an omnivorous diet and possesses weak claws with small, fine denticles and mechanical advantage (MA) of the claw's lever system < 0.3 , while the specialists, *Lophopanopeus bellus* (Stimpson), *Cancer oregonensis* (Dana) and *C. productus* (Randall), consume hard-shelled prey and possess large, powerful claws with broad, blunt molars and $MA > 0.3$. The claws of the generalist, *H. nudus*, exhibited weaker claw closing forces (5 N) than those of similar sized specialists (> 12 N). When crabs of similar weight were offered four size categories of *Littorina sitkana*, the generalist, *Hemigrapsus nudus*, exhibited a consistent preference for the smallest size categories, while the three specialists attacked all size classes offered. *Hemigrapsus nudus* took significantly longer (134 s) than the specialists (30–52 s) to break open a 4 mm *L. sitkana*. This difference in shell-breaking time between the generalist and the specialists increased with increasing prey size. The rate of successful attacks on increasingly larger *L. sitkana* decreased with prey size in the generalist (70% on 4 mm, 37% on 6 mm, and 0% on 8 mm snails), but remained high in the specialists (70–100%). Strength limitation of the claws is the best hypothesis to explain the avoidance of large snails by the generalist, *H. nudus*.
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1. Introduction

The design of a predator's feeding structure can influence a predator's success, and therefore the size structure and population dynamics of its prey. For example, the geometry and morphology of the grasping foreleg of praying mantids, beaks of birds, crushing mouthparts of fishes, and the claws of decapod crustaceans can affect the type and size of prey they select, and consequently the size–structure of their prey populations (Holling, 1964; Sanchez-Salazar et al., 1987; Wainwright, 1987; Benkman, 1993). Predators that prey on only one type of prey often possess more specialized feeding structures than predators with broader diets. For example, the beaks of red crossbills (*Loxia curvirostra*), with their mandibular crossings, are specialized to pry open the closed seed cones of conifers, while the more generalized beaks of pine siskins (*Carduelis pinus*) are less efficient at opening these cones (Benkman and Lindholm, 1991). Similarly, tropical crabs that feed primarily on heavily armored gastropods typically possess more powerful and more specialized claws than more omnivorous crabs (Zipser and Vermeij, 1978; Bertness and Cunningham, 1981; Hughes, 1989). Crabs with claw morphologies specialized for opening hard-shelled prey can select for predator-resistant shell morphologies in the prey, which in turn can select for crabs with even more specialized claws. Such an arms race may be responsible for the greater resistance of tropical Pacific gastropods to tropical crab predators relative to gastropods from the tropical Atlantic that normally experience less specialized crab predators (Vermeij, 1976). Here we test the hypothesis that crabs with powerful, specialized claws are more efficient predators on shelled snails than crabs with weaker, more generalized claws.

Biomechanical analyses of decapod crustacean claws have shown that it is mechanically impossible to design a claw that is both fast and strong (Alexander, 1968; Warner, 1977). Claws that are long relative to their height have a high tip velocity per unit distance contracted by the muscles attached to the apodeme, but a low mechanical advantage. These fast claws typically have fine, sharp denticles and fast muscles with short sarcomeres. Strong claws, on the other hand, have greater propal heights and widths, a higher mechanical advantage, blunt, broad molars, and more slowly contracting strong muscles with long sarcomeres (Alexander, 1968; Atwood, 1973; Warner, 1977). The claws in some families, such as the Grapsidae and Cancridae, are monomorphic, while those in others, such as the Xanthidae and Portunidae, are dimorphic with each crab possessing both a fast and a strong claw (Warner, 1977). This claw dimorphism may allow these latter species to potentially feed on both fast and hard prey (Abby-Kalio and Warner, 1984). Despite this diversity of decapod claw form, there has been little investigation into how claw morphology translates into prey size selection and feeding efficiency.

Many factors play a role in prey size selection in crabs including: the size relationship between crab and prey, degree of satiation, claw gape, claw strength, dentition and total prey-handling time. Experimental studies with crabs in a laboratory setting have shown that starved crabs will open very large prey items, but satiated crabs select prey within a limited size-range (Elner and Hughes, 1978; Boulding, 1984; Lawton and Hughes, 1985; Hughes, 1989; Juanes and Hartwick, 1990). To some extent prey size selection is a

consequence of the geometry of the crab's claw relative to that of the shell of the prey. For example, *Cancer pagurus* uses two methods of opening *Littorina littorea* depending on the relationship between the diameter of the prey's shell and the gape of the crab's claw (Lawton and Hughes, 1985). Snails small enough to fit within the gape are crushed outright by a contraction of the claw. There is little variation in the shell-breaking time for shells being crushed outright, although thick-shelled snails may require repeated applications of force (Lawton and Hughes, 1985). Snails that are too large to fit within the gape, or those with thick shells, must be 'peeled' by progressively breaking back the lip of the shell aperture. The propus (fixed finger) or dactyl (movable finger) of one claw is inserted into the shell aperture and used to grasp the columella, the other claw is used to apply force repeatedly to the apertural margin (Lawton and Hughes, 1985). Repeated force application to the apertural margin of the shell results in the chipping of a spiral channel up the center of the outer lip of the aperture. The time required to peel thick-walled gastropod shells increases exponentially with shell length (Lawton and Hughes, 1985). This substantial increase in shell-breaking time is probably an important cause of size selection by crabs, especially by generalists.

The objectives of this study are three-fold: (1) to classify five common species of Northeastern Pacific crabs as either mollusc specialists or generalists, using morphological criteria derived from the literature, (2) to compare claw morphology, claw closing forces, prey size selection, shell-breaking time and total prey-handling time in generalist and specialist crabs using the common intertidal snail, *Littorina sitkana* as the prey, (3) to relate claw parameters and feeding efficiency to prey size selection, and to speculate on the differential demographic impact that generalist and specialist crabs may exert on their prey populations. We predict that specialist crabs require less time to open large snails, and thus have a potentially greater demographic effect per predator on mollusc prey than generalists of equal size and abundance. All experiments were carried out at the University of Washington Marine Laboratories at Friday Harbor, on San Juan Island, Washington (48°33'N, 123°01'W).

2. Methods

2.1. Predator 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- and high-tidal zones while *Lophopanopeus bellus* (Stimpson) (Brachyura: Xanthidae), *Cancer oregonensis* (Dana) (Brachyura: Cancridae), and 1 year-old *Cancer productus* (Randall) (< 60 mm carapace width) live and forage in the low intertidal zone (Kozloff, 1983). Older juvenile and adult *Cancer productus* (60–150 mm carapace width) move into the mid- and high-tide zones with the incoming tide to forage (Robles et al., 1989; Behrens Yamada and Boulding, 1996). Adult males in all five crab species possess larger claws than females. The difference is most pronounced in *Hemigrapsus* sp., and non-existent in the juvenile *C. productus* that

we used in our studies (Orensanz and Gallucci, 1988, pers. obs.). Sexual dimorphism is an indication that claws are multifunctional tools used in defense and reproduction, as well as feeding (Orensanz and Gallucci, 1988; Seed, 1993). In order to achieve valid feeding comparisons among species, Orensanz and Gallucci (1988) suggest using only female crabs. Since the extremely small claws of *Hemigrapsus* sp. females would trivialize this comparison, we decided to use male crabs.

The grazing snail, *Littorina sitkana* Philippi 1846 (Prosobranchia: Littorinidae), was chosen as the prey organism. This species has a moderately thick-walled, spherical shell, often with heavy spiral ridges (Boulding et al., 1993). On San Juan Island, Washington this snail is abundant and encompasses a large size range making it an ideal experimental prey organism. Shell length was measured as the maximum distance between apex and outer lip (Behrens Yamada, 1989).

