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Feeding biology and ecological aspects of a cancroid crab Cancer Oregonensis (Dana) Rathbun (decapoda, brachyura)

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FEEDING BIOLOGY AND ECOLOGICAL ASPECTS OF A CANCROID CRAB: CANCER OREGONENSIS (DANA) RATHBUN (DECAPODA, BRACHYURA)

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FEEDING BIOLOGY AND ASPECTS OF THE POPULATION STRUCTURE OF *CANCER OREGONENSIS* (DANA) RATHBUN (DECAPODA, BRACHYURA)

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INTRODUCTION

In the San Juan Archipelago, *Cancer oregonensis* (Dana) Rathbun (Fig. 1) is abundant and distributed from the low intertidal zone to -435 m subtidally (Rathbun, 1904). Ricketts and Calvin (1974) refer to *C. oregonensis* as the most common *Cancer* species in this area.

Subtidally, according to Kozloff (1974), the crab is commonly found within the hollowed-out shells of the barnacle, *Balanus nubilus* (Fig. 1). With one exception (Knudsen, 1964), a perusal of the literature reflects little on the biology of *C. oregonensis*. There is a lack of ecological information on cancroid crabs in general, with most of the investigations concerned about the marketability of certain species (Butler, 1960, 1961; Edwards, 1964; Poole, 1965; Scarratt and Lowe, 1972).

The purpose of this study was to examine the feeding biology and aspects of the structure of intertidal and subtidal populations of *C. oregonensis*. The population characteristics studied, as well as feeding, will help explain the success of this species in the San Juan Archipelago. This investigation was conducted over a period of three months (March, April, and May) in 1976.

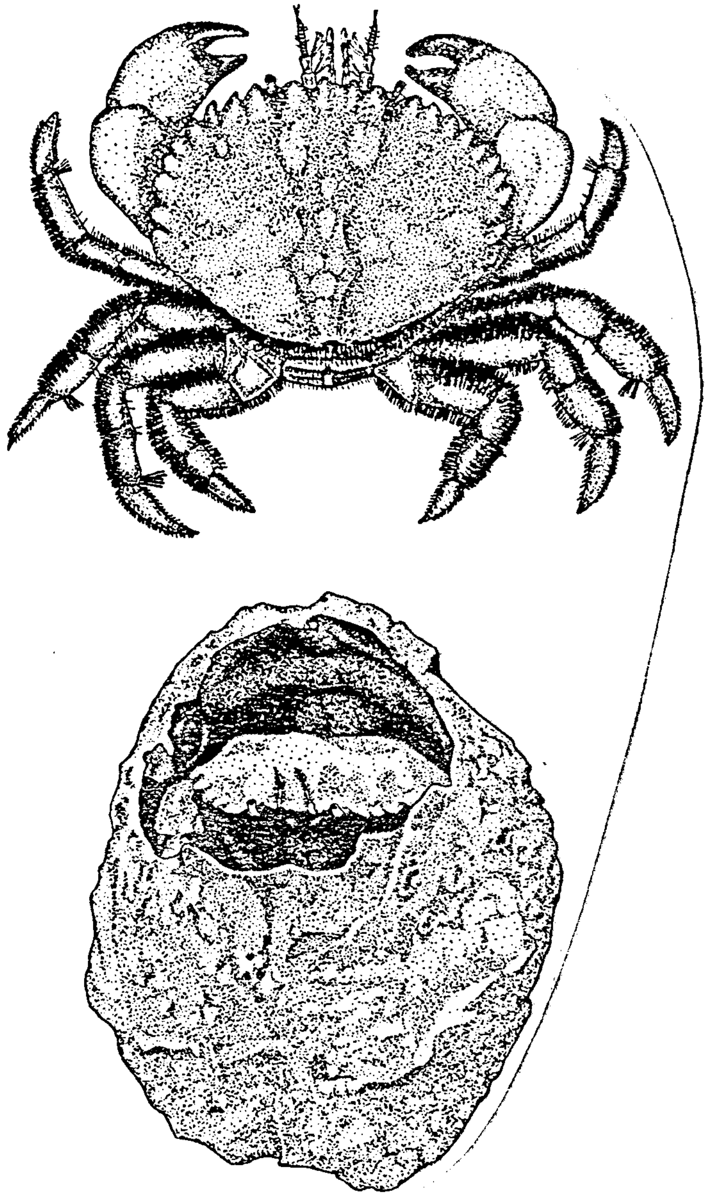

Figure 1. Cancer oregonensis. Dorsal view (above X 1), as found subtidally in Balanus nubilus shells (below X 0.6).

MATERIALS AND METHODS

Study Areas

Subtidal and intertidal populations of C. oregonensis were examined separately but not always in the same area. Subtidal populations were collected at Cantilever Pier by the use of SCUBA and at various locations in the San Juan Archipelago by dredge samples. Intertidal populations were examined at Cattle Point, Lonesome Cove, and near the Cantilever Pier site. A third group was studied on the floating docks at Snug Harbor. The latter group, however, was used for feeding analysis and not for population studies.

The Cantilever Pier study site is located at San Juan Island, near the Friday Harbor Laboratories of the University of Washington on the northern part of the harbor (Fig. 2). The area is characterized by rocky cliffs which extend to -20 m (mean sea level = +2 m), level off, and then continue to -45 m where they level off again. The solid, rocky outcrop substratum is interspersed with areas of silt, sand, and loose rock. Wherever the slope isn't steep, these silty areas become more predominant, i.e., at approximately -15 m and continuous at -20 m and -45 m. The actual collection sites were located on rocky outcrops where the encrusting barnacle, Balanus nubilus, is common

