PREDATION ON AN INTRODUCED MARINE SNAIL BY NATIVE CRABS

by

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Ceratostoma inornatum is an introduced marine snail in Puget Sound, Washington. Two of five native species tested as possible predators ate *Ceratostoma*. These two species, the crabs *Cancer gracilis* and *Lophopanopeus bellus*, did not eat native snails similar to *Ceratostoma*, but ate native and introduced bivalves more than *Ceratostoma*. The reasons for the differences in predation seemed to be explained by shell strength of the prey species. The presence of *Ceratostoma* adds a new type of prey to the menu of the two crab species at the sites studied.

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INTRODUCTION

An introduced species is often thought to alter the resource partitioning of the ecosystem it invades, usually in terms of what resources it uses (Chapman and Banner, 1949; Woelke, 1956; Carlton, 1979; Maciolek, 1984; McKay, 1984). By its presence, however, the introduced species also provides a new resource that native consumers may or may not be able to use. It might be expected that a consumer would prefer the food resource that it coevolved with, especially if morphological or behavioral adaptations are involved in the detection, capture, handling, and assimilation of the food resource by the consumer. Nonetheless, many examples exist of native consumers significantly incorporating introduced species into their diets (Glude, 1964; Recher, 1966; McKechnie and Fenner, 1971; Bourne and Lee, 1974; Carlton, 1979).

Experimental studies of native predators on introduced prey have been few, however. Only rarely have attempts been made to explain why a native consumer will incorporate an introduced species into its diet, often in preference to native species that it evolved with. New types of potential dietary items rarely naturally enter a consumer's community, and introduced species provide an opportunity to test the extent to which a specific consumer is coupled to its food resorces.

Will a native consumer ignore, incorporate, or prefer an introduced potential food species? One null hypothesis is that the native consumer will ignore the introduced species. A second null hypothesis is that if given a choice between a native food species and the introduced species, the native consumer will prefer the native food species.

The Japanese oyster drill, *Ceratostoma inornatum* (Recluz, 1851)(*Ocenebra japonica* in older literature) (Figure 1), a muricid gastropod, was unintentionally introduced to the Pacific coast of North America with shipments of young Pacific oysters, *Crassostrea gigas* (Thunberg, 1795). In Puget Sound, Washington, it was first reported in 1922 in oyster beds, and by the 1940's had become the most serious predator on the native oyster, *Ostrea lurida* Carpenter, 1864 (Chapman and Banner, 1949). Chapman and Banner (1949), Chew and Eisler (1958), Chew (1960), Koganazawa (1963), and Squire (1972), review the biology of *Ceratostoma inornatum*.

Ceratostoma occurs in *Ostrea* beds in the southern Puget Sound with a number of native predators known to eat shelled mollusks, and with a number of native shelled mollusks similar in size to *Ceratostoma*. The predators include the neogastropods *Nucella lamellosa* (Gmelin, 1791) (Thaididae) and *Searlesia dira* (Reeve, 1846) (Buccinidae), the anomuran crab *Pagurus samuelis* (Stimpson, 1857) (Paguridae), and the brachyuran crabs *Lophopanopeus bellus* (Stimpson, 1860) (Xanthidae), and *Cancer gracilis* Dana, 1852 (Cancridae). Native shelled mollusks that provide similar but alternate prey items to *Ceratostoma* include the neogastropods *Nucella* and *Searlesia*, the mesogastropod *Crepidula*

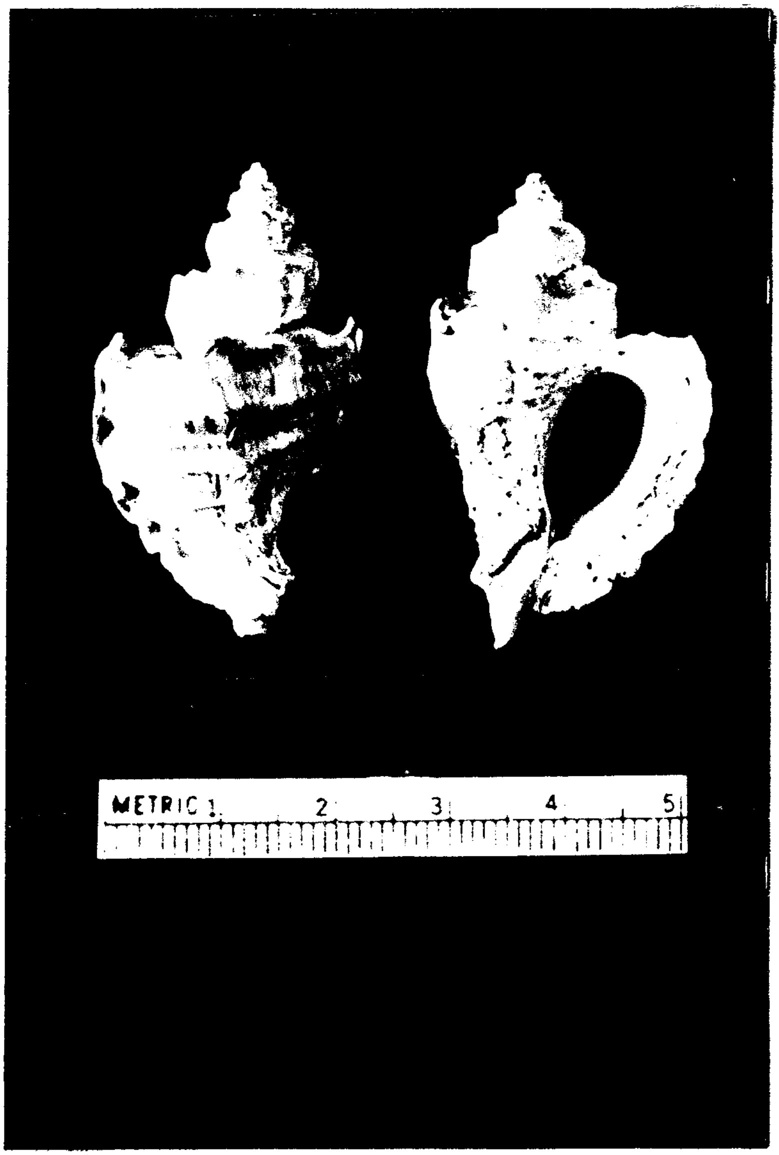

Figure 1: Ceratostoma inornatum

fornicata Linnaeus, 1758 (Calyptraeidae), and the bivalves Macoma inquinata (Deshayes, 1855) (Tellinidae), Tapes japonica Deshayes, 1853 (Veneridae), Mytilus edulis Linnaeus, 1758 (Mytilidae) and Ostrea. For further details on the Ostrea bed habitat and reasons these species were considered as predator or prey species, see Appendix A.

The major questions and corresponding hypotheses addressed by this study are as follows:

I. Will any of the native predators tested (Nucella, Searlesia, Pagurus, Lophopanopeus, and Cancer) prey upon the introduced gastropod Ceratostoma under laboratory conditions?

Hypothesis I: None of the predators will prey upon Ceratostoma.

II. If Ceratostoma is eaten by a native predator, will there be a difference in predation frequency relative to predation on native species?

Hypothesis II: There will be no difference between the predation frequency on Ceratostoma and on native prey.

III. If Ceratostoma is preyed upon either more or less frequently than native species, what causes the difference?

Hypothesis IIIA: The difference will not be due to chemical deterence by the prey.

Hypothesis IIIB: The difference will not be due to prey shell parameters.

Hypothesis IIIC: The difference will not be due to relative energetic rewards of the prey.

METHODS AND MATERIALS

Field work was done in the southern Puget Sound of Washington State, U.S.A. (long. 123 deg. 0 min.; lat. 47 deg., 1 min.). Most experimental specimens were collected from here. Sites were *Ostrea* beds at about the mean low low tide level on the western sides of Mud Bay and Oyster Bay (Figure 2).The beds are nearly level, terraced by concrete dikes, and tidal currents are very slight. There is no large freshwater discharge into either bay. Eight hundred *Ceratostoma* were collected by hand from the two sites together, and taken to laboratory facilities at the Oregon Institute of Marine Biology (University of Oregon) at Coos Bay, Oregon. Notes were made during collection of habitat preference and relative abundance of *Ceratostoma*. Because *Ceratostoma* of less than 20 mm in shell length were rare or absent from the sites, this study looked only at *Ceratostoma* and other shelled molluscan prey 20 mm or greater in shell length.

Specimens of *Lophopanopeus*, *Pagurus*, *Nucella*, *Searlesia*, *Crepidula*, *Mytilus*, *Ostrea*, *Macoma*, and *Tapes* were also collected by hand at these sites, and notes made of habitat preferences and relative abundances. *Cancer gracilis* is largely nocturnal and secretive (pers. obs.), and specimens of this species were collected by dip net at night in Dyes Inlet, a nearby arm of the Puget Sound with a less treacherous bottom,

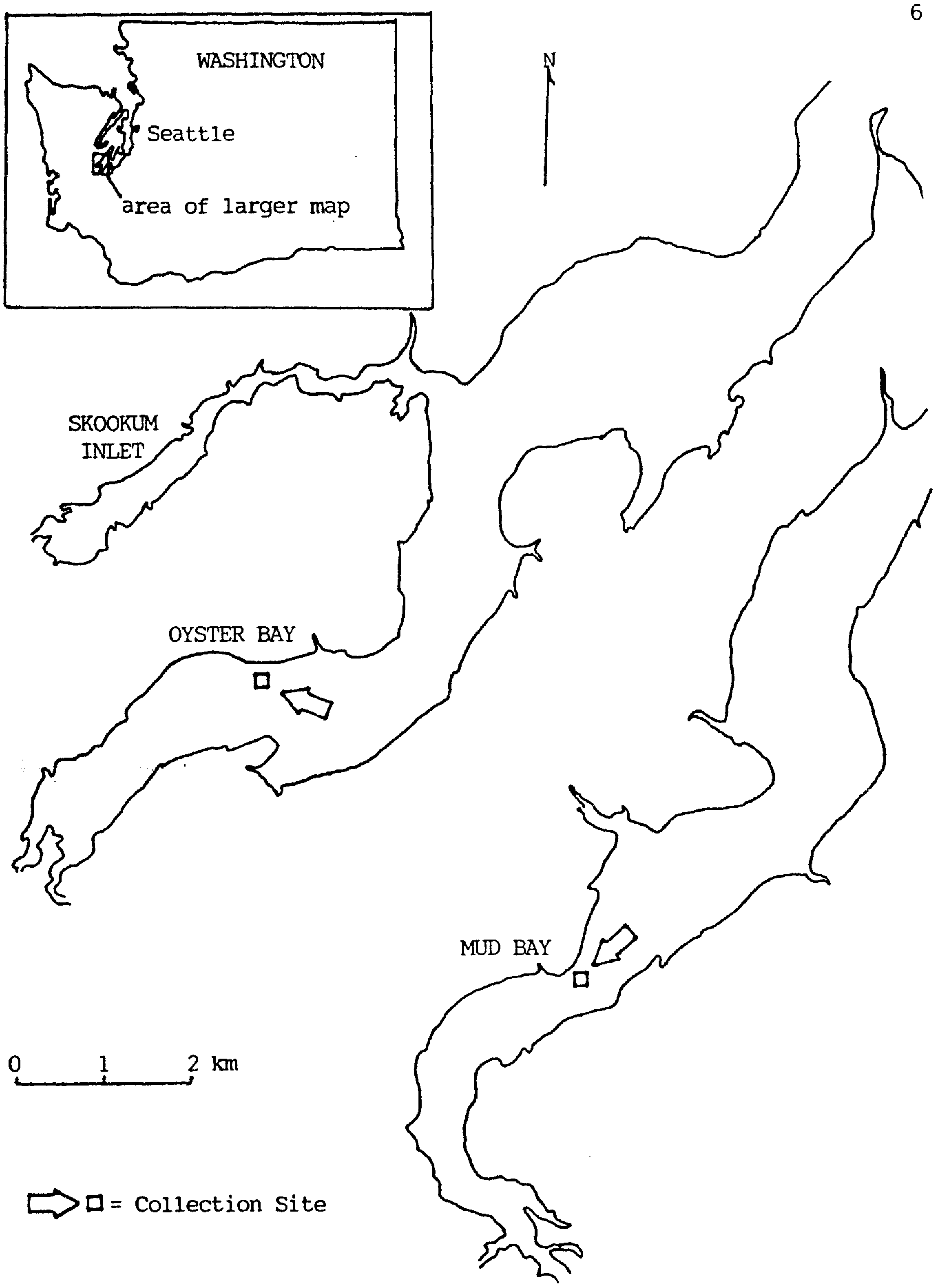

Figure 2: Map of Research Field Sites

essential for pursuing the agile decapod. Notes of the diet and feeding method of this crab were made during collection. Specimens of *Mytilus* and *Macoma* were also collected from Coos Bay, Oregon.