2.2. Claw morphology of mollusc generalist and specialist

We derived criteria for categorizing decapods as to the degree of specialization on hard-shelled prey from published studies on decapod claw morphology (Warner and Jones, 1976; Brown et al., 1979; Elner and Campbell, 1981). We ranked decapod species by the ideal mechanical advantage (IMA) of their claws' lever systems, and descriptions of the dentition pattern of the occlusal surfaces, and compared these to published data on the diet of the crustaceans (Warner and Jones, 1976; Brown et al., 1979; Gosner, 1979; Lawton and Hughes, 1985; West and Williams, 1986; Lawton and Lavalli, 1995). Based on these results, we categorized the decapods as mollusc specialist or not (Table 1).

We used MA and dentition pattern to rank our five species of Pacific NW crab on the degree of specialization on hard-shelled prey. We estimated MA of the claw's lever system from at least 17 live and preserved male crabs from each species by taking the ratio of two level arms: L_1 , fulcrum to the insertion of the closer apodeme, and L_2 , fulcrum to tip of the dactyl (Fig. 1, Warner and Jones, 1976; Seed, 1993). To determine whether crabs of a given weight are strength limited or gape limited in their prey size selection, two other claw parameters: propal height, and mid-dactyl gape were measured (Fig. 1). For each species we regressed propal height and claw gape against crab weight and calculated propal height and gape for crabs of a mean adjusted weight of 8.7 g. Claw closing forces (N) at the adjusted propal heights were calculated from the regressions in Fig. 3 (see below). Since claw morphology and ecology of *Hemigrapsus oregonensis* are very similar to that of *H. nudus* (Kozloff, 1983, pers. obs.), this species was not measured for propal height or claw gape, and was not used in the subsequent feeding trials.

2.3. Claw strength

We tested the hypothesis that the claws of mollusc specialists generate higher claw closing forces than generalists using an in vivo 'calibration device' (Fig. 2 in Boulding, 1984). A piece of heavy wire was bent into an Ω shape and a strain gauge (BEAN BAE-13-250BB-350SE) was glued to a piece of 0.76 mm steel shimstock and hot-melt glued to the straight edge of the wire. A linear relationship was found between the force

Table 1
Correlation of claw morphology with diet in seven species of decapod crustaceans

Species	Claw	MA	Dentition	Diet	Degree of specialization on hard-shelled prey
<i>Procambus clarki</i> (Astacidae)	monomorphic	0.22 ^b	fine denticles sharp molars	omnivore scavenger ^b	somewhat
<i>Uca pugilator</i> (Ocypodidae)	'fiddle' claw	0.23 ^b	small, sharp denticles	detritivore ^d	not
<i>Liocarcinus depurator</i> (Portunidae)	strong fast	0.25 ^a 0.18 ^a	blunt, broad blunt, sharp	crustaceans, fish, thin-shelled molluscs ^a	somewhat
<i>Callinectes sapidus</i> (Portunidae)	strong fast	0.29 ^b 0.23 ^b	blunt, broad broad & fine	fish, snails, mussels ^{a,f}	somewhat
<i>Homarus americanus</i> (Astacidae)	strong fast	0.33 ^c 0.16 ^c	blunt, broad sharp, fine	hard-shelled prey, molluscs, crabs ^g	very
<i>Cancer pagurus</i> (Cancridae)	monomorphic	0.33 ^a	blunt, broad	molluscs ^{a,c}	very
<i>Menippe mercenaria</i> (Xanthidae)	strong fast	0.50 ^b 0.36 ^b	blunt, broad blunt, broad	oysters, shellfish ^b	extremely

The ranking was based on mechanical advantage of the claws' lever systems (IMA), and dentition as described by: ^a Warner and Jones, 1976, ^b Brown et al., 1979, and ^c Elner and Campbell, 1981. The claws of some species are monomorphic, while others are dimorphic with both a strong and a fast claw. Diets of decapods were obtained from the literature ^a Warner and Jones, 1976, ^b Brown et al., 1979, ^d Gosner, 1979, ^e Lawton and Hughes, 1985, ^f West and Williams, 1986, ^g Lawton and Lavalli, 1995).

exerted on the calibrating device by known weights and the output of the Wheatstone bridge containing the device's strain gauge. Claw closing forces were measured by positioning the mid-dactyl and mid-propal fingers of crab's claws into the upper and lower wire loops of the strain gauge and waiting for the crab to 'attack' so that it closed its claw and pulled the loops together. We selected crabs from the four species possessing propal heights between 4.5 and 13 mm. Both right and left claws of 11–15 individuals per species were measured repeatedly and the highest reading per crab was regressed against its weight. Non-cooperation is a problem with any static in vivo technique (see Elner and Campbell, 1981) and was a problem for *Cancer oregonensis*.

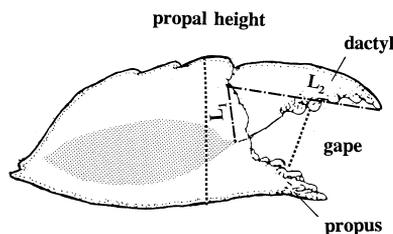


Fig. 1. Claw parameters used in interspecies comparisons. Mechanical advantage (MA) at the claw tip is given as the ratio of the lever arms L_1 and L_2 . Stippled area represents the closer apodeme plate to which the closer muscle is attached. Propal height, a measure of closer muscle mass, and mid-dactyl gape are indicated by broken lines.

2.4. Prey size selection and consumption rate

A laboratory trial was set up to compare prey size selectivity and consumption rates in male *H. nudus*, *L. bellus*, *C. oregonensis* and *C. productus*. Since in the previous field experiments small adult *H. nudus* were reluctant to feed on hard-shelled prey (Behrens Yamada and Boulding, 1996, unpubl. data), a special effort was made to find larger males, and acclimate them to laboratory conditions. Male *H. nudus* (22–37 mm carapace width, 5.6–20.6 g wet weight) were collected from large boulders at False Bay, a mud flat on San Juan Island. Crabs in this size range are extremely rare on the rocky shores around San Juan Island. Only those crabs that actively fed on *L. sitkana* in a preliminary 6 day feeding trial were selected. While the results from this trial allow comparison of the relative prey size selection among the 4 crab species, it should be noted that they greatly overestimate the actual consumption rate for average-sized *H. nudus* in the field (Behrens Yamada and Boulding, 1996). Individuals of the other three crab species were subsequently collected from other San Juan Island beaches. Since it was not possible to find crabs of all four species within the exact same weight range, the smaller *H. nudus* (5.6–14.5 g) were matched with the available size ranges of the other three species (*L. bellus* 5.4–8.2 g; *C. oregonensis* 7.2–11.9 g; and *C. productus* 9.2–12.4 g). Between 6 and 10 crabs of each species were assigned to individual plastic sandwich boxes (5 × 15 × 15 cm) with mesh sides for water circulation, while an additional 4 large *H. nudus* (14.7–20.6 g) and 4 *C. productus* 15.3–18.0 g) were each placed inside larger plastic boxes (9 × 22 × 22 cm) with mesh sides.

Separate 100 l sea water tanks were assigned to each of the four crab species in sandwich boxes and to the two species in the larger boxes. This was done to prevent chemical stimuli from one species affecting the feeding pattern of another. Tank assignments were randomized in time every 2 days to prevent tank effects. Water temperatures ranged from 12 to 13°C while flow rates were raised to 4 l/min to prevent the build up of chemicals exuding from damaged prey. Crabs inside the sandwich boxes were offered 3 snails from each of the following non-overlapping size classes: 4–5 mm, 5.5–7 mm, 8–10 mm and 11–13 mm in length. The larger crabs inside the larger boxes were handled in the same manner with the exception that they received a larger size range of snails: 5.5–7 mm, 8–10 mm, 11–13 mm and 15–17.5 mm in length. Black plastic sheets covered all 6 tanks. Every 12 h, for 6 days, the shell remnants of consumed snails and snails with chipped lips were removed and replaced with intact live snails. The first 12 h served as an acclimation period, after which the number of snails in each size category that were peeled, crushed outright and punctured was noted.