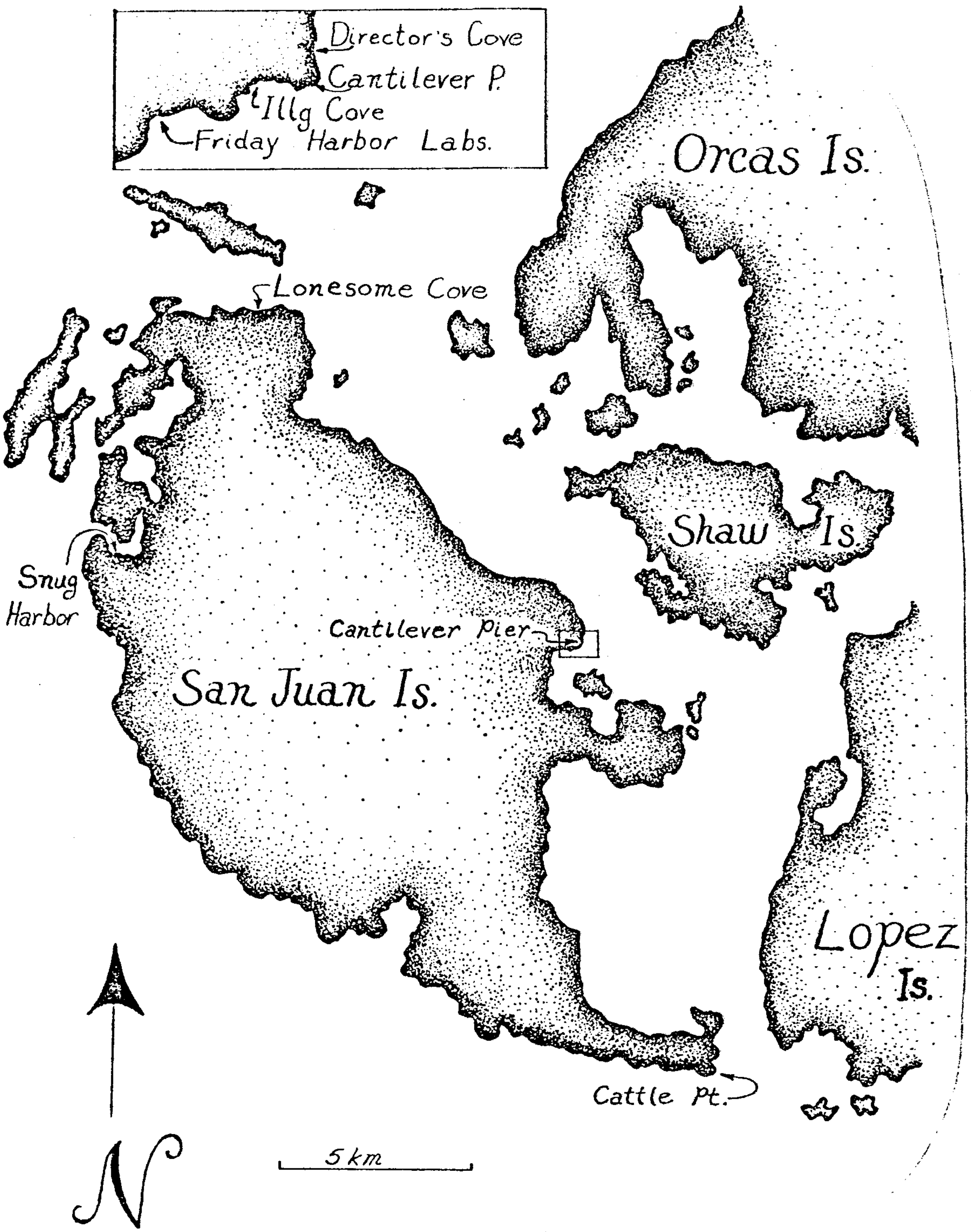

Figure 2. Cancer oregonensis. Study sites on and around San Juan Island. Insert shows detailed description of Cantilever Pier site.

to abundant. Along with B. nubilus, the predominant bottom fauna consists of the sea urchins, Strongylocentrotus drobachiensis and S. franciscanus, the sea cucumber, Parastichopus californianus, various tunicates, brachiopods, and sea stars.

Dredge samples were obtained by the M.V. Hydah (operated by the University of Washington) at depths ranging from -15 m to -30 m near Lopez Island in the San Juan Channel, and at Obstruction and Peavine passes near the mouth of East Sound, Orcas Island.

The main intertidal collecting took place at Cattle Point, which is located on the southern tip of San Juan Island (Fig. 2). This area is characterized by a sandy beach that slopes gradually, becoming more rocky with cobbles (15 to 30 cm across) in the low intertidal zone (zero to minus tides). The cobbles are amongst the fine (<1 mm), sandy mud and are mostly covered with the algae, Polysiphonia sp., Odonthalia sp., and Rhodomela sp. At Cattle Point the predominant fauna consists of various species of polychaetes in the sand and attached under rocks, as well as gammarid amphipods hidden in the algae.

The second intertidal study site is located at Lonesome Cove on the northern tip of San Juan Island (Fig. 2). Unlike Cattle Point, the substratum is not fine sand, but considerably coarser (i.e., 1 to 3 mm with pebbles up to 5 cm). The algal species are different, consisting primarily of Agarum sp. and Monostroma sp. The bottom fauna is not significantly different than that found at Cattle Point in relationship to the polychaetes and amphipods. There is, however, a considerable number of urchins, S. drobachiensis, and the cucumber, Cucumaria miniata.

The floating docks at Snug Harbor (Fig. 2) on the west side of San Juan Island offer a unique study site. This area is characterized by sponges, tunicates (especially the compound ascidian Distaplia occidentalis), dorid nudibranchs, polychaetes (both errantians and sedentarians), and anemones (Metridium senile).

Sampling Procedure

Animals were collected by hand intertidally, at Snug Harbor, and by SCUBA and dredge hauls subtidally. Collections were returned to the laboratory where they were maintained in aquaria with running, unfiltered sea water. Those individuals to be used for stomach analysis were placed immediately in 70% EtOH. The ethanol was used instead of formalin to facilitate ease of handling by the investigator. All of the animals were measured with vernier calipers for carapace width and sexed. Ovigerous females were noted and egg counts were conducted by removing the eggs from the pleopods, taking a wet weight of the total and a subsample. The subsample was counted with the use of a grid plate (marked in square centimeters for ease of reference) and a hand counter. The number of eggs per weight of subsample was considered a simple ratio of the total number of eggs per weight. Sexual maturity was determined by the smallest size ovigerous female and by gonad development in the male (Fasten, 1917).