Laboratory experiments were carried out in the running seawater facilities at the Oregon Institute of Marine Biology. The outlets from any tanks holding the *Ceratostoma*, *Crepidula*, or *Iapes* (species not found in Coos Bay) were screened, and drained into a freshwater pond to prevent accidental introduction. Egg cases laid by the snails while they were held were removed regularly and destroyed.

Ceratostoma Field Collection Analysis

Three parameters were measured on *Ceratostoma* taken from the field: size, severe shell wear, and the frequency of past unsuccessful crab attacks. These were done seperately for the specimens from each site.

Shell size was measured (to the nearest millimeter) as the length from the tip of the first whorl to the tip of the siphonal canal. Types of severe shell wear were noted, and the frequency of each type calculated. The presence of an uneven scar on the shell was taken as evidence of a past attack by a crab (Vermeij, 1982). This could be seen consistently only on unworn shells, so only those shells were examined to obtain the frequency of past attacks.

Predation Experiments

Predation experiments were as follows:

I. Five species were tested as possible predators on Ceratostoma. Those that did not eat Ceratostoma were fed a known dietary item to determine if they would consume any food in the laboratory. Those that did prey on Ceratostoma went on to subsequent experiments.

II. Seven species for Cancer and five species for Lophopanopeus were tested as possible alternate prey of the predators (two crabs) which continued from I. Those that were not preyed upon were crushed and re-offered to the crabs to test for chemical deterence. The species that were preyed upon went on to the final set of experiments.

III. The alternate prey species that continued from II were matched one at a time with Ceratostoma and placed with the Ceratostoma predators (those continuing from I) to test for differences in relative predation.

All predators used in the experiments were measured. The shell length and width of the snails were measured, the right chela propodus length and the carapace width of the Pagurus were measured, and the length of both chela propodi and the maximum carapace width of Lophopanopeus and Cancer were measured. (Propodi lengths have the advantage over dactyli lengths in including the muscular region within the measurements). Sex of the last two species was also recorded. Only specimens with intact shells (in the case of the snails) or with both chela and missing no more than one walking leg (in the case of the crabs), were used in this study.

The first experiment for each predator was to place *Ceratostoma* ranging in length from 20 to 42 mm with at least ten adult specimens of the predator. Predators of both sexes were used and included some of the largest and smallest specimens found for each species. For *Nucella* and *Searlesia* the predator/prey ratio was 1:1, and for the other species, *Pagurus*, *Lophopanopeus*, and *Cancer*, the predator/prey ratio was 1:3. No other prey was placed with the predator for the duration of this experiment. If under these conditions the predator did not eat any of the living *Ceratostoma* within fourteen days, an ammount of crushed *Mytilus* was placed in the tank with the predator (small live *Mytilus* for *Nucella*) and the *Ceratostoma*, to determine if the predator was inclined to feed. If this was eaten readily by the predator, it was assumed that it would not or could not prey on the *Ceratostoma*, even if hungry, and was therefore unlikely to be a predator of this size range of *Ceratostoma* in the field. No further experiments were done with this catagory of predators.

If the predator did successfully prey on any of the *Ceratostoma* in the fourteen day period, the second experiment was conducted with that species. Alternate prey species were determined for each species of crab by exposing at least thirty of each of the potential prey species (*Nucella*, *Searlesia*, *Crepidula*, and *Mytilus*, *Ostrea*, and for *Cancer*, also *Tapes* and *Macoma*) to ten crabs for ten days. Care was taken to assure that both the alternate prey species tested and the crabs used represented the full range of sizes found in the field. If no individuals of a potential prey were eaten in this preliminary experiment, a number of crushed individuals were placed with the crabs to test for possible chemical deterence. This catagory of possible prey species was not used in subsequent experiments.

The final set of experiments consisted of isolating the crabs in individual test enclosures. The test enclosures were as follows: For *Lophopanopeus* 20 individual enclosures were made of perforated wood panels. Each enclosure was 20 x 15 cm by 12 cm deep (Figure 3). A rock or a *Crassostrea* shell was placed in each enclosure, and clear glass panels were placed over the tops, permitting a natural light cycle. For *Cancer* the enclosure design was similar, but larger (30 x 30 cm.); 5 cm of sand but no shell was placed in the bottom, and wooden panels with only small cracks for light were placed on top for this nocturnal species. Ten male and ten female adult *Lophopanopeus* of the full size range were used, and ten adult *Cancer* of both sexes ranging from 45 to 84 mm (carapace width) were used.

After the crabs were allowed to acclimate to their individual enclosures for several days, three randomly selected *Ceratostoma* from the Mud Bay collection and three randomly selected specimens of an alternate prey species from the field collections were placed together with each crab, to determine differences in predation frequency. The population sample that the alternate prey items were taken from was the same sample used for prey parameter experiments. Only one alternate prey species was matched with *Ceratostoma* at any one time. Clams (*Tapes* and *Macoma*) were buried at the bottom of the sediment; all other species were placed on the top of the sediment in the enclosures. The

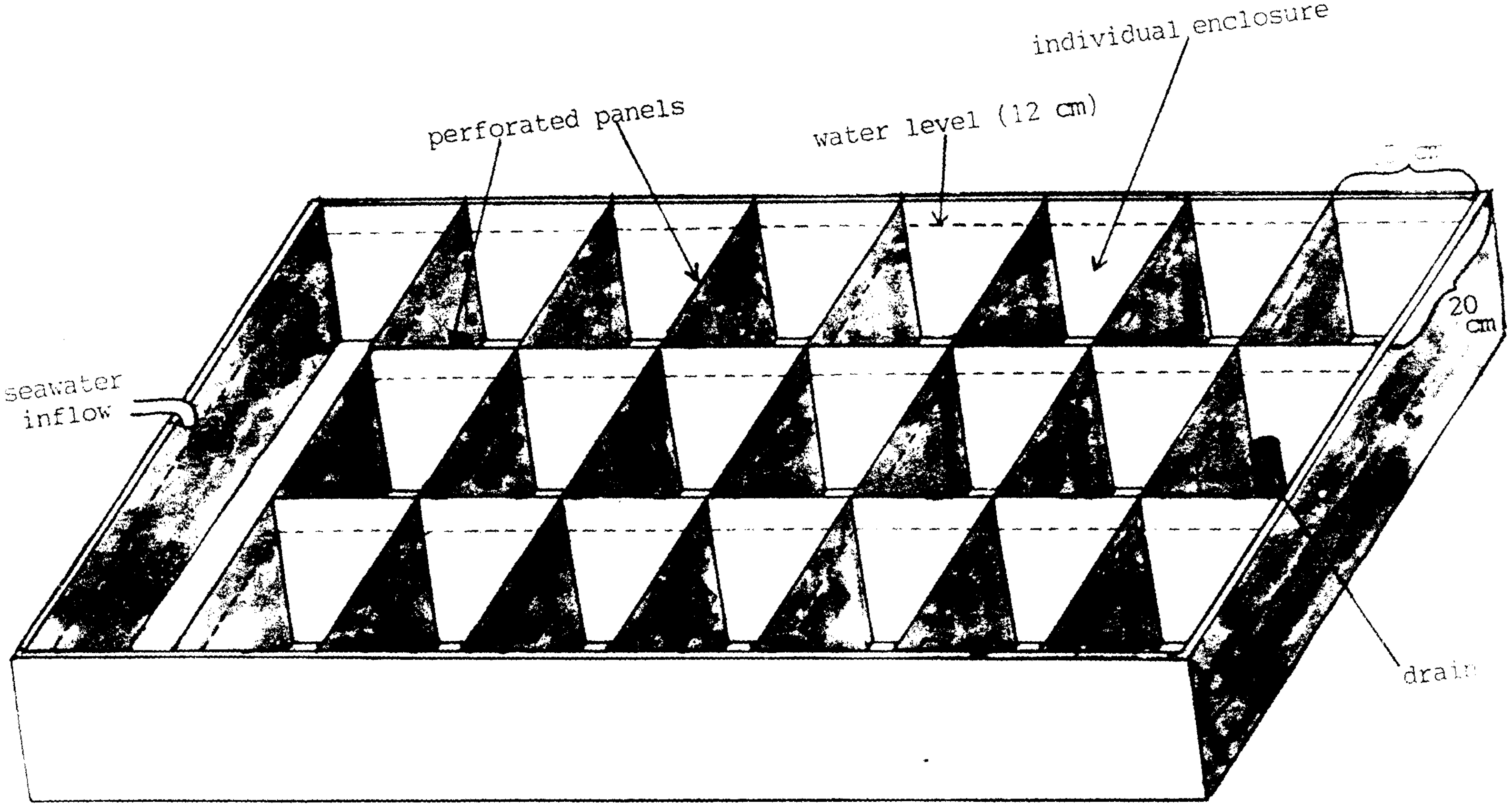

Figure 3: Diagram of _Lophopanopeus_ Experimental Enclosures

enclosures were checked daily, and any killed prey removed, recorded, and replaced with a living specimen of the same species selected randomly from the field collections. Ceratostoma that had crawled up the side of the enclosures were put back on the bottom. Killed prey, even if uneaten, was considered an incidence of predation. When possible, the predation was watched and the technique and time for a successful uninterrupted attack, from the discovery of the prey to the discarding of the remains, was recorded. Each of these experiments also ran ten days.

Three assumptions critical to the last set of experiments were that the crabs knew what was in their habitat, that they did not know the depth at which the clams were buried in the sediment, and that they did not discriminate against prey that they had previously handled but did not consume. For a discussion of these assumptions, see Appendix B.

Three major patterns were looked for in the predation experiment data: the effect of crab size on the maximum size of Ceratostoma eaten, differential predation upon Ceratostoma versus an alternate prey species, and relationships between parameters of different prey species and frequency of predation by crabs.

For the effect of prey parameters on predation by crabs, Ceratostoma and alternate prey species were converted to percentages of all prey killed for each choice trial and tested for significant differences. The percentages for all species were tested for relationships to shell size, shell strength, and relative reward.

Measurements of Prey Parameters

Shell size, shape, and crushing resistance, and the relative reward to a predator were recorded or measured for each of the species considered for these experiments, and in the case of Ceratostoma, for both unworn specimens and specimens with severe shell wear.

Average shell length was calculated for each species used. The shell shape, including sculpture, was observed qualitatively for typical specimens.