2.5. Shell-breaking and prey-handling time

Three limiting factors may cause a hungry crab to reject a given prey item: strength limitation, gape limitation and time limitation. While a crab may be able to peel a large snail, the time involved to extract the nourishment may be less than could be obtained by feeding on alternative food items. Thus time limitation could play a role in prey selection. We selected 20 male *Hemigrapsus nudus* (5–10 g) and over 10 similarly sized crabs from each of the three specialist species. Crabs were housed in a water table,

inside 1 l plastic beakers with mesh sides and offered 4–7 mm long *Littorina sitkana* each evening. Once crabs accepted snails as prey, the nightly feeding trials started. One 4–5 mm long *L. sitkana* was offered to each crab and shell breaking time, total handling time, or rejection time recorded using a stopwatch. We defined shell-breaking time from the time both chelae make contact with the snail to the time the shell breaks, even if the first break is only a chip. We recorded total handling time as time from initial attack to the time the crab consumed the prey. Thus, total handling time included shell-breaking time and eating time. Rejected prey, whether intact or with a chipped lip, were not used for subsequent trials. After a crab had a chance to successfully attack and consume at least one 4–5 mm snail, it was challenged with larger snails: 6–7 mm and 8–9 mm. The number of attempted attacks and percent of successful attacks on the different size categories of snails was tabulated for each species. Mean and 95% confidence interval of shell-breaking, and prey handling time for the 4 crab species on the three different size prey were calculated. The profitability of the different size snails consumed by the four crab species was calculated by dividing the dry biomass by the total handling time. We used 2.5, 6 and 15 mg for 4.5, 6.5 and 8.5 mm snails, respectively (Menge, 1972).

3. Results

3.1. Claw morphology of mollusc generalists and specialists

A tabulation of claw characteristics and diets of seven decapod crustaceans showed that *Homarus americanus*, *Cancer pagurus* and *Menippe mercenaria*, which feed primarily on hard-shelled prey, possess at least one claw with a high MA > 0.3, and blunt, broad molars. Less durophagous crabs, such as *Procambus clarki*, *Uca pugilator*, *Liocarcinus depurator* and *Callinectes sapidus*, which feed on detritus, fast moving prey, such as fish, other crustaceans, and smaller molluscs have at least one claw with a low MA < 0.3, and fine, sharp denticles (Table 1). This correlation between MA, claw dentition and diet enabled us to rank decapod species from generalist to specialist on hard-shelled prey (Table 1). *Menippe mercenaria* is an extreme specialist because it eats exclusively hard-shelled prey, and its master claw has a very high MA of 0.5 (Table 1).

Using the above criteria of MA and dentition, we examined the claws of our five species of Pacific NW crabs and classified them as either generalists or specialists on hard-shelled prey. None could be classified as extreme specialists (Table 2). The two generalists, *Hemigrapsus nudus* and *H. oregonensis*, have claws with occlusal margins lined with serrations used for scraping encrusting organisms off rocks (Fig. 2a). The three specialists, *Lophopanopeus bellus*, *Cancer oregonensis*, and *C. productus*, possess stout claws with blunt molar teeth (Fig. 2b Fig. 2c Fig. 2d). In the generalist the blunt tips of the two opposing claw ‘fingers’ abut, but in the three specialists the sharp tips overlap in a shearing cross bill-like fashion. The claws of the two generalists have an average IMA of 0.28, while those of the specialists range from 0.34 for *L. bellus* to 0.39 for *C. productus* (Table 2).

Published stomach analyses as well as field and laboratory feeding experiments confirm our classification (Table 2). The generalists, *Hemigrapsus nudus*, and *H.*

Table 2
 Classification of Pacific North West crab species as either generalists (G), or specialists (S) on hard-shelled prey based on Table 1 characteristics

Species	Claw	IMA		Dentition	Diet	Degree of specialization on hard-shelled prey
		Mean	Max			
<i>Hemigrapsus nudus</i> (Grapsidae)	monomorphic	0.28	0.33	fine denticles, blunt tips abut	omnivore	slightly, G
<i>Hemigrapsus oregonensis</i> (Grapsidae)	monomorphic	0.28	0.31	fine denticles, blunt tips abut	omnivore	slightly, G
<i>Lophopanopeus bellus</i> (Xanthidae)	slow fast	0.34 0.24	0.38 0.27	blunt, broad molars, sharp tips cross	molluscs, crustaceans	very, S
<i>Cancer oregonensis</i> (Cancridae)	monomorphic	0.36	0.41	blunt, broad molars, sharp tips cross	molluscs, barnacles crustaceans	very, S
<i>Cancer productus</i> (Cancridae)	monomorphic	0.39	0.42	blunt, broad molars, sharp tips cross	molluscs, barnacles crabs, sea urchins	very, S

The claws of at least 15 male crabs (5–11 g) were measured for mean and maximum IMA (see Fig. 1). In the generalist the tips of the two opposing claw ‘fingers’ are blunt and abut directly, but in the specialists, they are sharp and overlap in a shearing crossbill-like fashion.

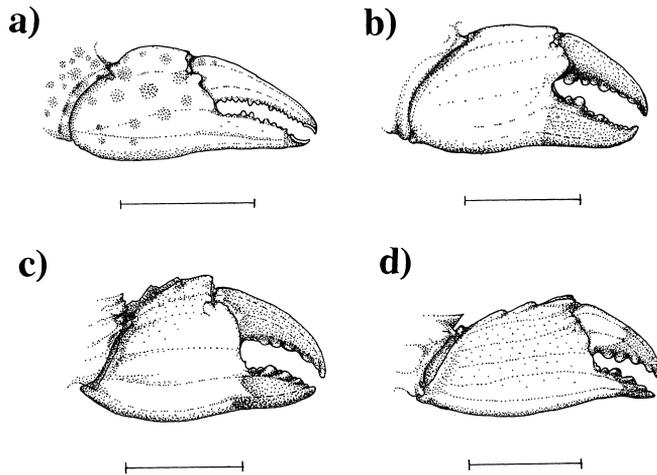


Fig. 2. Right claws of four intertidal crab species. (a) *Hemigrapsus nudus* (25 mm carapace width); (b) *Lophopanopeus bellus* (25 mm carapace width); (c) *Cancer oregonensis* (32 mm carapace width); (d) *Cancer productus* (45 mm carapace width). Note the fine serrations on the occlusal surfaces of the claw of *H. nudus* and the stout, blunt molar teeth of the other three species. The blunt tips of the opposing claw 'fingers' abut in *H. nudus*, while the sharp tips in the other three species overlap in a shearing cross bill-like fashion. Scale bar is 10 mm.

oregonensis, are omnivores whose diets includes macro- and microalgae as well as snails and seed oysters (Knudsen, 1964; Behrens Yamada, 1977; Quayle, 1988; Sousa, 1993; Behrens Yamada and Boulding, 1996). The specialists, *L. bellus*, *C. oregonensis*, and *C. productus*, routinely feed on hard-shelled prey such as barnacles, snails, mussels, clams,

Table 3

Comparison of propal heights (P.H.), mid-dactyl gapes and claw-closing forces in four species of crabs of adjusted mean weight = 8.7 g

Species	N	Propal height vs. weight	r^2	P	P.H.	$\pm 95\%$ CI	Force (N)
<i>H. nudus</i>	27	$y = 5.64 + 0.48wt$	0.93	<0.001	9.79	± 0.22	4.5
<i>L. bellus</i>	18	$y = 5.13 + 0.74wt$	0.71	<0.001	11.18	± 0.29	25.5
<i>C. oregonensis</i>	30	$y = 6.32 + 0.51wt$	0.74	<0.001	10.76	± 0.21	
<i>C. productus</i>	22	$y = 4.88 + 0.37wt$	0.91	<0.001	7.95	± 0.26	12.2

Ranking of propal height: CP < HN < CO = LB

Species	N	gape vs. weight	r^2	P	Gape	$\pm 95\%$ CI
<i>H. nudus</i>	27	$y = 2.65 + 0.36wt$	0.58	<0.001	6.21	± 0.41
<i>L. bellus</i>	18	$y = 2.99 + 0.57wt$	0.45	0.003	8.68	± 0.53
<i>C. oregonensis</i>	30	$y = 4.60 + 0.95wt$	0.13	0.047	6.16	± 0.39
<i>C. productus</i>	21	$y = 3.90 + 0.71wt$	0.13	0.112	4.37	± 0.49

Ranking of gape: CP < CO = HN < LB

Regressions were linear over the weight (wt) range examined (4–15 g). 95% CI indicates 95% confidence interval of propal height (P.H.) and gape. Claw closing forces (N) at the adjusted propal heights were calculated from the regressions in Fig. 3.