Stomachs were excised from those individuals that were preserved and the contents noted as nearly as could be detected with the aid of microscopes.

As collections were brought into the laboratory, some animals were found to be in the process of molting. When ecdysis was complete, the soft crab was removed and isolated, allowing it to harden. The exuded shell was measured, as well as the hardened crab, and an increment of growth calculated.

All animals were collected by simple random sampling techniques during the months of March through May, 1976.

Behavioral Patterns and Adaptations

Field conditions where *C. oregonensis* is found were reproduced (as near as possible) in the laboratory. Cattle Point was selected because of its accessibility as the model for the intertidal segment of the population, and dredge hauls furnished the materials necessary to recreate the subtidal environment. Visual observations were made on a 24-hour basis with the use of red light during periods of darkness. Each hour the number of active crabs was determined and a percentage calculated from a known number present in the experiment. The percentage served as an index (for comparison purposes) of the amount of activity (foraging, feeding, or reproductive) at any given time. This technique was also used to detect feeding behavior. Night observations, subtidally, were made by the use of SCUBA and photographic methods. A tripod with a Canon F-1 camera (with battery-operated motor drive and underwater housing) and Subsea strobe were installed at -22 m off Cantilever Pier. Pictures were taken every 3 minutes and analyzed for activity.

In further analysis of feeding behavior, an experiment was designed to ascertain which appendages were associated with food manipulation. Three crabs were fed nereid polychaetes that had been stained with toluidine blue (Caine, 1975). The crabs were separated from the prey after ten minutes of feeding and placed in the freezing compartment of a refrigerator. The appendages used in handling the food were stained with the toluidine blue.

Preliminary observations by the author indicated the possibility of detritus feeding for C. oregonensis. On this basis, an experiment was designed similar to Orton's (1927) to test this hypothesis. Ten crabs were maintained without a food source for 10 days in running, filtered sea water. At the end of this starvation period, 5 crabs were selected at random to be placed in clean dishes with detritus collected from -20 m off Illg Cove (Fig. 2). The remaining 5 crabs served as a control, being given the same conditions as the experimental group, but not being fed. The experiment was terminated at the end of 24 hours and the stomachs of the crabs analyzed.

The chemoreceptibility of C. oregonensis was tested by a Y-maze (Fig. 3) apparatus (Castilla and Crisp, 1970).

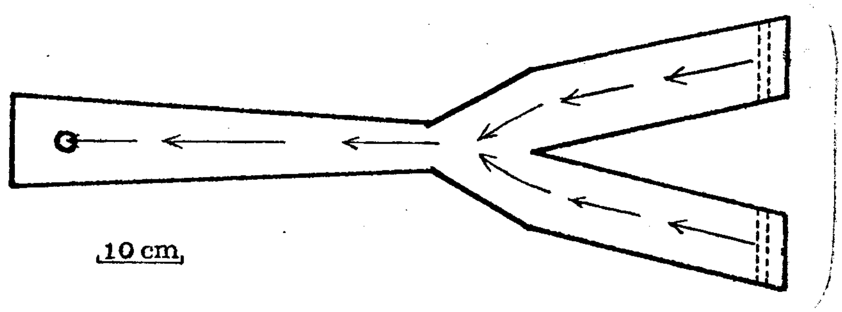

Figure 3. Cancer oregonensis. Y-maze apparatus for testing chemoreceptibility (after Castilla and Crisp, 1970). Arrows indicate flow of seawater.

Plexiglass baffles placed in each arm of the experimental chamber gave a uniform current flow of approximately 1.5 to 2.0 cm/sec. Flourescein (trademark for Braun-Knecht-Heimann-Co.) dye was used to detect whether the current from one arm entered the other. A prey species was placed in one arm, leaving the other as a control. The apparatus was cleaned between each run and the bait switched to the opposite arm to eliminate learning bias. The Y-maze was painted black and placed in an area completely surrounded with black plastic, so as to eliminate the possibility of visual orientation.

Because of the size of C. oregonensis, it was felt that some morphological adaptation might have evolved that would be advantageous in handling smaller prey organisms. An examination of setal types on the mouth parts, antennae, pereiopods, and carapace was compared with those found in the literature and on *Hemigrapsus oregonensis*. Regression lines of the ratio of the third maxilliped to carapace width were compared for five species of decapod crabs, and the results reported in the next section.

RESULTS

Sex Ratio

Recently, investigators have been examining sex ratio in crustaceans on the basis of size classes, as opposed to the overall population (Wenner, 1972; Ahmed and Mustaquim, 1974). This method of using size classes, according to its proponents, gives a more accurate and clear appraisal of the sex ratio and contributes more information about the ecological characteristics of the population.

The data for _C. oregonensis_ were treated accordingly, being divided into discrete size classes and the sex ratio calculated within each class. The results are found in Table 1 and show a deviation from a normal mendelian sex ratio, particularly in the 16 mm, 20 mm, and 40 mm size classes. A graphical representation, according to Wenner (1972), of the results in Table 1 is found in Figure 4. The significance of this "probability curve" will be discussed in a later section of this paper.

Further treatment of the data by constructing a histogram (Fig. 4) indicates a bimodal distribution of males and a unimodal distribution of females. Both graphs in Figure 4 indicate the possibility of a size dimorphism in the population.

Table 1. *Cancer oregonensis*. Percent males within discrete size classes.