Sites on the shells tested for crushing resistance were those as close as possible to those where the crabs attacked. If no successful attacks were made on a species, sites tested for shell strength corresponded to those on the most similar species attacked. The device used to measure shell crushing resistance consisted of a steel spike with a surface area of 1 mm^2 near the fulcrum of a lever arm. The spike was rested against the shell being tested, and lead weights placed on the platform at the other end of the lever arm until the spike broke through the shell (Figure 4, top). This was converted to the crushing power per square millimeter required to break the shell by the equation $P = [(Wp + Lp + Lb)/f - p] + L + W$, where P = the pressure per mm^2 required to break through the shell, W = the weight upon the platform + the weight in grams of the platform (40.2), L = the weight of the lever arm (93.7 g), p = the distance bc (32.2 cm) (Figure 4, bottom), b = 1/2 the distance ac (17.2 cm), and c = the distance bd (37.9 cm). This equation simplifies to $P = W \times 6.649 + 340.3$ g. The points tested for each species corresponded to those points attacked by crabs on that

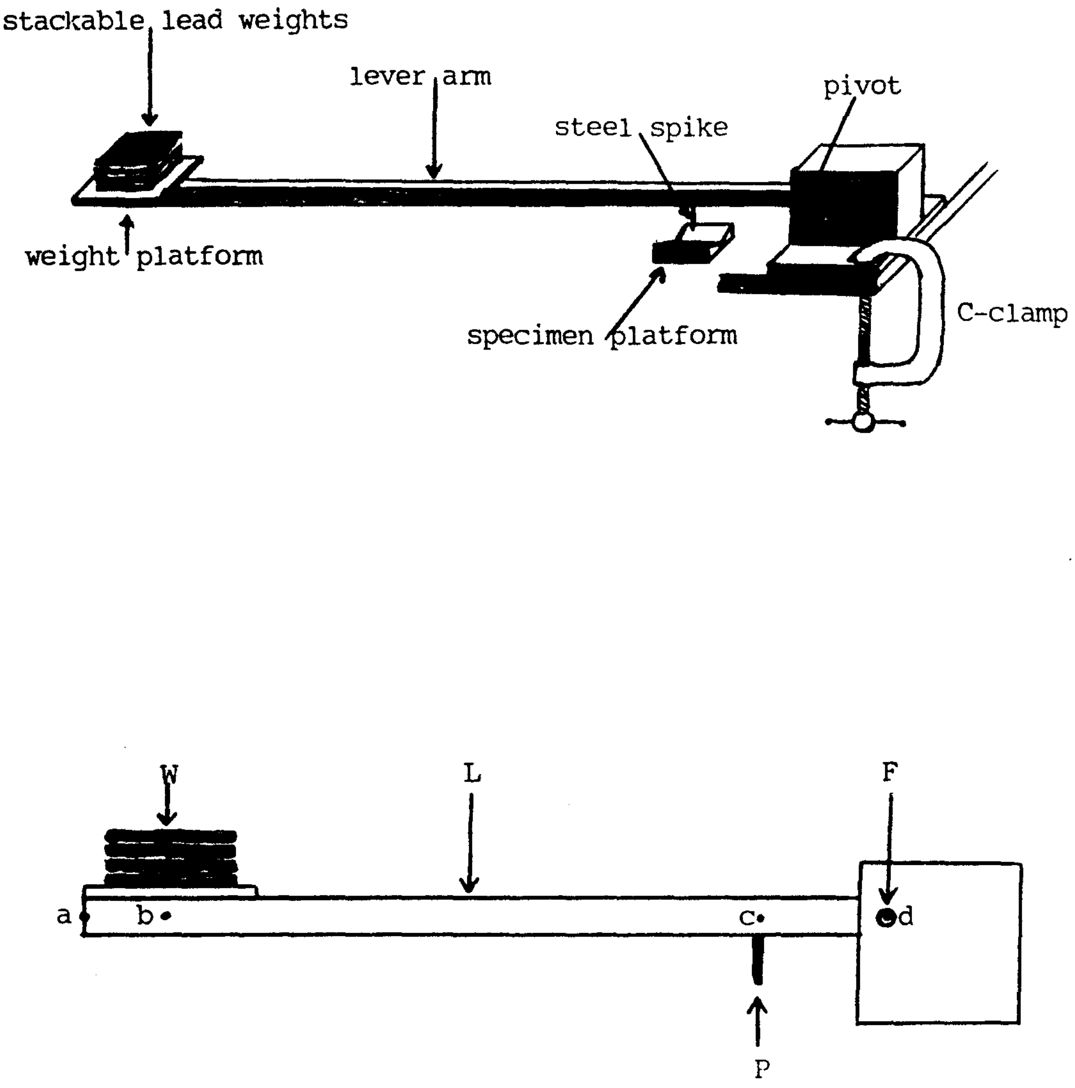

Figure 4: Device for Testing Shell Crushing-Resistances

species, or in the case that the crab did not prey on that species, on spots corresponding to those on the most similar prey eaten by the crab. Live or preserved whole specimens were used in every case.

An estimate of the relative reward of all the prey species tested was made using ten live whole specimens randomly selected for shell length of each species. These were weighed alive, then killed by boiling, the flesh extracted (opercula were discarded) and dried under a lamp for three days at 30 deg. C until completely dried, and reweighed. The relative reward was taken as the percent dried tissue per whole animal, averaged for the ten individuals of each species.

If shell strength or relative reward was significantly correlated to shell size for any species, it was corrected to the length of the smallest average for any of the alternate prey species using the equation of the correlation.

RESULTS

Field Observations

Ceratostoma was abundant but patchily distributed on concrete dikes and *Crassostrea* shells, but virtually absent on *Ostrea* shells, at both the Mud Bay and Oyster Bay sites. Along a 1 m stretch of concrete dike numbers of individuals could range from 0 to 100.

Cancer less than 50 mm in carapace width could be seen in the high subtidal during the day at all sites, and at night *Cancer* of all sizes came up to this level, to a density of about one per square meter at Dyes Inlet and slightly less in Mud Bay. At Dyes Inlet *Cancer* was observed to eat *Tapes* and *Macoma*, taking from 3 to 10 minutes, with an average of three minute (5 observations) to dig up either species.

Lophopanopeus was found incidentally in rubble at the base of the dikes, but more frequently under *Crassostrea* shells or shell clusters. About one half of these shells or shell clusters had one to three *Lophopanopeus*. This species was found only at Oyster Bay.

Pagurus was abundant subtidally or in pools created by the dikes. Abundance was difficult to estimate, but *Pagurus* probably outnumbered *Lophopanopeus* by at least a factor of ten at both sites.

Nucella and *Searlesia* were found in the same habitat as *Ceratostoma*, but were outnumbered by the latter by at least 30:1 at either site. *Searlesia* was more abundant than *Nucella* at Mud Bay but was absent at Oyster Bay. *Crepidula* was very abundant in the upper intertidal, but much less common in the *Ostrea* beds. There were about 1-10 *Crepidula* stacks per square meter, attached to clam shells, oyster shells, or rocks, at either site.

Tapes and *Macoma* numbers were difficult to estimate, since they were buried, but both were abundant, up to 50 per square meter adjacent to the *Ostrea* beds at both sites.

Mytilus was very abundant in the upper intertidal but relatively scarce in the *Ostrea* beds, numbering about 10-100 per square meter at both sites. *Ostrea* made up over 90 percent of the surface biomass on the oyster bed and about 25 % of the biomass on the dikes, at both sites.

Ceratostoma Field Collection Analysis

The mean shell length of *Ceratostoma* at Mud Bay was 33.0 mm (s = 4.16; n = 364) and ranged from 20 to 44 mm. At Oyster Bay the mean size was 35.8 mm (s = 5.26, n = 104), and the size range from 20 to 44 mm. Sizes were distributed normally over these ranges at Mud Bay, but were skewed towards larger snails at Oyster Bay.

Three types of severe shell wear were observed: heavy infestations of a boring polychaete ,*Polydora* sp. (Blake and Evans, 1973) (Spionidae); wear on the inner lip where the operculum rubbed (hereafter called the "worn lip syndrome"); and intervarix infestation of an endolithic filamentous green alga. (Figure 5). Infection rates for each type at Mud Bay and Oyster Bay are shown in Table 1. All three of these shell-wearing mechanisms were present on the other neogastropods, *Nucella* and *Searelsia*, but were never observed to cause more than very slight wear.

Table 1: Rates of Severe *Ceratostoma* Shell Wear for Mud and Oyster Bays

Site	*Polydora*	Worn Lip Syndrome	Alga
Mud Bay (n= 208)	11.5% (n=24)	52.4% (n=109)	53.4% (n=111)
Oyster Bay (n=286)	0.7% (n=2)	4.5% (n=13)	1.4% (n=4)

The rate of crab attack as measured by shell scars was 31.6% (25/79) in Mud Bay specimens and 32.7% (18/55) in Oyster Bay specimens. Figure 6 shows a typical shell scar on *Ceratostoma*. The attacking species could not be determined from this.

Predation Experiments

Cancer (Figure 7) used ranged in size from 45 to 84 mm in carapace width, with the right chela propodi lengths from 23 to 46 mm. Chela size correlated perfectly with carapace size. The right and left chelae were identical in size in most specimens, and except for irregular, slight wear, were also identical in shape (Figure 8). Originally two

Figure 5: Types of Severe *Ceratostoma* Shell Wear; (left to right) *Polydora*, Worn Lip Syndrome, Endolithic Alga.

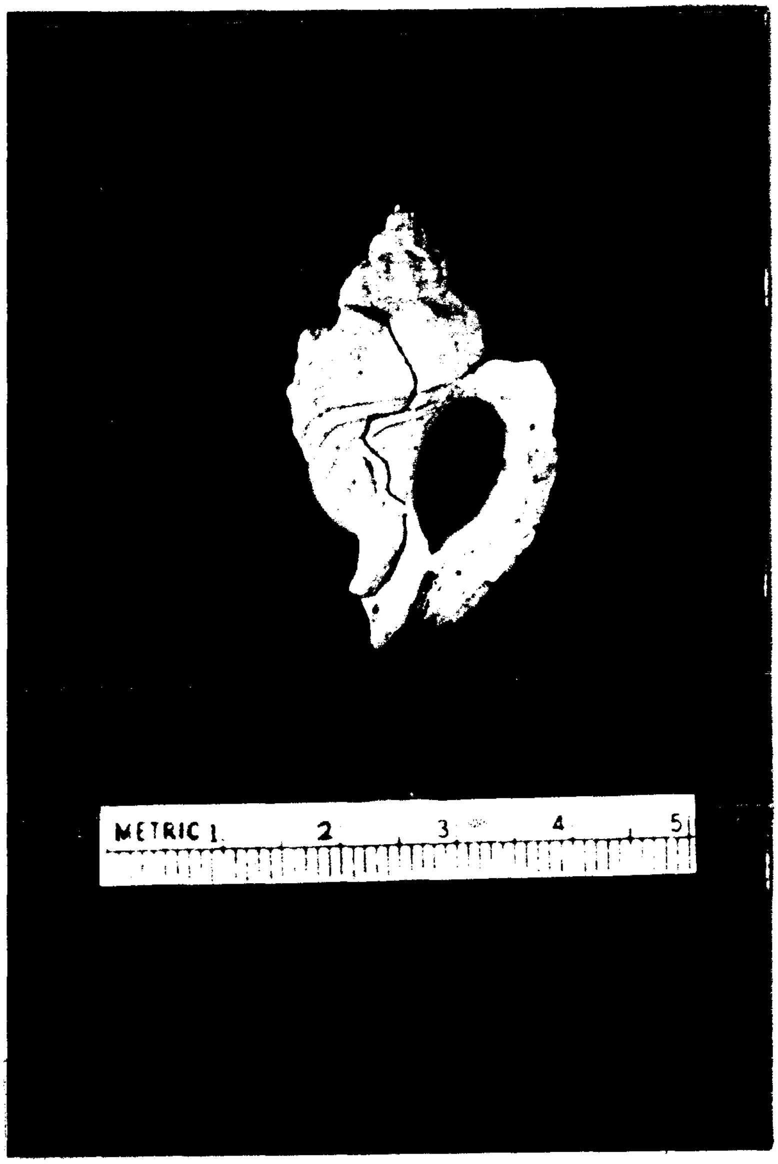

Figure 6: Scar on <u>Ceratostoma</u> Shell

Figure 7: <u>Cancer</u> <u>gracilis</u> (top) and
<u>Lophopanopeus</u> <u>bellus</u>