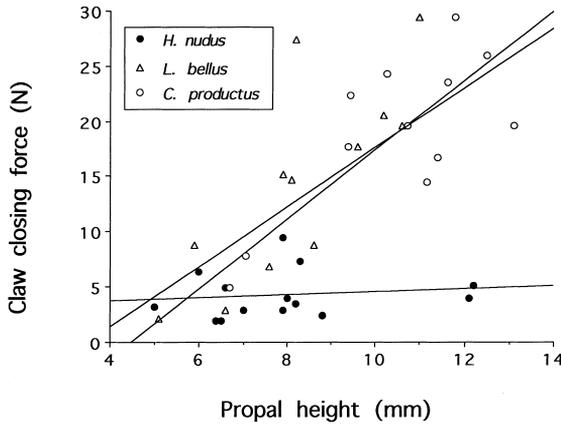


Fig. 3. Regressions of claw closing forces (N) versus claw propal height for three crab species. Crabs were tested repeatedly, and the maximum force reading per crab was plotted against its propal height. Regressions for *Lophopenopeus bellus* ($y = -16.89 + 3.79x$) and *Cancer productus* ($y = -9.31 + 2.70x$) were significant at $p < 0.005$, with $R^2 > 56$; that for *Hemigrapsus nudus* ($y = 3.17 + 0.14x$) was not significant.

oysters and sea urchins (Knudsen, 1964; Bernard, 1979; Boulding, 1984; Palmer, 1985; Robles et al., 1989; Behrens Yamada et al., 1993; Walker and Behrens Yamada, 1993; Behrens Yamada and Boulding, 1996).

Claw size as a function of crab weight varied greatly among the four species of crabs.

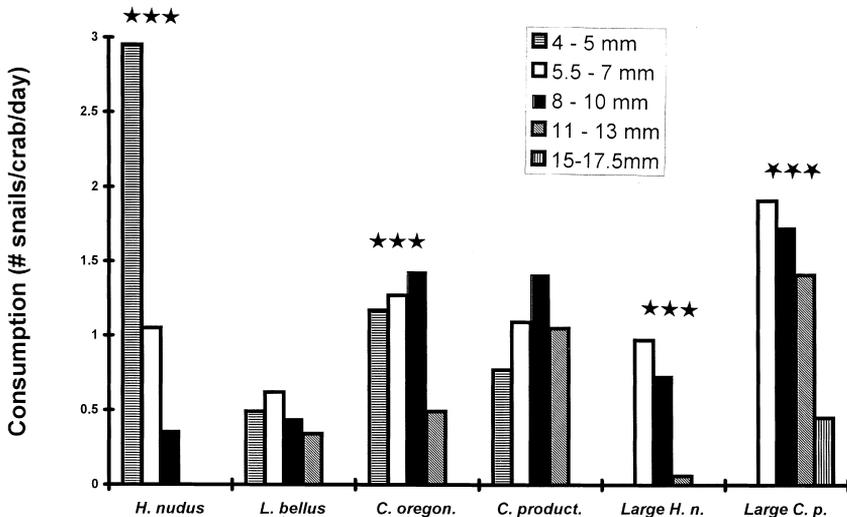


Fig. 4. Prey size selection in *Hemigrapsus nudus*, *Lophopenopeus bellus*, *Cancer oregonensis*, *C. productus*, large *H. nudus* and large *C. productus* in laboratory feeding trials. Each crab was offered three individuals of each of the four size classes of *L. sitkana* every 12 h. The four species of small crabs received four size classes of snails between 4 and 13 mm, while the large *H. nudus* and the large *C. productus* received snails between 5.5 and 17.5 mm. Three asterisks indicate significant prey size selection: $\chi^2 > 17.9$, $df = 3$, $p < 0.001$.

The regressions of propal height against weight explained over 70% of the variation, and were highly significant for all four species of crabs, while those of gape against weight explained less than 60% of the variations (Table 3). This discrepancy is due to the fact that claw gape is very difficult to measure in a living crab. When propal height and gape were adjusted at 8.7 g (the mean weight of all the crabs), *L. bellus* emerges with the largest propal height and gape, and *C. productus* with the smallest (Table 3). Thus for a given weight, juvenile *C. productus* possess smaller claws than the other three species.

3.2. Claw strength

Claw closing forces increased rapidly with propal height in both *Lophopenopeus bellus* and *Cancer productus*, but not in *Hemigrapsus nudus* (Fig. 3). Thus for similar sized claws, the difference in claw closing forces between the two specialists and the generalist increased with crab size. When we compare crabs of similar weight (8.7 g), the two specialists generate greater claw closing forces than the generalist: 25.5 N for *L. bellus* and 12.2 N for *C. productus* versus 4.5 N for *H. nudus* (Table 3).

3.3. Prey size selection and consumption rate

Regardless of size of crab tested, the generalist, *H. nudus*, exhibited a consistent preference for the smallest snails offered, and a total avoidance for the largest ($p < 0.001$) (Fig. 4). Only one *Littorina sitkana* > 10 mm in length was eaten by a large *H. nudus*. The three specialist crab species, however, ate all four size classes of snail offered (Fig. 4). Neither *Lophopenopeus bellus*, nor small (9–12 g) *C. productus*

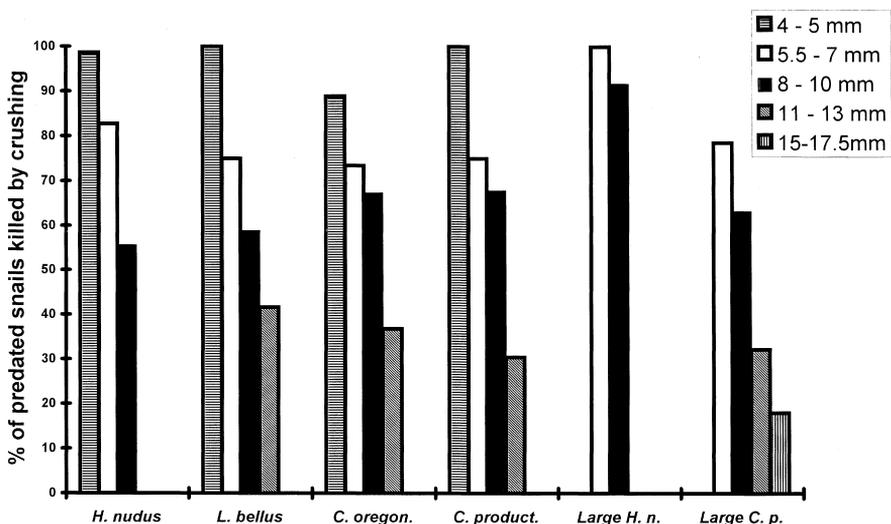


Fig. 5. Percent of predated snails in each size category that were killed by outright crushing. As prey size increased, all species of crabs switched from the crushing to the peeling technique.