Size class[a]	Sample size	Males	Females	% Males
4- 7.99	8	8	-	100
8-11.99	55	36	19	66
12-15.99	112	65	47	58
16-19.99	98	37	61	38
20-23.99	93	25	68	27
24-27.99	78	33	45	42
28-31.99	78	48	30	62
32-35.99	43	27	16	63
36-39.99	20	10	10	50
40-43.99	7	5	2	71
Total	592	294	298	50

[a]Determined on the basis of carapace width in mm.

Mean Sizes

The size range for *C. oregonensis*, based on carapace width, was found to be 5.6 mm to 42.5 mm. The mean size of the total population was 21 mm. The most frequent carapace width for males was 13.7 mm, whereas females were most abundant with a carapace width of 20.7 mm.

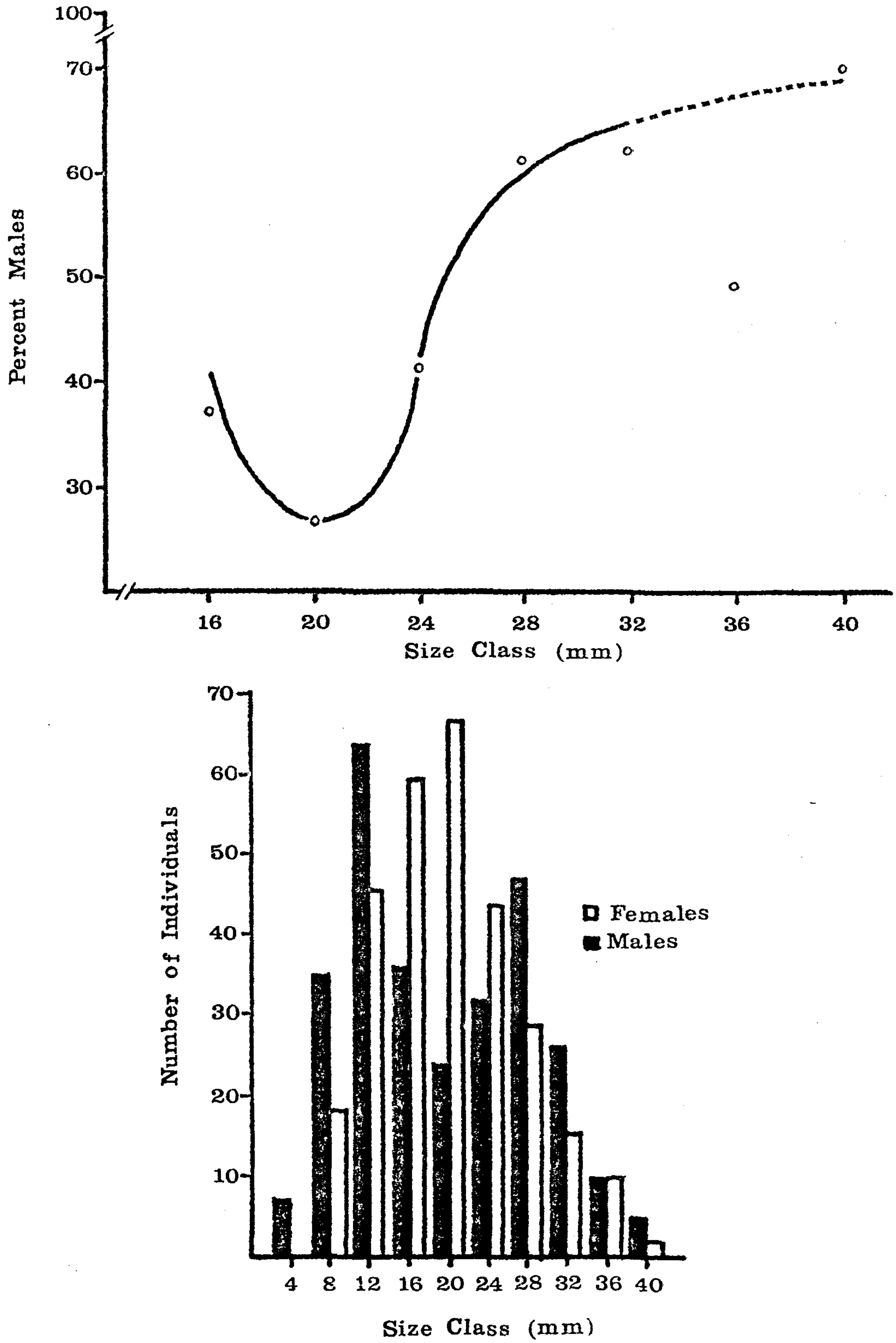

Figure 4. Cancer oregonensis. Sex ratio (above) expressed as the percent of mature males in the population for all data combined and (below) as the number of mature and immature individuals within each size class.

Growth

Growth increments from molting data have been reported for decapod crabs by Smaldon (1972), and specifically for cancroid crabs by Butler (1961), Poole (1965), and Scarratt and Lowe (1972). Increments of growth for _C. oregonensis_ were obtained from recently molted specimens and the data are shown in Table 2. The data indicate a tendency toward decreasing growth increments with increasing size of crab.

Size at Maturity

The size at maturity for females (16 mm) was determined by the minimum-sized individual carrying eggs (Ahmed and Mustaquim, 1974; Krouse, 1972; and Smaldon, 1972). Male sexual maturity was determined by examining gonadal development. Fasten (1917) determined that in mature _C. oregonensis_ the testis almost fills the lateral lobes of the cephalothorax, and the vas deferens is a thick, coiled structure between the heart and intestine. Results of the gonadal development investigation indicated that the males became sexually mature in the same size class as the females (16 mm).

Table 2. *Cancer oregonensis*. Growth increments based on recently molted specimens.

	Pre-molt[a]	Post-molt[a]	Width increment[a]	% Increase
Males	15.5	19.3	3.8	24.5
	23.8	28.7	4.9	20.5
Females	15.0	21.0	6.0	40.0
	17.0	21.4	4.4	25.9
	17.8	20.0	2.2	12.4
	26.4	29.6	2.6	12.1
	28.8	32.0	3.2	11.1
	31.6	36.7	5.1	16.1

[a]Measured for carapace width and expressed in mm.