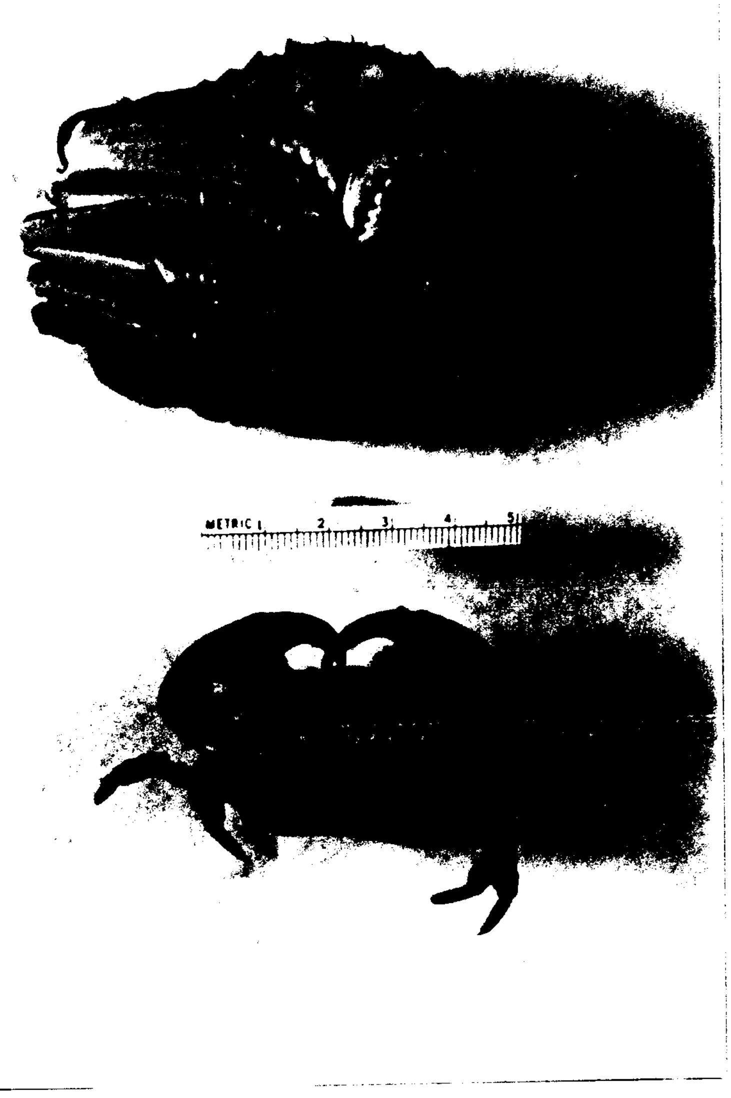

Figure 8: Chelae of <u>Cancer</u> (top) and <u>Lophopanopeus</u>

males and eight females were used, but one male died and was replaced with another male halfway through the experiments.

Lophopanopeus (Figure 7) used ranged in size from 22 to 34 mm (mean = 27.2 mm) in carapace width for males and 27 to 18 mm for females (mean = 22.0 mm). The size of the largest chela propodi correlated very closely to carapace size (r = 0.899), and ranged from 13 to 27 mm. Usually the right chela was larger and blunter (Figure 8), but in one case this was reversed.

Pagurus used ranged from 6 to 12 mm in carapace width and from 7 to 16 mm in right chela propodus length. The right chela was always larger, and chela size corresponded perfectly to carapace width. *Searelsia* used as predators ranged from 33 to 48 mm in shell length, and *Nucella* used as predators ranged from 38 to 49 mm in shell length.

The first predation experiment established that of the five predator species used, only *Cancer* and *Lophopanopeus* preyed upon *Ceratostoma*. *Pagurus* and *Searlesia* readily ate crushed *Mytilus*, and *Nucella* readily ate small *Mytilus*, when these were placed with them at the end of the first experiment.

Cancer readily ate *Ceratostoma*, and over the course of the experiments nine crabs ate a total of 107 *Ceratostoma*. *Lophopanopeus* did not as readily eat *Ceratostoma*: over the course of the experiments only 23 were eaten by 10 crabs. The effect of crab size on the maximum size of *Ceratostoma* preyed upon is shown in Table 2 and Figure 9.

Table 2: Largest *Ceratostoma* Eaten by each Crab

Crab Species	Carapace Width	Largest *Ceratostoma* Eaten
Cancer	50 mm	23 mm
Cancer	52 mm	24 mm
Cancer	58 mm	32 mm
Cancer	73 mm	34 mm
Cancer	75 mm	35 mm
Cancer	77 mm	39 mm*
Cancer	81 mm	38 mm
Cancer	82 mm	41 mm*
Cancer	84 mm	38 mm*
Lophopanopeus	24 mm	25 mm
Lophopanopeus	25 mm	25 mm
Lophopanopeus	25 mm	31 mm
Lophopanopeus	26 mm	28 mm
Lophopanopeus	26 mm	29 mm
Lophopanopeus	27 mm	35 mm
Lophopanopeus	29 mm	35 mm
Lophopanopeus	30 mm	30 mm
Lophopanopeus	34 mm	34 mm

* This was the largest *Ceratostoma* offered to this crab.

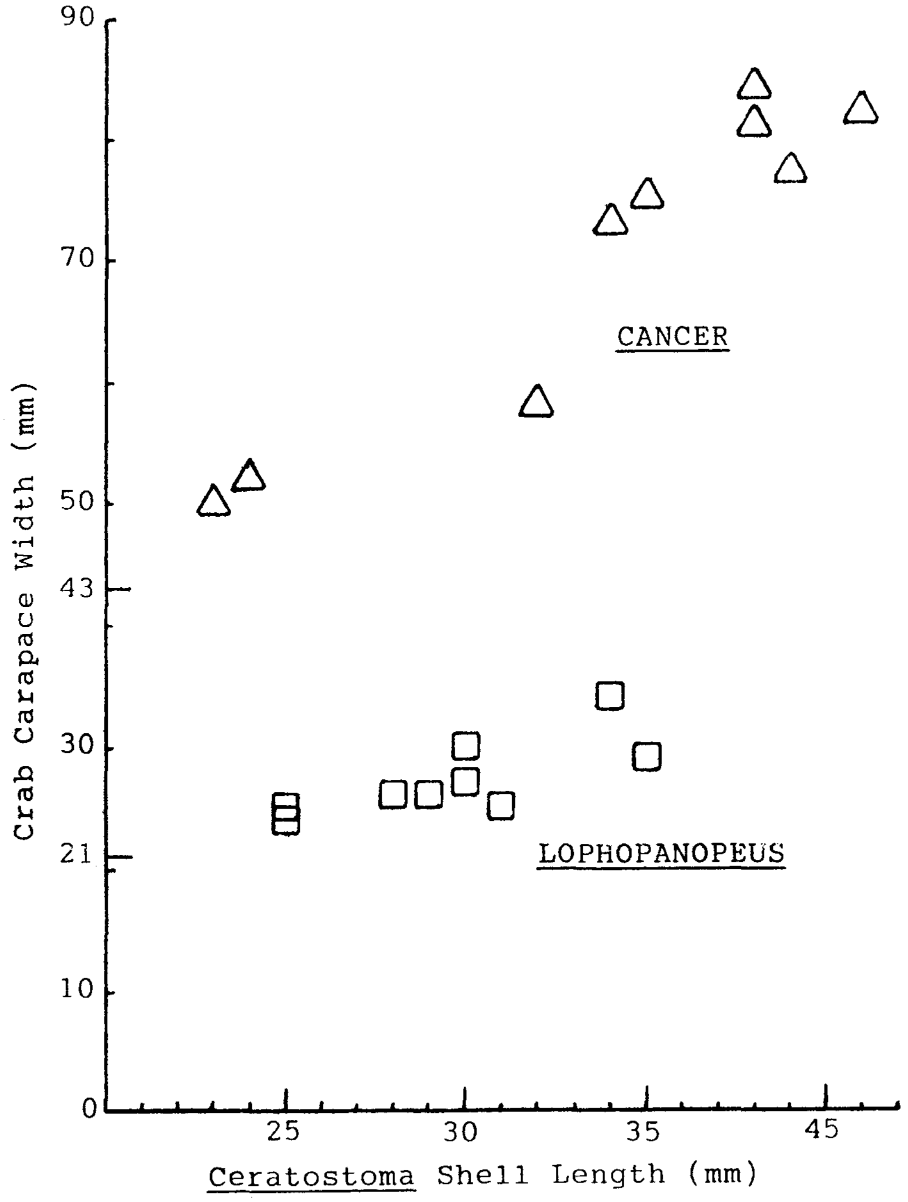

Figure 9: Effect of Crab Size on Maximum Size of Ceratostoma Preyed Upon.

Cancer preyed upon *Ceratostoma* by holding it with one chela and attempting to crush it with the other. If the attempt was unsuccessful the crab would shift the snail and try again, often switching the attacking chela. Generally this would result in a large hole in the shell, but complete crushing or chipping spirally from the terminal varix (Figure 10), were also common. *Lophopanopeus* was similar in its attack methods, except that the larger chela made almost all of the crushing attempts. The effect on the *Ceratostoma* shell was the same for either species of crab.

Of the alternate prey species *Cancer* did not eat any intact *Nucella*, *Searlesia*, or *Crepidula*, but was observed to attack all three species, and readily ate crushed specimens of all three species. It ate *Mytilus* to the exclusion of *Ceratostoma*; *Tapes* and *Macoma* were eaten more than *Ceratostoma*; and *Ostrea* was eaten about equally to *Ceratostoma*. *Lophopanopeus* did not eat any *Nucella* or *Searlesia*, although it attacked both, and did kill and eat a small number of *Crepidula*. Crushed *Nucella* was eaten readily, but crushed *Searlesia* was never eaten. *Lophopanopeus* ate *Mytilus* to the exclusion of *Ceratostoma*, although those crabs under 23 mm in carapace width could not eat *Mytilus* larger than about 25 mm in shell length, and it ate very few *Ostrea*. This information, combined for all crabs of each species, is given in more detail in Table 3.