Table 4

Rate of successful attacks by four crab species on three sizes classes of *Littorina sitkana*

Crab species	Snail size (mm)	No. of crabs	No. attacks	% successful attacks
<i>H. nudus</i>	4	14	71	70
<i>H. nudus</i>	6	12	46	37
<i>H. nudus</i>	8	12	32	0
<i>L. bellus</i>	4	13	21	71
<i>L. bellus</i>	6	10	20	70
<i>L. bellus</i>	8	10	22	77
<i>C. oregonensis</i>	4	22	60	93
<i>C. oregonensis</i>	6	21	55	96
<i>C. oregonensis</i>	8	19	48	100
<i>C. productus</i>	4	13	26	88
<i>C. productus</i>	6	12	19	100
<i>C. productus</i>	8	11	16	100

exhibited any significant size selection ($p > 0.20$), but *Cancer oregonensis* and large (15–18 g) *C. productus* ate significantly fewer of the largest size class (11–13 mm and 15–17.5 mm, respectively) than expected ($\chi^2 > 19.9$, $df = 3$, $p < 0.001$).

All crabs, with the exception of two *H. nudus*, consumed snails during the feeding trial (Appendix A). The results from these non-feeding crabs and those from two molting *C. productus* were not included in the analysis. When snails in the size range from 4 to 13 mm were offered, the somewhat smaller *L. bellus* ate an average of only 1.8

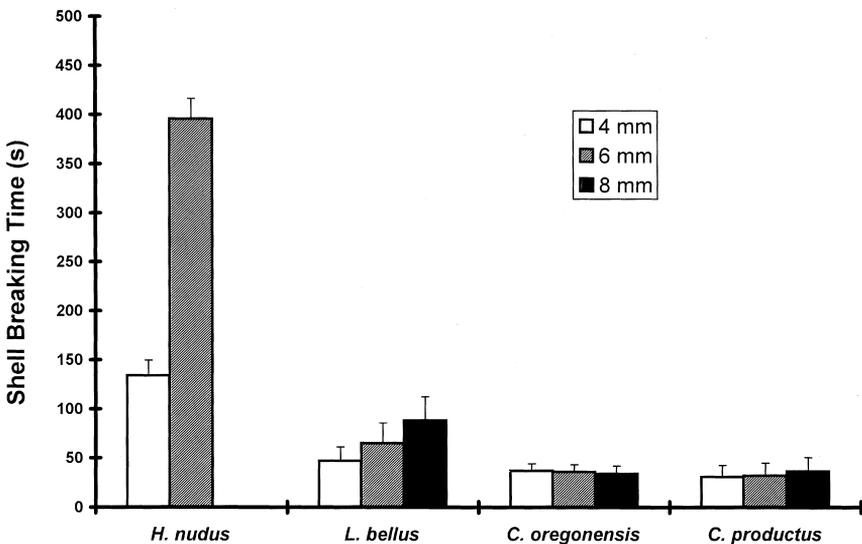


Fig. 6. Time (s) required to break three size classes of *Littorina sitkana* by four crab species. Shell breaking time increased with snail size for *Hemigrapsus nudus* and *Lophopenopeus bellus*, but not for the two *Cancer* species. Shell breaking time was significantly greater for *H. nudus* than for the other three species. None of the *H. nudus* were successful in breaking 8 mm snails. Error bars indicate 95% confidence interval of the mean.

snails/day while all the other three crab species ate an average of 4.3 to 4.4 snails/day. When prey and crab size increased, large (15–21) *H. nudus* ate an average of only 1.8 snails/day, while large (15–18 g) *C. productus* ate 5.5 snails/day (Appendix A). Consumption rate varied greatly within a species, especially for *H. nudus*. While two crabs ate no snails in 6 days, some ate an average of >7 /day (Appendix A). Comparison of mean daily biomass consumption among the crab species yielded the following ranking: *Hemigrapsus nudus* (19 mg) $<$ *Lophopenopeus bellus* (25 mg) $<$ *Cancer oregonensis* (53 mg) $<$ *C. productus* (71 mg) (Appendix A). The larger *C. productus* consumed over 6 times more snail biomass than larger *H. nudus* (130 vs. 20 mg/day).

All four species of crabs changed their mode of attack from outright crushing to peeling as prey size increased (Fig. 5). Thus, the larger a successfully attacked snail, the more likely it will be peeled. The specialists attacked any size class, even if they needed peeling over 50% of the time. *Hemigrapsus nudus*, however, avoided larger snails (Fig. 5).

3.4. Shell breaking and prey-handling time

The difference in prey size selection between the generalist and the specialists crabs is directly related to the efficiency with which they break shells. The percent of successful attacks on *L. sitkana* by *H. nudus* decreased dramatically with snails size: from 70% on

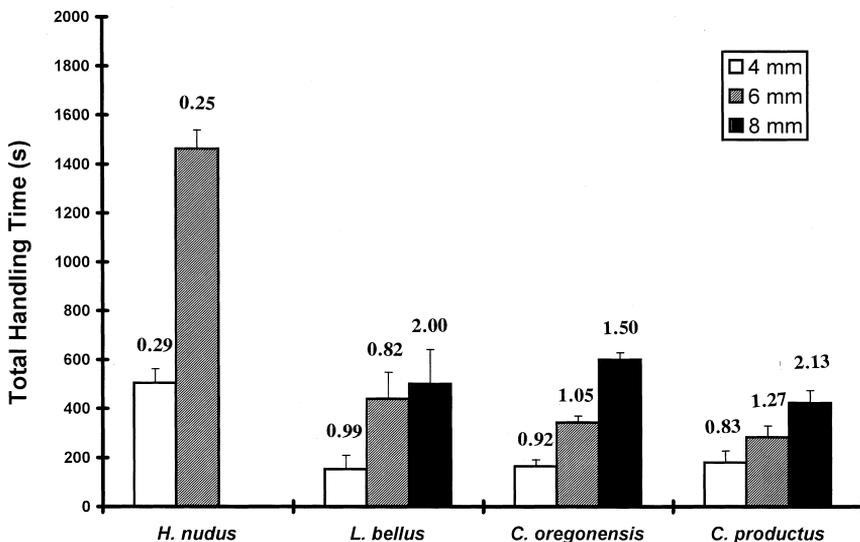


Fig. 7. Time required to break and consume three size classes of *Littorina sitkana* by four species of crabs. Consumption time increased with snail size for all crab species. Consumption time was significantly greater for *H. nudus* than for the other three species. Numbers above bars indicate prey profitability as measured by biomass (mg)/total handling time (min).

4, 37% on 6, and 0% on 8 mm snails, while *Lophopanopeus bellus*, *Cancer oregonensis* and *C. productus* were highly successful at all snails sizes (70–100%) (Table 4).

The generalist, *H. nudus*, took an average of 134 s to break open the shell of a 4 mm *Littorina sitkana*, while the three specialist crabs took only 31 to 52 s (Fig. 6). This difference in shell breaking time between the generalist and the specialists was even greater for 6 mm snails: 396 s vs. 32–65 s (Fig. 6). None of the 12 *H. nudus* successfully attacked a 8 mm snail. Shell breaking times on 8 mm snails increased to 113 s for *Lophopanopeus bellus*, but remained low (<40 s) for the two *Cancer* species (Fig. 6). Total prey-handling time increased with prey size for all crab species (Fig. 6). It took these specialists < 10 min (422–599 s) to break and consume an 8 mm *L. sitkana*, while the generalists took over twice as long, > 24 min, (1463 s) to break open and consume a 6 mm *L. sitkana* (Fig. 7). Prey profitability, as measured by dry biomass/total handling time, increased with prey size in the specialist: from 0.8 to 1.0 mg/min on 4 mm, to 1.5 to 2.13 mg/min on 8 mm snails (Fig. 7). In the generalist, *H. nudus*, profitability remained below 0.3 mg/min for both 4 and 6 mm snails.