Recruitment

All individuals collected that were less than 16 mm (size at maturity) could be considered juveniles (Scarratt and Lowe, 1972) or first-season recruits. Population success for the intertidal and subtidal habitats can be calculated from proportions of immature crabs to the total number found in each location. The results of these calculations are found in Table 3. Although a higher percentage of success is shown for the subtidal habitat, an analysis of variance for the data indicates no significant difference between intertidal and subtidal habitats.

Table 3. *Cancer oregonensis*. Percent larvae becoming juveniles.

Habitat	No. juveniles	% Juveniles in population
Intertidal	86	25.9
Subtidal	89	34.4
Total	175	29.6

Mating Behavior

Mating and courtship behavior for *C. oregonensis* was found to be similar to that of other cancroid crabs as reported in the literature (Butler, 1960; Edwards, 1964; Naylor, 1962; Scarratt and Lowe, 1972; Snow and Neilsen, 1966). Mating pairs were not found until mid to late May. However, one pair was found mid-March, and Knudsen (1964) reported mating pairs as early as April. Continuous observations indicated the one pair found by the author in mid-March most likely was a rare occurrence, and it is believed that Knudsen's (1964) findings may be influenced by locality (further south than the San Juan Archipelago). The one mating pair found was brought into the laboratory, and on March 15 it was observed that the female's epimeral line was broken open preparatory to ecdysis. The female was still in the possession of the male and remained so during the entire molting process and throughout copulation. As the shedding of the female's exoskeleton progressed, the male grasped the female's abdominal flap at the proximal end with his cheliped, and while pulling, used his pereiopods to push the old exoskeleton away. Along with the chelipeds, the pulling motion was augmented with the third maxillipeds. The male continued to assist the female in this way until ecdysis was complete, whereupon copulation began. The entire process took approximately 8 hours to complete.

Fecundity

The ovigerous females found ranged in size from 16 mm to 40 mm (Table 4), although there was no evidence that individuals greater or equal to 40 mm were incapable of laying eggs. The percent ovigerous by size class remains fairly evenly proportional (Table 4; Fig. 5), with exceptions in the 20 mm and 28 mm size classes.

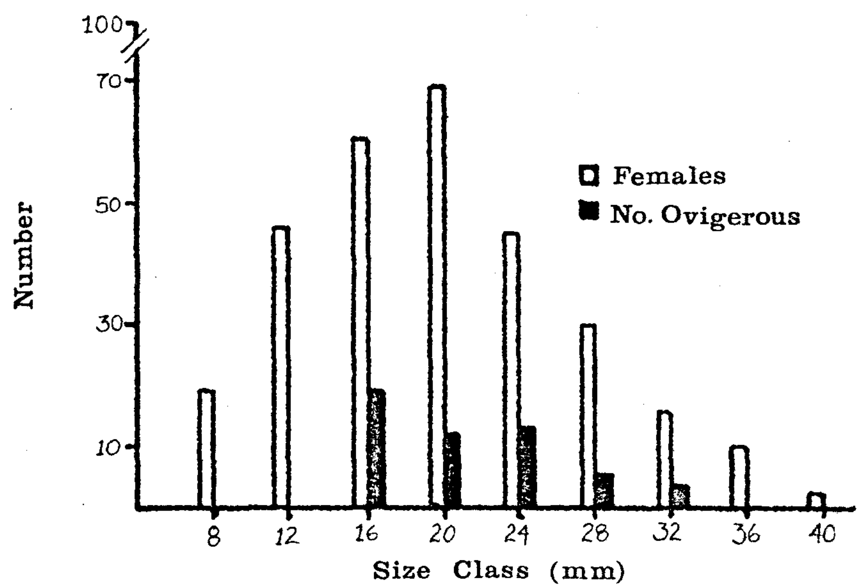

Figure 5. Cancer oregonensis. Histogram showing the number of ovigerous females in each size class.

Table 4. *Cancer oregonensis*. Number of gravid females in each size class.

Size class[a]	Sample size	Females	No. ovigerous	% Ovigerous
4- 7.99	8	-	-	-
8-11.99	55	19	-	-
12-15.99	112	47	-	-
16-19.99	98	61	19	31
20-23.99	93	68	12	18
24-27.99	78	45	13	29
28-31.99	78	30	5	17
32-35.99	43	16	5	31
36-39.99	20	10	3	30
40-43.99	7	2	-	-

[a]Determined from carapace width in mm.

Table 5. *Cancer oregonensis*. Summary of ovigerous females by month.

	March	April	May
Females	63	94	141
No. ovigerous	31	19	6
% Ovigerous	49.2	20.2	4.3

A large number of ovigerous females were taken in March with noticeable hatching occurring in April. Table 5 illustrates the degree at which ovigerity decreases with time, e.g., with nearly half of the females found in berry in March, less than a fourth in April, and a very small (4.3%) number in May.

Cancer oregonensis females produce a tremendous number of eggs. Knudsen (1964) counted eggs on 17 females between the sizes of 17 mm and 26 mm, and found corresponding egg numbers of 10,000 to 33,000. Specimens in this study of the 16 mm to 40 mm range were found to have 3,000 to 82,000 eggs per female, a regression of which is represented in Figure 6.