Figure 11 shows the effect of *Cancer* predation upon the four bivalve species it ate. Attacks on all of these species were stereotyped. *Cancer* would hold the bivalve beneath it with its walking

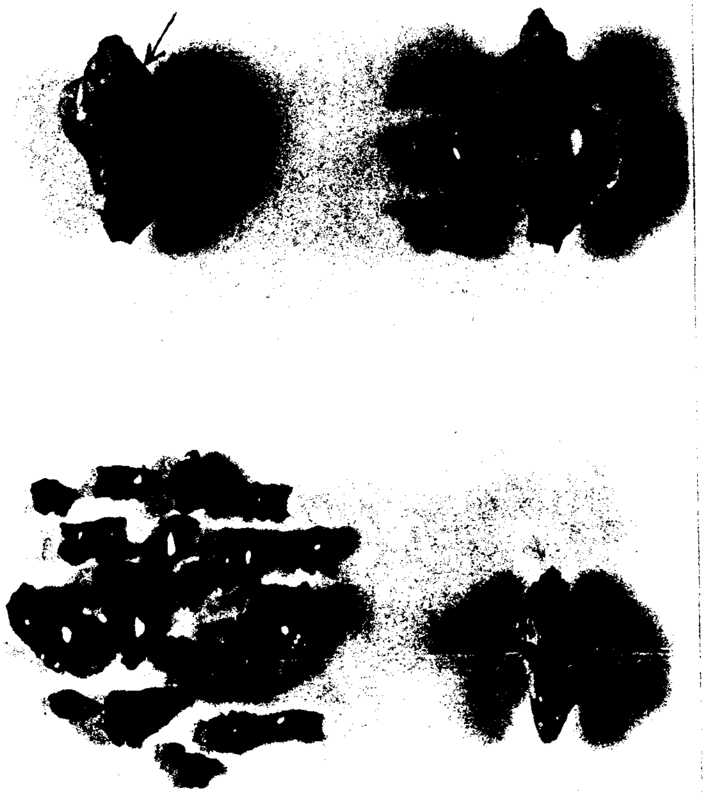

Figure 10: The Effects of Crab Predation on Ceratostoma Shells

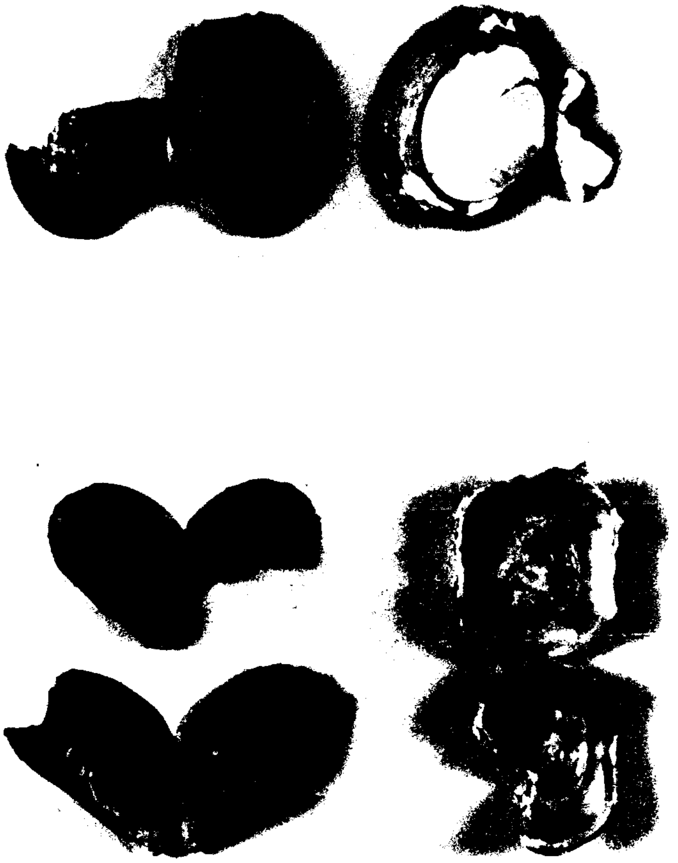

Figure 11: The Effects of Crab Predation on Bivalve Shells

Table 3: Amount of Alternate Prey Killed as a Percent of all Prey Killed per Trial

Prey Species	Killed by *Cancer*	Killed by *Lophopanopeus*
Nucella	0	0
Searlesia	0	0
Crepidula	0	71% (5:2)
Tapes	80% (20:5)	not tested
Macoma	77% (24:7)	not tested
Mytilus	100: (51:0)	100% (35:0)
Ostrea	45% (13:16)*	67% (4:2)*

*Not significant at $p = 0.05$.

legs and attack it with its chelae. *Tapes* was attacked by chipping at the edge of the shell in an attempt to wedge the chela between the valves. This was often but not always followed by breaking one of the valves from the inside out. *Macoma* and *Ostrea* were both attacked by crushing the edge of the shell, and *Mytilus* was attacked either at the edge of the shell or at the area of byssal attachment. This information plus times taken for successful attacks is summarized in Table 4.

Lophopanopeus attacked *Mytilus* and *Ostrea* in a manner similar to *Cancer*, but no times for successful attacks were recorded. *Crepidula* was attacked by breaking through the shell that the snail resided on (in these cases a vacant *Crepidula* shell). Only the bottom *Crepidula* of a stack was therefore ever eaten.

Table 4: Method and Time of Successful Attacks On Prey Species by Cancer

Prey Species	Method of Attack	Time for Attack (n = 5)
Worn Ceratostoma	Crushing	10-60 min (avg 30 min)
Unworn Ceratostoma	Crushing	60-360 min (avg 180 min)
Tapes	Chipping/Wedging	6-30 min (avg 15 min)*
Macoma	Crushing Edge	6-30 min (avg 11 min)*
Mytilus	Crushing Edge/Byssal Area	1-5 min (avg 3 min)
Ostrea	Crushing Edge	10-60 min (avg 30 min)

* Includes time to excavate clam.

Prey Parameters

The results of prey parameter measurements are given in Table 5, for shell size, shell strengths, (crushing resistance in kg) and relative reward. Only Mytilus showed a skewed size distribution: the size distribution was slightly to the left (towards smaller). The areas tested for shell strength were as follows: for randomly selected Ceratostoma, worn Ceratostoma (using specimens that exhibited both severe intervarix wear and worn lip syndrome), unworn Ceratostoma, Nucella, and Searlesia the inner lip and the intervarix regions of both the largest and second largest whorl were tested; for Crepidula, which came in "stacks" of 2-5 individuals, the lip of the shell of the bottom-most Crepidula was tested; for Tapes the seam where the two valves met was tested (only live animals were used); for Mytilus the edge of the valves and the area near the byssus were tested; and for Macoma and Ostrea the edge of the shell was tested. These are all shown in Figures

Table 5: Prey Parameters

Prey Species	Avg. Size	Crush.-Resist.(kg/mm^2)	Rel. Reward
Ceratostoma	33 mm (s = 4.2, n = 208)	6.14 kg (s = 2.08, n = 50)	0.070 (s = .025, n = 10)
worn *Cer.*	34 mm (s = 3.8, n = 50)	2.71 kg (s = 1.05, n = 50)	0.050 (s = .011, n = 10)
unworn *Cer.*	33 mm (s = 4.6, n = 50)	11.37 kg (s = 2.68, n = 50)	0.081 (s = .012, n = 10)
Nucella	47 mm (s = 5.8, n = 34)	14.86 kg* (s = 2.76, n = 50)	0.040 (s = .013, n = 10)
Searlesia	40 mm (s = 2.8, n = 30)	15.00 kg (s = 2.50, n = 30)	0.076 (s = .011, n = 10)
Crepidula	42 mm (s = 3.4, n = 50)	3.77 kg* (s = 3.27, n = 50)	0.070 (s = .019, n = 10)
Tapes	41 mm (s = 3.9, n = 50)	12.25 kg (s = 4.20, n = 50)	0.048 (s = .006, n = 10)
Macoma	35 mm (s = 6.5, n = 50)	2.22 kg* (s = 1.25, n = 50)	0.070* (s = .012, n = 10)
Mytilus	32 mm (s = 6.8, n = 50)	2.26 kg* (s = 0.73, n = 50)	0.035* (s = .003, n = 10)
Ostrea	41 mm (s = 4.0, n = 50)	6.43 kg (s = 3.50, n = 50)	0.033 (s = .010, n = 10)

* This parameter is significantly correlated at $p = 0.1$ to length: reported value is corrected to a shell size of 32 mm.

12 and 13, which also show the shapes of typical specimens of each species used. In some cases the crushing resistance exceeded the capacity of the measuring apparatus (17.80 kg/mm^2); when this happened, the point tested was assigned the value of 19 kg.

Figures 14, 15, and 16 compare predation by *Cancer* to shell size, shell crushing resistance, and relative reward, respectively. Predation is shown as relative to predation on *Ceratostoma*, and is scored as follows: 5 = eaten to exclusion of *Ceratostoma*, 4 = eaten more than but not to the exclusion of *Ceratostoma*, 3 = eaten equally to *Ceratostoma*, 2 = eaten, but not as much as *Ceratostoma*, and 1 = not eaten.

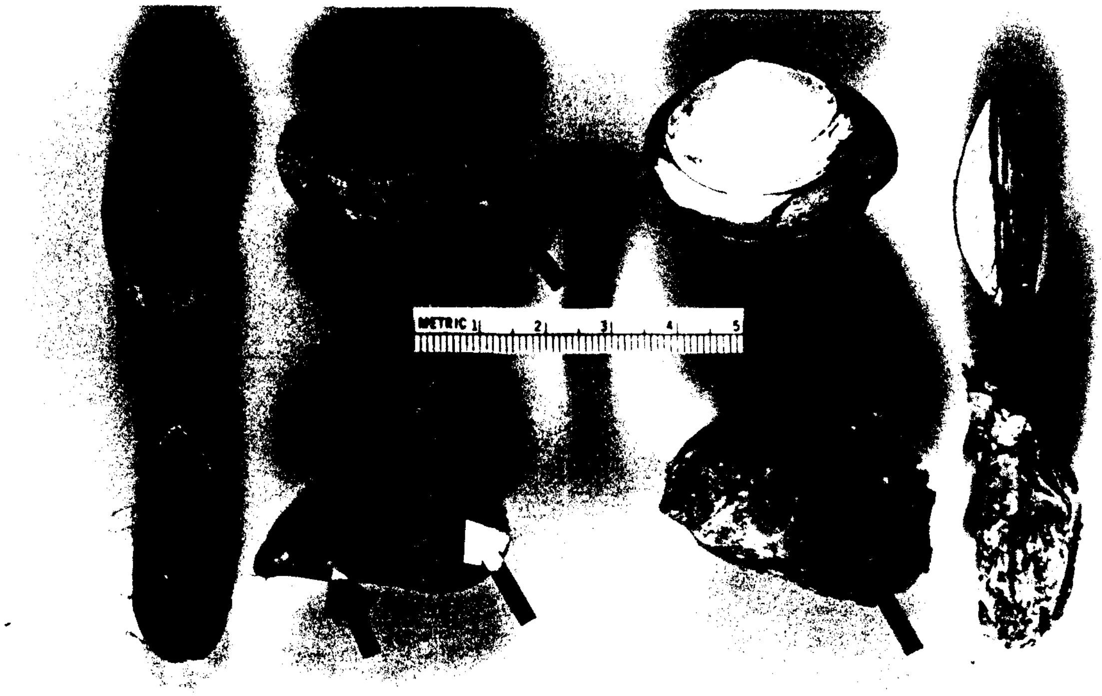

Figure 12: Bivalve Prey Species; (clockwise from top left) Tapes, Macoma, Ostrea, and Mytilus, With Sites Tested for Crushing-Resistance (arrows)

Figure 13: Gastropod Prey Species (clockwise from top left)
Ceratostoma, Nucella, Crepidula, and Searlesia,
With Sites Tested for Crushing-Resistance (arrows)