4. Discussion

4.1. Generalist versus specialist predators

Crabs range in their foraging patterns from generalists to specialists on hard-shelled prey. The generalists possess slender claws with fine denticles and ideal mechanical advantage of the lever system ($IMA < 0.3$), while the specialists possess at least one powerful claw with broad, blunt molars and $IMA > 3.0$. The blunt tips of the claw fingers abut to form a scoop in the generalist, *Hemigrapsus nudus*, but the sharp tips overlap in a shearing crossbill-like fashion in the specialists, *Lophopanopeus bellus*, *Cancer oregonensis* and *C. productus*. The generalist, *Hemigrapsus nudus*, took around three times as long as the three specialists to break a 4 mm *Littorina sitkana*. This difference between the two groups of crabs increased to 6 times as long for 6 mm snails. Prey profitability, as measured by biomass extracted/total prey handling time, on 4 and 6 mm snails was around 3 times greater in the specialists than in the generalist.

While it is not surprising that a predator with a specialized feeding apparatus is more efficient at attacking its prey than a generalist of similar size, only a few other studies have quantified this difference (e.g. Schluter, 1982; Benkman and Lindholm, 1991). The large ground finch, *Geospiza magnirostris*, with its large, thick beak is three times more efficient at opening the large, hard, mature seeds of *Bursera graveolens* than is the smaller beaked medium ground finch, *Geospiza fortis* (Schluter, 1982). Crossbills (*Loxia curvirostra*) specialize in extracting the seeds from closed conifer cones. The beaks of crossbills are similar to the beaks of the generalist seed predator, the pine siskin, except that the tips of the mandibles extend until they cross. Crossbills took four times longer to remove seeds from reclosed western hemlock cones after the crossed part of their mandible was removed (Benkman and Lindholm, 1991).

4.2. Claw parameters and prey-size selection

Prey size selection in crabs of similar weight depends on claw size (propal height or gape), claw dentition, MA and claw closing force. *Lophopenopeus bellus* with largest claws generated the greatest closing forces and exhibited no significant prey size selection. The claws of *Hemigrapsus nudus* have a greater propal height, and greater claw gape than those of similar sized *C. productus*, but *H. nudus* preferred smaller prey, and consumed a lower snail biomass. Even though *H. nudus* have a relatively large claw gape, they avoided snails > 10 mm in length, but *C. productus*, with a smaller gape, peeled snails up to 17.5 mm. Since the smaller claws of *C. productus* have a higher MA and generated greater claw closing forces than the larger claws of *H. nudus* of the same weight, it appears that *H. nudus* is not gape limited, but strength limited in the largest prey they can successfully attack. Mollusc-crushing fishes, such as the hog fish, are also strength limited, while predators such as pike, perch and salamanders, which feed on soft prey, are gape limited (Wainwright, 1987; Maret and Collins, 1996; Persson et al., 1996).

4.3. Mechanics of shell-breaking efficiency

The crabs that are efficient shell-breakers have large blunt claw molars and sharp shearing tips. The large claw molars may enable the crab to concentrate all of the force generated by the claw muscles onto one region of the prey's shell (Brown et al., 1979). This force concentration may greatly increase the local stresses in the shell material per unit force exerted which may increase the rate of microcrack propagation in the shell (Boulding and LaBarbera, 1986). Crabs may open large shells by a cumulative process of extending microcracks until the shell breaks (Elner, 1978; Boulding and LaBarbera, 1986). The shape of the molars is important. Crabs with worn molars take longer to open prey (Juanes and Hartwick, 1990).

The specialist crabs exerted considerably more force on the crab force calibrator than did the generalist crab. For crabs of similar weight (8.7 g), *Hemigrapsus nudus* generated a force of 4.5 N, whereas *L. bellus* and *C. productus* generated 25.5 N and 12.2 N, respectively. Boulding (1984) recorded forces of 60 N from a strain gauge attached to the middle of the claw of a *C. productus* (carapace width 86 mm, propus height 19 mm) attacking a clam. Elner and Campbell (1981) recorded a maximum force of 256 N from a strain gauge attached to the middle of the crusher dactyl (propus height 101 mm) of a 172 mm lobster, a specialist on hard-shelled prey.

Hemigrapsus nudus may prefer small snails because they are poor at peeling snails. Since *H. nudus* have weak claws without sharp shearing tips, they may select snails small enough to crush outright. This view is supported by the observation that one *Lophopenopeus bellus* with worn chelal tips was unable to break open a 6 mm snail.

4.4. The role of hunger, learning and strength conditioning

While claw morphology and size determine the largest snail a given crab can successfully attack, other factors such as hunger level, learning, and strength con-

ditioning, can modify the expected result. If starved for long periods in the laboratory, *H. nudus* could be forced to open 12 mm *L. sitkana* but they rarely ate this size of snail in field experiments (Behrens Yamada and Boulding, 1996, unpubl. data). In laboratory experiments crabs persist trying to open a shelled prey item for a certain period and then give up (Lawton and Hughes, 1985; Hughes, 1989). In the laboratory the absence of alternative prey results in the crab re-attacking the same prey item and may finally result in the crab opening it even if it takes many attack bouts over several days (Boulding, 1984). In the field where alternative prey are abundant, crabs are less likely to re-attack a prey item they have unsuccessfully attacked. Crabs appear to have shorter persistence times when prey density is high (Eggleston, 1990). This response to prey density could result from selection for optimal foraging or from selection for avoidance of prey that cause excessive wear to their claw molars.

Complex shell opening behavior can sometimes compensate for limited crushing forces (Seed and Hughes, 1995). We observed great individual variation in the snail consumption rate in *H. nudus* (0–7/day). We believe that learning to effectively crush and peel snails contributes to this variation. While a few *H. nudus* readily attack and consume *L. sitkana*, most required at least a week of conditioning before they accept the snails as prey. We also observed that not all *H. nudus* learn to peel shells effectively. Those that learn consume more biomass per day than those that fail to learn this technique (unpub. data). Cunningham and Hughes (1984) found that after green shore crabs had successfully broken 5–6 prey items, they required 30% less time to break open subsequent prey of the same type and size. These observations strongly suggest that learning is involved in becoming a more efficient predator.

Since crustaceans' exoskeletons grow incrementally, the external claw dimensions are not always reflections of closer muscle mass and strength. For example, *Carcinus maenas* in late intermolt exert greater claw closing forces (22 N) than similar sized crabs in early intermolt (17 N) (Kaiser et al., 1990). Smith and Palmer (1994) found that claw strength increases with use. By immobilizing one claw, they were able to increase the strength of the free claw. Conversely, muscle tension and sarcomere length were significantly reduced in *Carcinus maenus* that were fed on soft food for 6 months (Abby-Kalio and Warner, 1984).

4.5. Demographic effects of generalists and specialists on prey populations

Generalist and specialist predators can exert distinctly different per capita demographic effects on their prey (Schluter, 1982). In our system, adult *Littorina sitkana* have a partial size refuge (Paine, 1969, 1976) from the generalist predator, *Hemigrapsus nudus*, but not from the specialists. All size classes of *L. sitkana* are vulnerable to attack by the three specialists. Both *Lophopanopeus bellus* and *Cancer oregonensis* are interstitial species found in shelters below the 0 m tidal. Their effect on intertidal prey species is minimal compared with that of the more abundant, larger and mobile *Cancer productus* (Behrens Yamada and Boulding, 1996). Not only do young juvenile *C. productus* consume more prey per unit body weight than the other two mollusc specialists, but older juvenile and adult *C. productus* are highly mobile. They forage throughout the intertidal, aggregate in areas of high prey abundance, and select larger *L.*

sitkana (Boulding and Hay, 1984; Robles et al., 1989; Behrens Yamada and Boulding, 1996). Results from a previous study indicate that on beaches with a high abundance of adult *Cancer productus*, *L. sitkana* can persist only in high intertidal and supratidal refuges (Behrens Yamada and Boulding, 1996).