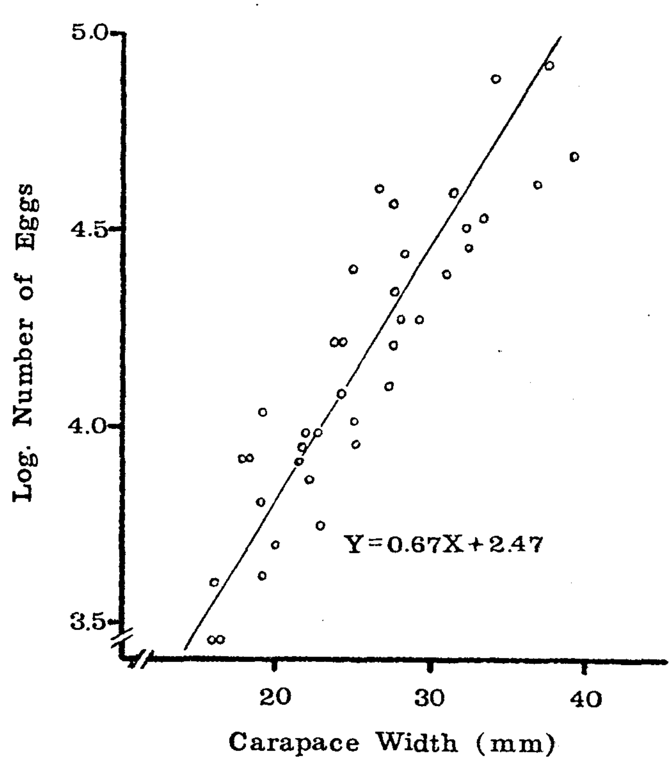

Figure 6. Cancer oregonensis. Linear regression line for (log) number of eggs vs. carapace width.

Activity Periods

Visual observations of *C. oregonensis* crabs in reconstructed subtidal and intertidal habitats (previously described), gave results indicating a preference to nocturnal patterns of activity for the intertidal crabs, but this was not so subtidally. A mean percent of activity during daylight, nighttime, and twilight hours was calculated for both habitats and compared with an ANOVAR. It was found that in the intertidal habitat there is a significant increase in crab activity during the dark hours at the .05 percent level. The subtidal habitat, however, showed no activity difference between diurnal and nocturnal time periods. This evidence was supported by underwater photographs taken during the hours of darkness.

Stomach Contents

Cancer oregonensis stomachs were removed from approximately 17% of the total sample. Qualitative examination indicated an omnivorous diet for the crabs with feeding preferences according to availability within a habitat. The results of this analysis are found in Table 6.

Stomach contents are indicated in the table as to type and frequency of occurrence. Some stomachs may have contained two, three, or more of the items listed. Detritus is listed separately from diatoms since, once in the intertidal samples and at Snug Harbor, diatoms were present in the stomach without detritus. However, in all other samples the two were found together.

The stomach contents data for the intertidal habitats tend to indicate a preference toward crustaceans, particularly amphipods.

Table 6. *Cancer oregonensis*. Results of stomach contents analysis.

Contents	Intertidal	Floating Docks	Subtidal
Empty	6	2	1
Unidentified	8	3	7
Crustaceans	20	1	10
Amphipods	11		
Polychaetes	11	4	5
Detritus	8	-	15
Diatoms	3	1	14
Sand	11	-	5
Algae[a]	5	-	6
C. oregonensis eggs	-	-	3
Sponge spicules[b]	-	5	-
Miscellaneous			
Eggs	1	-	-
Urchin spines	-	-	1
Mollusc radula	-	-	1

[a]Includes filamentous algae.

[b]Other than those possibly being picked up with detritus.

Polychaetes were the second most preferred prey group, and considering the method by which they were caught (to be discussed later), probably accounted for the amount of sand found in the stomachs.

A large number of sponge spicules were found in stomachs from the Snug Harbor floating dock habitat, however, C. oregonensis was not observed feeding on sponges. Most likely the sponge and/or spicules are taken in during the process of foraging for polychaetes that are found in and amongst the sponges (personal observation), or while feeding on detritus or diatoms on the surface of sponges.

Subtidally, crabs were found to ingest a large amount of detritus. This may have been a result of foraging for small sediment-dwelling crustaceans (which were also found in the stomachs in high numbers). However, not all crab stomachs contained both crustaceans and detritus.

Prey Association

In an effort to correlate the stomach contents of intertidal crabs with potential prey species, ¼ m^2 quadrats were placed randomly at Cattle Point and Lonesome Cove. Presence and absence data were collected for those groups that were commonly found with C. oregonensis. Those found in the stomach analysis as well are shown in Table 7 with their frequency of occurrence. The data tend to correspond to the frequency of prey organisms found in the stomach analysis. Numerous complications and inefficient methods of collecting sediment by hand (unique to SCUBA collecting) prevented the same type of comparative analysis for the subtidal habitat.

Table 7. Prey groups associated with *Cancer oregonensis*.

Associate	No. quadrats	No. of times present	% Associated with *C. oregonensis*
Polychaetes	8	8	100
Amphipods	8	8	100
Other crustaceans	8	6	85.7

Structural Morphology

Four species of brachyurans (*Cancer magister*, *C. productus*, *Hemigrapsus nudus*, and *H. oregonensis*) as well as *C. oregonensis* were sturcturally compared on the basis of the third maxilliped to carapace width ratio. The third maxilliped is the principal appendage involved in the handling of food items. In consideration of the types of food ingested (i.e., small prey items and detritus), it may well be that a morphological adaptation of this appendage has evolved in the case of *C. oregonensis* to successfully utilize the smaller prey species available. A regression analysis was performed for all five species showing a high ($.885 \leq R \leq .996$) correlation value between the variables considered, with the results shown in Figure 7. The steeper the regression slope, the wider the third maxilliped would be in relationship to carapace width (or size of crab). Homogeneity of the slopes in Figure 7 was tested at the .05 percent level, comparing each one with C. oregonensis. The results of the slope comparisons show no significant difference between C. oregonensis and H. oregonensis, which might be expected on the basis of similar habitat (Gude, 1961), and feeding (Knudsen, 1964). A significant difference does occur, however, in comparing C. oregonensis with H. nudus, C. productus, and C. magister. The latter two, being larger crabs, are active predators and scavengers, using their chelae to capture the prey and their maxillipeds to push pieces of such into their mouths (Knudsen, 1964; Marshall and Orr, 1960).