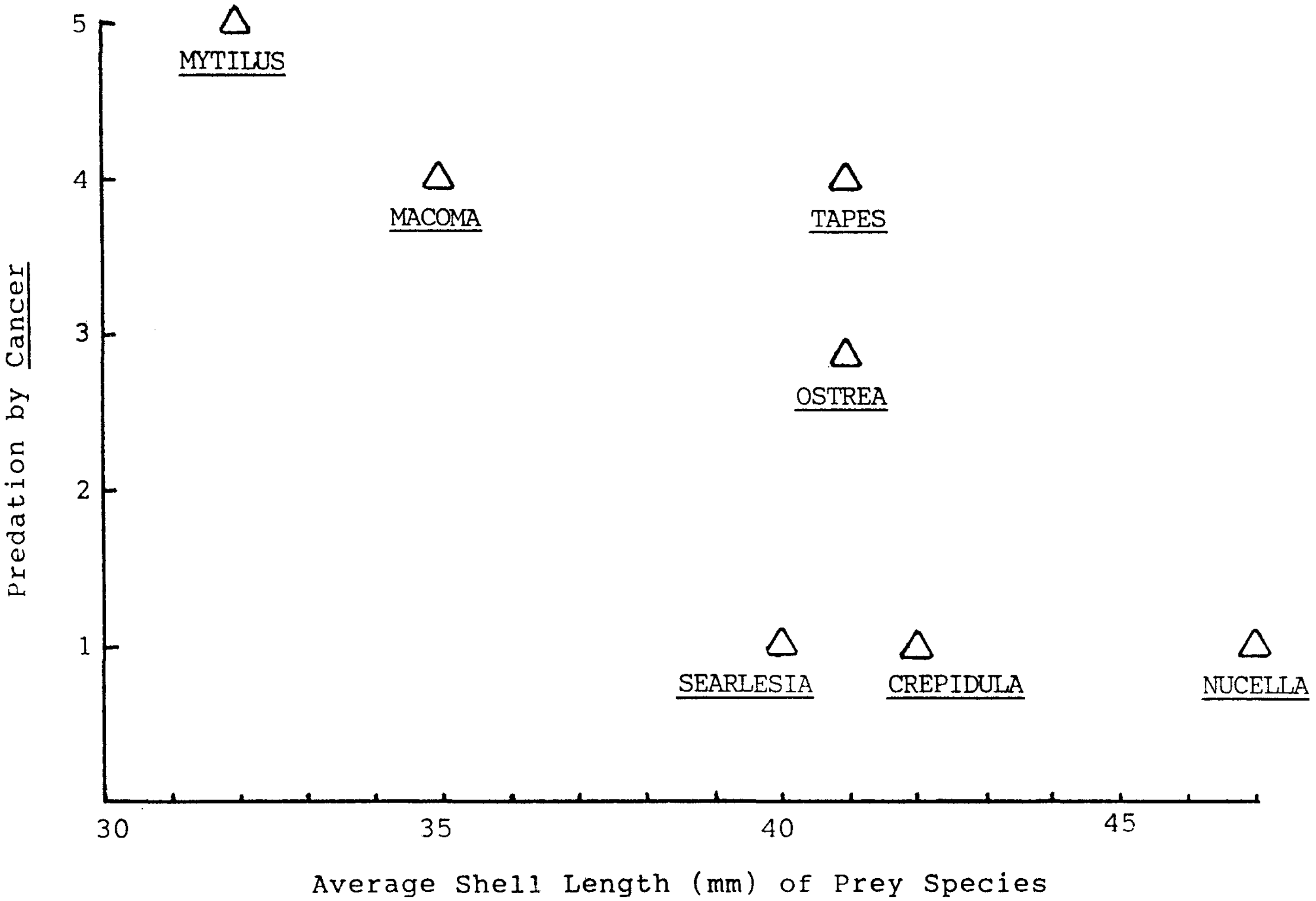

Figure 14: The Effect of Prey Shell Size on Predation by <u>Cancer</u> Relative to Predation on <u>Ceratostoma</u>.

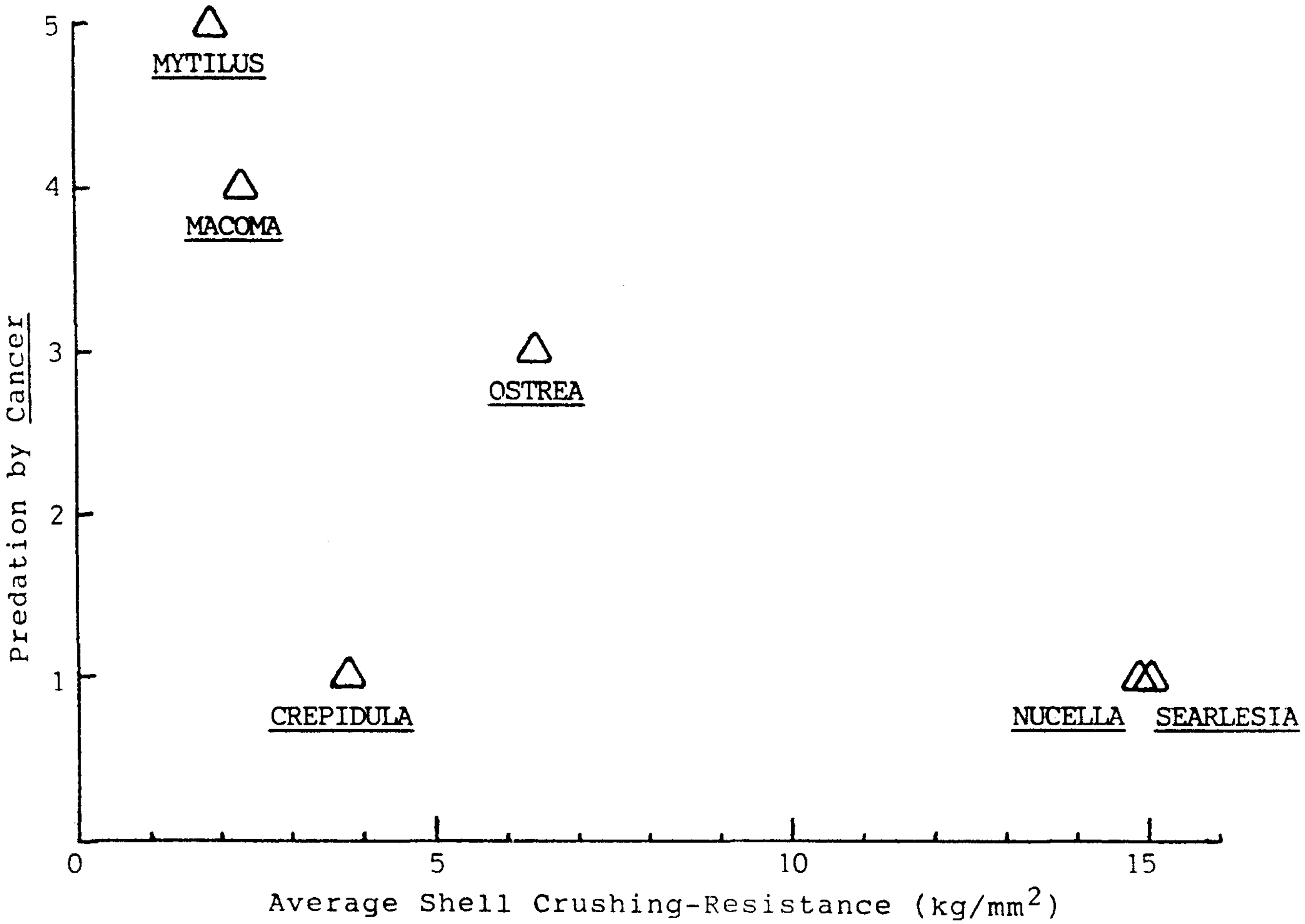

Figure 15: The Effect of Prey Shell Crushing Resistance on Predation by *Cancer* Relative to Predation on *Ceratostoma*

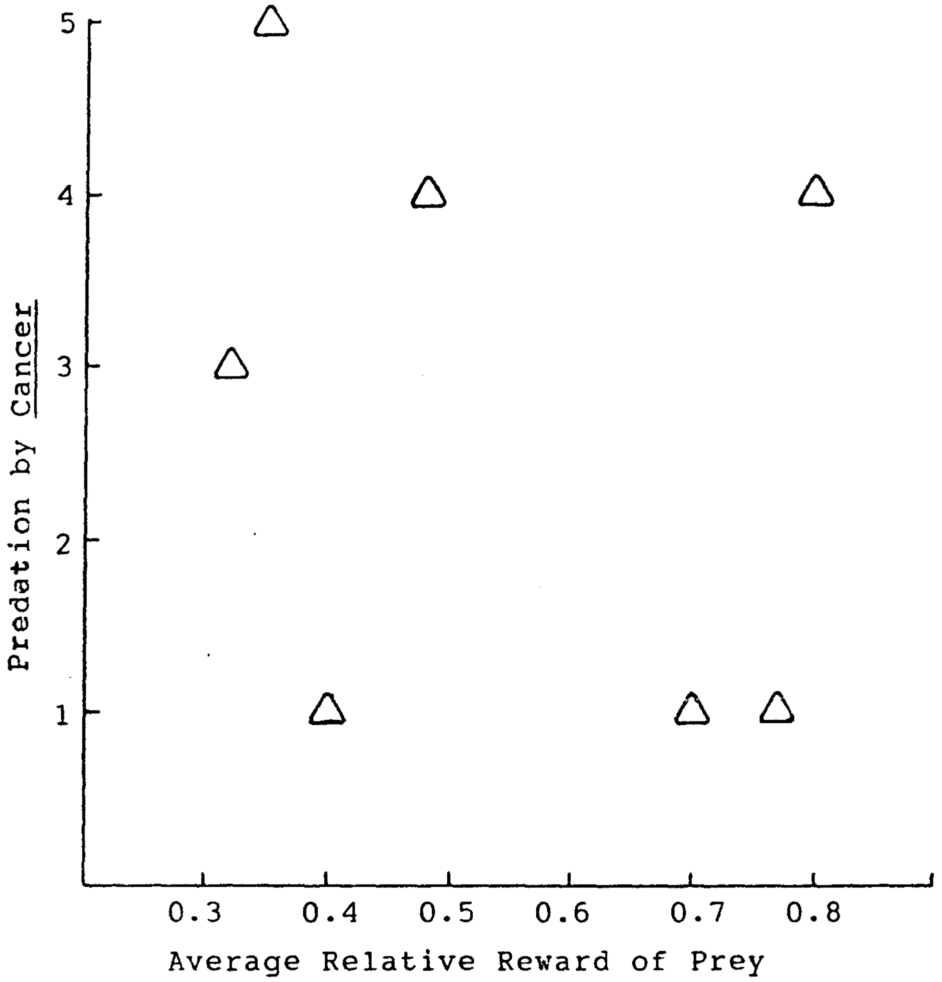

Figure 16: The Effect of Relative Reward of Prey on Predation by *Cancer* Relative to Predation on *Ceratostoma*.

DISCUSSION

Field Analysis

Dobson and May (1986) and Myers (1986) suggested that one reason an introduced species can successfully invade a system is the lack of parasites or pathogens adapted to that species in the host ecosystem. Ceratostoma inornatum has successfully invaded oyster beds of the Puget Sound, has persisted for half a century, and is by far the most abundant neogastropod in oyster beds. Clearly, however, it is more affected by several shell-eroding parasites or diseases than are the native neogastropods, Nucella lamellosa and Searlesia dira, the most similar species to Ceratostoma in the oyster beds. Based on shell-eroding agents, therefore, it does not appear that a lack of parasites or diseases is a requirement for continued existence of Ceratostoma in the Puget Sound.

It could be argued that these shell-eroding agents do not affect Ceratostoma survival, and are therefore not parasitic or pathogenic from the viewpoint of the snail. Shell erosion can be severe, however, covering large areas of the shell (Figure 5), and causing drastic shell weakening in those areas, based on the shell strengths experiments done in this study on worn and unworn specimens of Ceratostoma. If shell strength is related to susceptibility to predators, as suggested by

Vermeij (1979) and Palmer (1985), severe shell erosion could have significant importance to a population of *Ceratostoma* if the frequency of

shell erosion is high, such as at Mud Bay.