While the direct lethal effects of specialist predators are easy to document, those of generalists are more subtle. On some beaches, both species of *Hemigrapsus* predators and *L. sitkana* prey coexist at high densities (Behrens Yamada and Boulding, 1996). This association, however, does not necessarily imply that these generalist crabs have no effect on the demography of the snail populations. More than 90% of the *H. nudus* at our study sites on San Juan Island are less than 15 mm in carapace width and half of the remaining 10% are females with smaller claws (Behrens Yamada and Boulding, 1996). These crabs would have to peel any snails greater than 4 mm in shell length (unpubl. data). While snails larger than 5 mm effectively have a size refuge from predation by *H. nudus*, smaller snails may not. When *Hemigrapsus nudus* (20–26 mm carapace width) from the west coast of Vancouver Island were offered 2.0 mm *L. sitkana*, they averaged 10 snails/day while one crab consumed up to 60 snails/day (Holst and Boulding, unpub. data). If smaller crabs eat even smaller *L. sitkana*, or their egg masses, then this generalist predator could have a profound effect on its prey populations. Supporting evidence for this view comes from oyster growers. Both *Hemigrapsus nudus* and *H. oregonensis* are classified as pests in oyster culture because they feed on small, newly-planted ‘seed’ oysters (Quayle, 1988). Other effects of *H. nudus* on *L. sitkana* are interference, behavior alteration and growth depression (Behrens Yamada, unpublished data). In a field caging experiment the presence of *H. nudus* had no effect on the abundance of *L. sitkana*, but many snails had their lip chipped by unsuccessful predation attempts. Snails in *Hemigrapsus nudus* cages altered their foraging patterns and exhibited a 35% depression in their growth rate (Behrens Yamada, unpublished data).

In summary, the generalist predators, *Hemigrapsus nudus* and *H. oregonensis*, and the mollusc specialist, *Cancer productus*, are abundant enough to affect mollusc prey populations in the mid- and upper-intertidal zone on Northeastern Pacific beaches (Behrens Yamada and Boulding, 1996). While *Hemigrapsus* sp., with their weaker, slender claws affect only small molluscs, juvenile *C. productus*, with their stronger, molariform claws, successfully attack all sizes of *Littorina sitkana*, and adult *C. productus* actively select larger snails (Behrens Yamada and Boulding, 1996; Behrens Yamada et al. (1998)).

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Appendix A

Size selection and consumption rate (number and mg dry weight per crab per day) of *Littorina sitkana* by four crab species in concurrent laboratory trials. Crabs were offered 3 snails from 4 size classes every 12 h for 5.5 days. Total consumption for each size class are given for each crab species. Laboratory-conditioned *Hemigrapsus nudus* males

Crab species	Weight (g)	Carapace width (mm)	Propal height (mm)	Claw gape (mm)	Size selection (size class of <i>Littorina sitkana</i> consumed)					Consumption rate	
					4–5 (mm)	5.5–7 (mm)	8–10 (mm)	11–13 (mm)	15–17.5 (mm)	No./day	mg/day
<i>Hemigrapsus nudus</i>	7.2	25.5	9.5	4.6	6	0	0	0	0	1.1	2.7
	6.5	24.5	8.7	4.5	28	8	3	0	0	7.1	29.8
	6.1	22.8	8.7	4.0	0*	0*	0*	0*	0	0*	0*
	5.6	22.3	8.6	4.0	26	3	0	0	0	5.3	14.5
	9.5	27.2	9.8	6.5	14	13	2	0	0	5.3	24.7
	14.5	30.8	12.3	7.5	27	8	7	0	0	7.6	42.5
	11.6	29.2	11.3	6.0	21	3	0	0	0	4.4	12.3
	13.5	30.9	12.5	7.0	13	4	1	0	0	3.3	12.8
	12.6	31.2	10.9	6.8	1	1	0	0	0	0.4	1.4
	12.4	29.4	12.2	7.2	10	12	5	0	0	4.9	31.8
					146	52	18	0	0	4.4 (2.4)	19.2 (13.9)
	18.6	36.5	14.0	8.5		0*	0*	0*	0*	0*	0*
	20.6	34.7	14.3	9.8		5	8	1	0	2.5	37.5
	14.8	31.1	12.3	8.6		10	3	0	0	2.4	18.9
	14.7	32.3	12.2	7.3		1	1	0	0	0.4	4.2
<i>Lophopanopeus bellus</i>	6.5	24.1	10.5	8.8		16	12	1	0	1.8 (1.2)	20.2 (16.7)
	7.6	25.5	11.2	8.6	2	1	2	0	0	0.9	8.4
	6.8	24.2	10.5	7.7	7	5	1	3	0	1.1	15.5
	5.8	23.9	9.8	6.5	2	1	1	4	0	2.9	31.2
	8.2	26.4	10.3	7.7	3	6	5	3	0	1.5	32.0
	7.1	25.6	10.4	6.4	3	4	4	2	0	3.1	43.4
	5.4	23.5	9.8	5.8	1	5	2	0	0	2.4	31.5
					19	24	17	13	0	1.5	11.5
<i>Cancer oregonensis</i>	10.5	31.8	12.7	7.7	1	8	12	2	0	1.8 (0.9)	24.8 (13.0)
	11.2	31.8	10.2	5.0	5	1	9	2	0	4.2	60.5
	11.9	32.3	11.9	7.0	9	8	5	5	0	3.1	46.1
	8.0	28.3	9.6	5.5	6	4	4	2	0	4.9	61.4
	7.5	29.6	9.4	4.0	11	14	13	2	0	2.9	32.9
	7.5	29.7	8.7	4.5	9	8	5	0	0	7.3	74.9
	7.2	26.5	10.2	5.7	4	6	7	6	0	4.0	27.7
					45	49	55	19	0	4.2	70.5
<i>Cancer productus</i>	11.7	43.71	8.9	5.5	6	8	9	8	0	4.4 (1.5)	53.3 (18.1)
	9.2	41.3	8.3	4.3	2*	1*	1*	1*	0	5.6	93.3
	9.5	41.9	8.5	4.0	4	10	5	4	0	0.9*	11.8*
	10.6	44.7	9.2	5.4	3	2	10	7	0	4.2	54.2
	12.3	47.6	9.6	5.5	2*	2*	2*	2*	0	4.0	83.0
	12.4	45.5	9.8	5.0	4	4	7	4	0	1.5*	22.7*
					17	24	31	23	0	3.5	55.3
	17.4	53.5	11.3	6.0		16	18	10	1	4.3 (0.9)	71.5 (19.7)
18.0	52.0	10.8	5.0		14	5	12	4	8.2	155.5	
15.3	48.4	10.4	5.8		6	6	6	5	6.4	169.5	
15.4	48.0	10.1	4.8		6	6	6	5	4.2	140.0	
					6	9	3	0	3.3	55.1	
					42	38	31	10	5.5 (2.2)	130.1 (51.4)	

were selected to span the size ranges of the other three crab species. No significant regression of consumption rate (mg/day) against crab weight ranging from 5.4 to 14.5 g was found for any of the 4 species. Means and (standard deviations) of daily consumption rates are given for feeding, non-molting crabs. Asterisks indicate two non-feeding *Hemigrapsus nudus*, and 2 molting *Cancer productus* that were omitted from the analysis.