Comparative structural morphology was also evident in the examination of setae on the various appendages of C. oregonensis. Setae of the carapace, pereiopods, third maxillipeds, and antennae resembled those described by Roberts (1968) for Pagurus longicarpus and P. pollicaris. The pereiopods, carapace, and antennae of C. oregonensis were found to have Roberts' "type 5" plumose setae, whereas the maxillipeds have both plumose, serrated (Roberts' "type 2"), and Roberts' "type 6" setae (Fig. 8). The plumose setal type apparently has the ability to filter out large amounts of silt and detritus, as evidenced from the abundance of such material on the setae of all specimens examined. The serrated setae, located on the endopodite of the third maxilliped, are "comb-like" and most likely

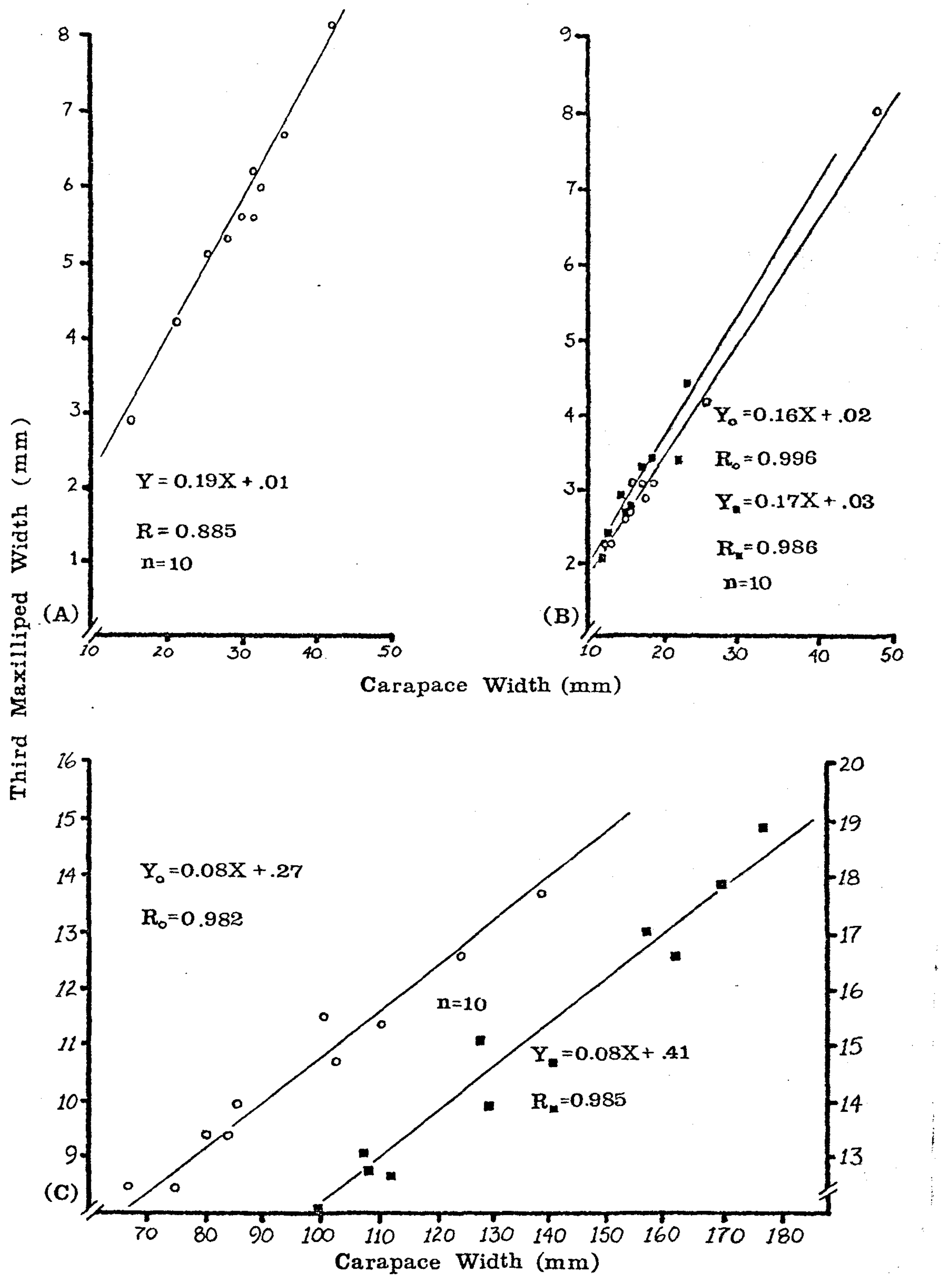

Figure 7. Regression analysis: third maxilliped width vs. carapace width for (A) C. oregonensis, (B) (∘) Hemigrapsus nudus and (▪) H. oregonensis, (C) (∘) C. productus and (▪) C. magister.

function in a cleaning capacity to remove detritus and silt from the appendages and to transfer these materials to the mouth.

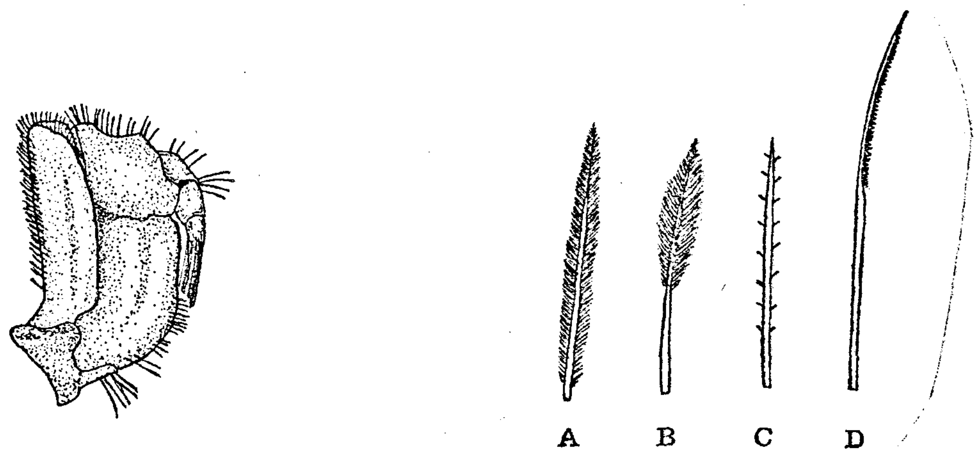

Figure 8. Cancer oregonensis. Third maxilliped (left) and setal types (A) plumose, Roberts' "type 5;" (B) plumose as found on antennae; (C) Roberts' "type 6;" (D) serrated, Roberts' "type 2."