Shell scars on *Ceratostoma* are frequent at both sites looked at. Theoretically these could be a result of a number of agents, such as gull or crow predation, wave damage, or crab predation. The waters of the southern Puget Sound are very calm, however, so wave action is very unlikely as a mechanism. Gulls and crows have been observed to prey on gastropods by dropping them, but shell damage inflicted by dropping *Ceratostoma* from the second floor of a building results very different scars than those found on *Ceratostoma* (Figure 6) (personal observation). Scars found on *Ceratostoma* more closely resemble damage by the crabs *Cancer* and *Lophopanopeus* in this study (Figure 9, lower right). The frequency of shell scars on living snails cannot be used as a direct measure of crab predation, since each scar represents an ultimately unsuccessful attack, but it indirectly demonstrates that crabs frequently attack *Ceratostoma* in oyster beds.

Predation on Ceratostoma

Of the five species tested as possible predators of *Ceratostoma*, three (the anomuran *Pagurus samuelis* and the predatory neogastropods *Nucella lamellosa* and *Searelsia dira*) ate none of the *Ceratostoma* offered them. Two species tested (*Cancer gracilis* and *Lophopanopeus bellus*) did prey upon *Ceratostoma*.

Cancer appears to prey more readily upon Ceratostoma than does Lophopanopeus, eating several times more snails than Lophopanopeus in the same time period, but since Cancer is much larger than Lophopanopeus this is not unexpected. It is unexpected, however, that Lophopanopeus ate Ceratostoma at all, since the largest Lophpanopeus used was much smaller than the smallest Cancer that preyed on Ceratostoma. Figure 9, showing the largest size of Ceratostoma eaten by each crab of both species, show that members of both species eat Ceratostoma of the population average size of 33 mm. Using the slope of the crab size versus Ceratostoma size, it is possible to predict the smallest crab of each species that will prey on Ceratostoma of 20 mm in length, the smallest size considered in this study. For Cancer the slope = 1.96 and the y-intercept = 4.16; the smallest crab that is predicted to be able to prey on a 20 mm Ceratostoma is 43 mm in carapace width. For Lophopanopeus the slope = 0.677 and the y-intercept = 7.25; the smallest crab that is predicted to be able to prey on a 20 mm Ceratostoma is 21 mm.

The diet overlap of Cancer and Lophopanopeus may be due to the overlap in chelae size. The chelae of Lophopanopeus are relatively much larger and more robust than the chelae of Cancer (Figure 8), and the dactyl and propodus of the chela of Lophopanpeus meet at only two points, rather than along the length of the dactyl. This would allow the smaller crab to exert more force on a single point.

Predation on Alternate Prey

There are three alternate hypotheses predicting how a native predator will view a native species versus a similar introduced species: the predator will favor the native species it has evolved with and adapted to eat, or the predator will reject the native species in favor of the introduced species, or the predator will not differentiate between the native and the introduced species. There seem to be examples of all three in the literature (Hillson, 1976; Taylor et al., 1984; Lloyd et al., 1986). In this case, neither species of crab eats either of the neogastropods tested here (_Nucella_ and _Searlesia_), but both eat the introduced prey (_Ceratostoma_). This suggests that the native snails have evolved defenses against _Cancer_ and _Lophopanopeus_.

One possible defense is shell strength. Both _Nucella_ and _Searlesia_ have significantly stronger shells than even unworn _Ceratostoma_. Although the reported values in this study are crushing-resistances of about 15 kg/mm^2 for either of the native species, they are conservative since the crushing resistance of the shells often exceeded the capacity of the testing device (17.8 kg/mm^2). Even with this limitation, they are stronger than unworn _Ceratostoma_ (11.4 kg/mm^2), the strongest group of that species. The native species might escape predation simply by being too hard to crush, an antipredator strategy proposed by Vermeij (1979) and Palmer (1985).

Another possible antipredator mechanism is shell shape and scupture. Vermeij (1979) suggested that relatively lower-spired shells are more difficult for crabs to prey on. _Searlesia_ is clearly higher-spired than

Ceratostoma, although *Nucella* is not. *Ceratostoma*, on the other hand, does have large varices, which was believed to be an antipredator strategy in gastropods by Bertness and Cunningham (1981) and Vermeij (1982), but *Searlesia* has none, and the varices on *Nucella* are relatively small and fragile. In this case the varices of *Ceratostoma* may actually serve to enhance predation by *Cancer* and *Lophopanopeus* by providing "handles" for the crabs to manipulate the shell with. Predation differences, therefore, do not seem to be accounted for by shell sculpture alone.

Crepidula is anomalous by being relatively fragile (crushing resistance of 3.8 kg/mm), but not eaten by *Cancer* (although the crabs readily ate crushed *Crepidula*). Furthermore, a few *Lophopanopeus* did eat *Crepidula*, by breaking through the shell of the dead individual on the bottom of the stack. *Cancer* may be incapable of preying on *Crepidula*, or it may lack the experience. The latter is doubtful, since this crab showed a readiness to eat a variety of other mollusks in the laboratory, and the individuals had been exposed to *Crepidula* in their natural environment. It is difficult to imagine the other alternative either, however, in which *Lophopanopeus* could prey upon *Crepidula* but *Cancer* could not. This problem deserves further study.

Both crabs ate all of the bivalve species offered, and with the exception of *Ostrea*, ate them significantly more than *Ceratostoma*. Here again the explanation for these preferences seems to be shell strength. *Macoma* and *Mytilus* both had more fragile shells than *Ceratostoma*, and *Ostrea*, which is the only entirely sessile species, had a shell thickness similar to *Ceratostoma*. *Iapes* appeared to have a much stronger shell than the other species from the shell strength data, but this appears to be an artifact of how shell crushing resistance was measured. *Cancer* preyed on this species by alternately chipping and prying at the edges of the valves until the clam could be pried open, and then if the shell broke, it would break from the inside. This could not be duplicated quantitatively by the author, so the shell strength data is unreliable for *Iapes* in this context, and is probably an overestimate.

The fact that only *Mytilus* was eaten to the exclusion of *Ceratostoma* probably reflects a second strategy by *Macoma* and *Iapes*. The latter two species are buried a few centimeters below the surface. This may increase searching time by *Cancer*, and it adds several minutes to the handling time by forcing the crab to excavate its prey. *Mytilus* does not have this defense, which may explain why this species forms dense monospecific mats in the upper intertidal of the southern Puget Sound, but is scattered and much less abundant in the oyster beds (personal observation).

For *Ostrea* to be successful in the lower intertidal, one could predict that it would be relatively predator-resistant. Although this was not specifically tested in this study, it appears that *Ostrea* was not preyed upon as readily as the other bivalves, and was not eaten significantly more than *Ceratostoma* by either crab species. Furthermore, the crushing resistance of *Ostrea* (6.4 kg/mm) was greater than that of *Mytilus* or *Macoma* (1.8 and 2.1 kg/mm , respectively).

There is clearly a pattern for predation on shelled mollusks by *Cancer*, and perhaps *Lophopanopeus* as well, based on shell strength. Figure 17 is similar to Figure 15, but *Iapes*, for which crushing resistance was measured unreliably, is left out. The correlation is significant ($r = -0.734$), with a slope of -2.54. It is possible to predict from this, based on shell strength, which species of shelled, slow-moving or sessile invertebrates will be eaten by *Cancer*, and approximately how much they will be eaten in the presence of other prey. Using this, the author predicts that severely worn *Ceratostoma* will be eaten relatively more than average *Ceratostoma*, and unworn *Ceratostoma* will be eaten less than average *Ceratostoma* (Figure 17).

There seemed also to be a pattern for predation based on average shell size (Figure 14), but if this was the controlling factor one would expect the smallest individuals of the uneaten species to be preyed upon at least occasionally. This was not the case, and by correcting crushing resistance for those species in which it was correlated significantly to shell size to the size of the smallest average of any species tested (32 mm), it is shown that shell strength could explain differential predation without size differences. Relative reward, although it varied significantly, was not correlated to predation (Figure 16). Chemical deterence seemed not to be present in any of the species tested, except possibly *Searlesia*, which *Lophopanopeus* did not eat crushed specimens, but since *Cancer* did eat crushed *Searlesia*, this needs more study.

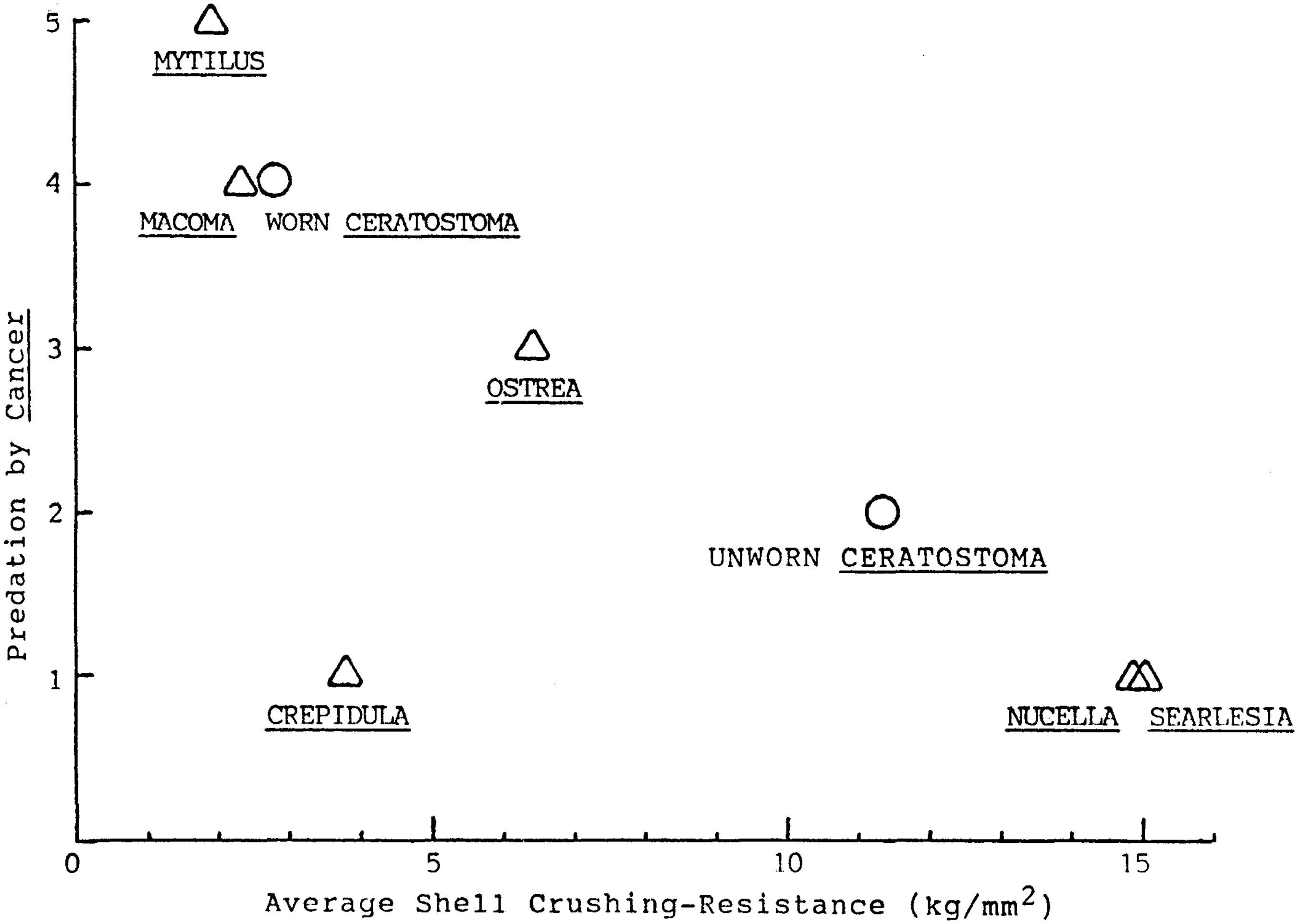

Figure 17: The Effect of Prey Shell Crushing Resistance on Predation by *Cancer* Relative to Predation on *Ceratostoma*

Answers to the questions and hypotheses posed at the end of the Introduction are as follows:

I. Two of the native predators tested (*Lophopanopeus* and *Cancer*) preyed upon *Ceratostoma* under laboratory conditions, but the remaining three (*Nucella*, *Searlesia*, and *Pagurus*) did not.