References

- Abby-Kalio, N.J., Warner, G.F., 1984. Effects of two different feeding regimes on the chela closer muscles of the shore crab *Carcinus maenas* (L.). Mar. Behav. Physiol. 11, 209–218.
- Alexander, R.McN., 1968. Animal Mechanics, Sedgewick and Jackson, London.
- Atwood, H.L., 1973. An attempt to account for the diversity of crustacean muscles. Am. Zool. 13, 357–378.
- Behrens Yamada, S., 1977. Geographic range limitation of the intertidal gastropods *Littorina sitkana* and *L. planaxis*. Mar. Biol. 39, 61–65.
- Behrens Yamada, S., 1989. Are direct developers more locally adapted than planktonic developers? Mar. Biol. 103, 403–411.
- Behrens Yamada, S., Boulding, E.G., 1996. The role of highly mobile crab predators in the intertidal zonation of their gastropod prey. J. Exp. Mar. Biol. Ecol. 204, 59–83.
- Behrens Yamada, S., Metcalf, S.H., Baldwin, B.C., 1993. Predation by the crab, *Cancer oregonensis*, inside oyster trays. J. Shellfish Res. 12, 89–92.
- Behrens Yamada, S., Navarette, S.A., Needham, C., 1998. Predation induced changes in behavior and growth rate in three populations of the intertidal snail, *Littorina sitkana* (Philippi). J. Exp. Mar. Biol. Ecol. 220, 213–226.
- Benkman, C.W., 1993. Adaptation to single resources and the evolution of crossbill (*Loxia*) diversity. Ecol. Monogr. 63, 305–325.
- Benkman, C.W., Lindholm, A.K., 1991. The advantages and evolution of morphological novelty. Nature 349, 519–520.
- Bernard, F.R., 1979. The food of Hecate Strait crabs, August 1977. Manuscript Report, Fish. and Mar. Ser. Canada 1464, pp. 1–23.
- Bertness, M.D., Cunningham, C., 1981. Crab shell-crushing predation and gastropod architectural defense. J. Exp. Mar. Biol. Ecol. 65, 47–65.
- Boulding, E.G., 1984. Crab-resistant features of shells of burrowing bivalves: Decreasing vulnerability by increasing handling time. J. Exp. Mar. Biol. Ecol. 76, 201–223.
- Boulding, E.G., Buckland-Nicks, J., Van Alstyne, K.L., 1993. Morphological and allozyme variation in *Littorina sitkana* and related *Littorina* species from the Northeastern Pacific. Veliger 36, 43–68.
- Boulding, E.G., Hay, T.K., 1984. Crab response to prey density can result in density-dependent mortality of clams. Can. J. Fish. Aquat. Sci. 41, 521–535.
- Boulding, E.G., LaBarbera, M., 1986. Fatigue damage: Repeated loading enables crabs to open larger bivalves. Biol. Bull. Woods Hole Mass. 171, 538–547.
- Brown, S.C., Cassuto, S.R., Loos, R.W., 1979. Biomechanics of chelipeds in some decapod crustaceans. J. Zool., Lond. 188, 143–159.
- Cunningham, P.N., Hughes, R.N., 1984. Learning of predatory skills by shorecrabs *Carcinus maenas* feeding on mussels and dogwhelks. Mar. Ecol. Progr. Ser. 16, 21–26.
- Eggleston, D.B., 1990. Foraging behavior of the blue crab, *Callinectes sapidus*, on juvenile oysters, *Crassostrea virginica*: Effects of prey density and size. Bull. Mar. Sci. 46, 62–82.
- Elnor, R.W., 1978. The mechanics of predation by the shore crab, *Carcinus maenas* (L) on the edible mussel, *Mytilus edulis* (L). Oecologia 36, 333–344.
- Elnor, R.W., Campbell, A., 1981. Force, function, and mechanical advantage in the claw of the American lobster *Homarus americanus* (Decapoda: Crustacea). J. Zool. London 173, 395–406.

- Elnor, R.W., Hughes, R.N., 1978. Energy maximization in the diet of the shore crab *Carcinus maenas*. J. Animal Ecol. 47, 103–116.
- Gosner, K.L., 1979. A field guide to the Atlantic seashore from the Bay of Fundy to Cape Hatteras. The Peterson Field Guide Series, Houghton Mifflin, Boston, 329 pp.
- Holling, C.S., 1964. The analysis of complex population processes. Can. Entomol. 96, 335–347.
- Hughes, R.N., 1989. Foraging behavior of a tropical crab: *Ozius verreauxii*. Proc. R. Soc. London 237B, 201–212.
- Juanes, F., Hartwick, E.B., 1990. Prey size selection in Dungeness crabs: The effect of claw damage. Ecology 77, 744–758.
- Kaiser, M.J., Hughes, R.N., Reid, D.G., 1990. Chelal morphology, prey-size selection and aggressive competition in green and red forms of *Carcinus maenas* (L.). J. Exp. Mar. Biol. Ecol. 140, 121–134.
- 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. 18, 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 Washington Press, Seattle, 370 pp.
- Lawton, P., Hughes, R.N., 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. 27, 143–154.
- Lawton, P., Lavalli, K.L., 1995. Postlarval, juvenile, adolescent and adult ecology. In: Factor, J.R. (Ed.), Biology of the Lobster Homarus Americanus. Academic Press, San Diego, pp. 47–88.
- Maret, T.J., Collins, J.P., 1996. Effect of prey vulnerability on population size structure of a gape-limited predator. Ecology 77, 320–324.
- Menge, B.A., 1972. Foraging strategy of a starfish in relation to actual prey availability and environmental predictability. Ecol. Monogr. 42, 25–40.
- Orensanz, J.M., Gallucci, V.F., 1988. Comparative study of postlarval life-history schedules in four sympatric species of *Cancer* (Decapoda: Brachyura: Cancridae). J. Crust. Biol. 8, 187–220.
- Paine, R.T., 1969. The *Pisaster-Tegula* interaction: Prey patches, predator food preference, and intertidal community structure. Ecology 50, 950–961.
- Paine, R.T., 1976. Size-limited predation: An observational and experimental approach with the *Mytilus-Pisaster* interaction. Ecology 57, 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 27, 349–356.
- Persson, L., Anderson, J., Wahlström, E., Eklöv, P., 1996. Size-specific interactions in lake systems: Predator gape limitation and prey growth rate and mortality. Ecology 77, 900–911.
- Quayle, D.B., 1988. Pacific oyster culture in British Columbia. Fish. Res. Board Canada, Bulletin 218, 241 pp.
- Robles, C., Sweetnam, D.A., Dittman, D., 1989. Diel variation of intertidal foraging by *Cancer productus* in British Columbia. J. Nat. Hist. 23, 1041–1049.
- Sanchez-Salazar, M.E., Griffiths, C.L., Seed, R., 1987. The interactive roles of predation and tidal elevation in structuring populations of the edible cockle. *Cerastoderma edule*. Estuarine, Coastal and Shelf Science 25, 245–260.
- Seed, R., 1993. Crabs as predators of marine bivalve molluscs. In: Morton, B. (Ed.), Proceeding of the 1st International Conference on the Marine Biology of the South China Sea. Hong Kong University Press, Hong Kong, pp. 393–418.
- Seed, R., Hughes, R.N., 1995. Criteria for prey-selection in molluscivorous crabs with contrasting claw morphologies. J. Exp. Mar. Biol. Ecol. 193, 177–195.
- Schluter, D., 1982. Seed and patch selection by Galapagos ground finches: Relation to foraging efficiency and food supply. Ecology 63, 1106–1120.
- Sousa, W.P., 1993. Size-dependent predation on the salt-marsh snail *Cerithidea californica* Hademan. J. Exp. Mar. Biol. Ecol. 166, 19–37.
- Smith, D.L., Palmer, A.R., 1994. Effects of manipulating diet on size and performance of brachyuran crab claws. Science 264, 710–712.
- Vermeij, G.J., 1976. Interoceanic differences in vulnerability of shelled prey to crab predation. Science 260, 135–136.

- Wainwright, P., 1987. Biomechanical limits to ecological performance: Mollusc-crushing by the Caribbean hogfish, *Lachnolaimus maximus* (Labridae). *J. Zool.*, London 213, 283–297.
- Walker, S., Behrens Yamada, S., 1993. Implications for the gastropod fossil record of mistaken crab predation on empty mollusc shells. *Palaeontology* 36, 735–741.
- Warner, G.F., 1977. *The Biology of Crabs*, Elek Science, London.
- Warner, G.F., Jones, A.R., 1976. Leverage and muscle type in crab chelae (Crustacea: Brachyura). *J. Zool.*, Lond. 180, 57–68.
- West, D.L., Williams, A.H., 1986. Predation by *Callinectes sapidus* within *Spartina alterniflora* marshes. *J. Exp. Mar. Biol. Ecol.* 100, 75–95.
- Zipser, E., Vermeij, G.J., 1978. Crushing behavior of tropical and temperate crabs. *J. Exp. Mar. Biol. Ecol.* 31, 155–172.