II. *Ceratostoma* was preyed upon less than *Tapes*, *Macoma*, and *Mytilus*, and equally to *Ostrea* by *Cancer*, and less than *Mytilus* by *Lophopanopeus*.

III. The difference in predation was satisfactorily explained only by the difference in prey shell parameters, and specifically, by shell strength.

This was not a study of the actual diets of *Cancer* or *Lophopanopeus*, but was meant to compare predation upon an introduced species, *Ceratostoma*, by native predators, versus predation upon the most similar species available, within a certain size range. The results show that *Ceratostoma* is eaten by two native predators, the crabs *Cancer* and *Lophopanopeus* and expands their menus to include large predatory neogastropods, a group apparently otherwise uneaten by the crabs in oyster beds. This suggests that *Cancer* and *Lophopanopeus* are able to incorporate non-coevolved species into their diet, and are therefore not rigidly coupled to their prey species. *Cancer* also preyed upon the introduced *Tapes* and *Lophopanopeus* preyed upon the introduced *Crepidula*.

APPENDIX A

DISCUSSION OF *OSTREA* BED HABITAT

The Oyster Beds

The major *Ostrea lurida* beds are in slightly brackish reaches of the southern Puget Sound, in Mud Bay, Oyster Bay, and Skookum Inlet (see Figure 2). None of these have large freshwater inflows, and salinites range from about 26 ppt during the winter to about 28 ppt in the summer (Hopkins, 1937; McKernan et al., 1949). The beds are on soft, nearly level mud tidal flats from less than 0.3 m above mean low low tide, except where concrete dikes have been placed to hold water at low tide, to over a meter below mean low low tide. Currents are very slight over these beds. The *Ostrea* grow on older shells, and form a loose, fragile matrix with individual oysters rising about 5 cm above the mud. The adult *Ostrea* do not exceed about 5 cm, so all shelters for other, non-burrowing species are on that scale or smaller. Wood is kept off the beds by the oyster culturists, except for boards erected at the edges of some beds to deter the large predatory moon snail, *Polinices lewisii* (Gould, 1847) (Naticidae). There is a scattering of naturally set *Crassostrea gigas* and *Ostrea edulis* Linnaeus, 1758, another introduced oyster, which may form large clumps and provide shelters over 25 cm across for mobile epifauna. The other notable feature of *Ostrea* beds are the concrete dikes, erected before the 1920's (McKernan et. al., 1949), rising to 0.5 m above the surrounding flats and filled with crevices. Rock is scarce except at the base of these dikes.

Other abundant (>10/m) large sessile organisms in the *Ostrea* beds include the mussel *Mytilus edulis* Linnaeus, 1758, native clams of the genus *Macoma*, especially *M. inquinata* (Deshayes, 1855) (Tellinidae), the introduced clam *Tapes japonica* Deshayes, 1853 (Veneridae),and the introduced slipper shell, or "cup", *Crepidula fornicata* (Calyptraeidae: Mesogastopoda). None of these species are as abundant as *Ostrea*, except on the concrete dikes (pers. obs). All should be regarded as potential prey items to anything that would also prey on *Ceratostoma*.

Snails, including *Ceratostoma*, are found mostly on the concrete dikes or on the shells of larger introduced oysters. These include *Nucella lamellosa* and *Searlesia dira*, both about the same size as *Ceratostoma*. These also should be regarded as potential prey items to a *Creatostoma* predator, even though they themselves as predatory gastropods are possible predators of *Ceratostoma*. Other shelled gastropods, with the exception of *Polinices*, which does not seem to be able or inclined to enter dense *Ostrea* beds, are smaller or rarer than these.

Brachyuran and anomuran crabs, arranged in decreasing order of size, include *Cancer gracilis* Dana, 1852, *Lophopanopeus bellus*, the hermit crab *Pagurus samuelis* (Stimpson, 1857), and *Hemigrapsus oregonensis* (Dana, 1851). *Cancer magister* Dana, 1852, and *Cancer productus* Randall, 1839, rarely enter these *Ostrea* beds (pers. obs.; D.

McMillin, pers. comm.). One other crab, *Pugettia producta* (Randall, 1839) (Majidae), occasionally enters *Ostrea* beds.

Other predators within the *Ostrea* beds include sculpins (pers. obs.) (Cottidae: Scorpaeniformes), gunnels (pers. obs.) (Pholididae: Perciformes), and perch (D. McMillin, pers. comm.; J. Taylor,pers. comm.) (Embiotocidae: Perciformes), none of which often attains more than 20 cm in length. Gulls (Laridae), crows (Corvidae) and scaups and scoters (Anatidae) are also seasonally abundant (D. McMillin, pers. comm.). The sea star *Pisaster brevispinous* (Stimpson, 1857) is present but scarce.

Ceratostoma is present throughout the system in large numbers, but is concentrated on the concrete dikes and on *Crassostrea* shells, in close aggregations of up to fifty. Small *Ceratostoma*, however, here defined as those less than 20 mm in shell length, are very difficult to find, and are either rare or hidden (pers. obs.).

Possible Predators on Large *Ceratostoma*

Since small *Ceratostoma* were very difficult to find in the field sites examined, this paper discusses only predators on those *Ceratostoma* 20 mm or more in shell length. Some of the organisms mentioned above, therefore, are not considered major predators on this species for the purpose of this paper because their known diets do not include large gastropods. These predators include the crab *Hemigrapsus oregonensis* (Knudsen, 1964), and all three fish families mentioned (Caillet and Antrim, 1978; Quammen, 1984; and D. Varoujean, pers. comm.).

Several more species can probably be omitted as potential predators because of rareity. These include *Pisaster*, *Cancer magister*, *Cancer productus*, and *Pugettia*. *Polinices* is common at the periphery of the *Ostrea* bed, but it moves by "plowing", nearly completely buried, through the mud, and does not seem able or inclined to enter the *Ostrea* beds (personal observation). For purposes of this study, therefore, *Polinices* is considered too scarce to be a significant predator of *Ceratostoma* in the oyster beds.

Several species of gull (Laridae), are present, but rarely if ever in large flocks (D. McMillin, pers. comm.). Their diets can be checked by scatological examination. This has been done periodically by D. McMillin (pers. comm), and while *Ceratostoma* is occasionally present, it does not appear to be a regular part of the diet. Crows, *Corvus brachyrhynchos* Brehm, are present but not abundant (pers. obs.), and have been reported by Zach (1978) to prey upon *Nucella*, and by McMillin to prey upon *Ceratostoma*, but he believes this last to be incidental (pers. comm.). Since *Ceratostoma* congregates on concrete dikes, they would be easy prey for the gulls and crows, yet remain abundant (personal observation). Three species of ducks, the white-winged scoter, *Melanitta fusca* (Linnaeus, 1758), the black scoter, *M. nigra* (Linnaeus, 1758), and the greater scaup, *Aythya marila* (Linnaeus, 1761) are seasonally abundant, and prey regularly on *Ostrea* , although they prefer the introduced bivalve *Tapes*, and local oyster culturists have carried out extensive campaigns against the ducks. The stomach content of many of these were examined, and while *Ceratostoma* was occasionally found, it was incidental (D. McMillin, pers. comm.; J. Taylor, pers. comm.). On the basis of stomach content literature (Cottam, 1939; Gabrielson and Jewett, 1940; Baltz and Morejohn, 1977; and Goudie and Ankney, 1986) and on the reports by the local oyster culturists, therefore, none of the bird species are considered major predators of *Ceratostoma*, although the fact that all include this species in their diet deserves further study.

Although gastropods have not been reported in the diet of *Nucella lamellosa*, *Nucella lapillus* has been reported to prey on *Littorina littorea* (Linnaeus, 1758) (Dudley, 1980; and J. Carlton, pers. ref.). *Searlesia dira* is reported to prey on mesogastropods (Louda, 1975; Hoffman, 1981). *Pagurus samuelis* has not been reported to prey on gastropods, but other hermit crab have (Greenwood, 1972; Rutherford, 1977). *Pagurus* has the double motive of both food and shelter needs. The diets of *Lophopanopeus bellus* and *Cancer gracilis* have not been well studied, but related species to both are known gastropod predators (Powell and Gunter, 1968; Chilton and Bull, 1985; Lawton and Hughes, 1985; and Palmer, 1985). Unlike the bird species discussed earlier, the diets of these species in estuaries has not been reported, and they cannot be eliminated as possible significant predators on *Ceratostoma* until tested.

APPENDIX B

DISCUSSION OF ASSUMPTIONS

Three assumptions critical to the predation choice experiments were as follows: first, that all individuals of either species of crab knew what prey items were in the habitat with them; second; that the *Cancer* did not know to what depth in the sediement the bivalves were buried, and third; that the crabs did not discriminate against individual prey specimens that they had previously handled and not eaten.

The first assumption is important because it eliminates the possibility that the crabs preyed only upon prey individuals that they randomly encountered with their appendages. This would then introduce prey behavior as another variable, even though the prey moved much more slowly than the crabs.

This assumption was supported by empirical observations of the two species of crabs. They did not seem to "see" the generally immobile prey species, but spent a large part of their time moving around the habitat, and encountered all the above-sediment prey items at least several times a day (if they did not eat them sooner). It is not known how *Cancer* detected the buried bivalves, but field observations of *Cancer* indicated that they did not dig randomly. Possibly they detected the clam siphons by chemoreception. The habitats were large enough that there was a low probability that the crabs would encounter the bivalves by random burrowing. Cancer individuals spent part of their time buried, but each individual tended to chose the same corner of its enclosure to do so.

The second assumption is important because it might be argued that if the crabs knew that the clams were buried at only 4-5 cm, rather than the typical 15-20 cm, they would be more likely to excavate them. This argument depends, however, on the crabs having a neural mechanism to evaluate this problem, which in itself is not a safe assumption. Even if the crabs did, and even if they encountered the bottom when they buried themselves, large smooth rocks, shells, or pieces of wood are abundant in the crabs' natural habitat, resembling the bottom of the artificial habitat at any point, so that the crabs would not neccesarily associate the bottom of the habitat with maximum sediment depth. Furthermore, there is no evidence that even if the crabs can detect clams chemically, they can gauge the depth at which the clam is buried.

The third assumption is important because if the crabs were somehow biased against prey individuals that they had handled but had not eaten, these individuals would cease to become prey options in the crabs' point of view. To argue against this assumption, it is neccesary that the crabs remember and recognize prey individuals as having been previously "unchosen", and to continue to remember this from day to day. Although crabs generally ignored uneaten prey individuals of any species when observed, they attacked these same prey if they were removed momentarily and then replaced, or if the crabs' violently disturbed the prey. This suggests that the crabs do not recognize the prey individuals themselves, or at least for time periods of more than a few hours.

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