Feeding Behavior

Sundry observations of C. oregonensis in the laboratory, revealed several species of prey not specifically identified in the normal stomach analysis, including ophiuroids, shrimp (Pandalus danae), the rock oyster, Pododesmus cepio, and the barnacles, Balanus cariosus and B. nubilus. The methods of feeding on the above species were generally the same. The process of removing flesh from them was accomplished by the chelae, which then transferred the food to the maxillipeds. In particular, it was noted that some of the B. cariosus and the smaller B. nubilus were entirely broken open. With those that were not broken open, C. oregonensis would reach into the open end, e.g., of the barnacle, pick off the flesh, and pass it to the third maxillipeds. In the handling of large B. nubilus, a crab will move inside the barnacle before the flesh is completely removed, and leave the tergal plates of the barnacle inside where they fell.

Scavenging was observed where C. oregonensis was found to feed upon animals that had recently died, but would not continue to feed upon such matter when the material began to decay.

The chemoreceptibility of C. oregonensis was tested, in part, by the Y-maze experiment and subjected to chi-square analysis (Bliss, 1967; Ostle, 1963). Balanus cariosus that had been recently broken open was used as the prey, and the results (Table 8) clearly indicate that the crabs are capable of detecting a food source that is up current. Another aspect of C. oregonensis' sensory ability will be shown in the methods of polychaete feeding.

Results of the toluidine blue experiment supported observations that the principle appendages involved in handling the prey are the chelae, pereiopods (especially the 2nd and 3rd pair), and the third maxillipeds (particularly the medial edge of the basal segments).

The starvation experiment patterned after Orton (1927) and described in materials and methods, compared the stomach contents of control and experimental animals.

Table 8. Cancer oregonensis. Chi-square analysis for Y-maze chemoreceptibility test.

Positive	Negative	R.L.[a]	Chi-square	Conclusion
18	1	3.84[b]	13.47	Reject H_0[c]

[a]Rejection level.

[b]Associated chi-square value for α=.05.

[c]H_0: p=0.5.

The results clearly indicate detritus feeding in C. oregonensis. Control crab stomachs were empty, whereas the experimental crab stomachs contained detritus and spicules identical to those found in stomachs analyzed and reported in Table 6.

As one can see from the stomach contents data in Table 6, the dominant or principal prey species of the intertidal zone are gammarid amphipods and polychaetes. The methods of capturing these prey species are described below. Amphipods are noticeable abundant amongst the algae, Polysiphonia sp., Odonthalia sp., and Rhodomela sp. It is here where C. oregonensis successfully captures them by positioning themselves under the algae. As amphipods dart rapidly in and out amongst the algae, the crabs' mouth parts grasp them with the medial edges (assisted by the endopods) of the third maxillipeds. It was also found that C. oregonensis will move in close to the prey and after 2 to 3 seconds of no noticeable movement, suddenly lunge toward the amphipod prey with extended, spread chelae, grasping the victims and transferring them to the mouth parts.

In capturing burrowed polychaetes, C. oregonensis appears to use its chemoreceptibility found on the dactyl segments of the pereiopods (Case, 1964). The foraging behavior consists of the crab slowly moving laterally along the substratum. During this movement the dactyls of the second and third pairs of pereiopods are placed 2 to 3 mm below the surface of the sand or mud. When above a worm the crab will suddenly stop, pause for 1 to 2 seconds, then begin a frenzied, rapid, digging movement using the second and third pereiopods. The worm is then moved to the third maxillipeds and ingestion follows.

Predator-Prey Relationships

The major predators of C. oregonensis were found to be large crabs in the intertidal zone and fish in the subtidal zone. At the Lonesome Cove sampling site C. productus was found in 25% of the quadrats in which C. oregonensis was sampled. The Cattle Point site included C. magister as well as C. productus in most samples, although C. magister was not quite as abundant as C. productus. Knudsen (1964) reported that C. productus would prey upon smaller crabs of the same or other species, and it was observed in the laboratory that C. productus would prey upon C. oregonensis. The larger species of Cancer crabs apparently play little or no role in predation subtidally upon C. oregonensis, at least at the Cantilever Pier site. After approximately 40 hours of SCUBA observations at Cantilever Pier, neither larger Cancer species, nor evidence thereof (except for one C. productus carapace molt), were observed living with C. oregonensis. This may be due, in part, to the presence of two species of large octopods, Octopus dofleini and Octopus sp., that frequent the area.

Fish predation is apparently very effective subtidally and may be important intertidally during nocturnal high tides. Fish activity increases during the hours of darkness as clearly documented by continuous photographic data (Braithwaite, unpublished data). A fish survey of the San Juan Islands was made between July, 1974 and September, 1975 by the Department of Ecology at the University of Washington (Miller, Simenstad, and Moulton, 1976), which presented data indicating a high predation level on C. oregonensis by the Ratfish, Hydrolagus colliei, and the Black Rockfish, Sebastes melanops (Table 9). The stomach of a Red Irish Lord (Hemilepidotus hemilepidotus) taken by the author contained C. oregonensis, Petrolisthes eriomerus, and one shrimp. Another fish taken, a Great Sculpin (Myoxocephalus polyacanthocephalus), contained 5 C. oregonensis.

It is evident from these data that the major predator pressure subtidally, is exerted by fish rather than invertebrates.

Table 9. Fish predators[a] of *Cancer oregonensis*.

Predator	Frequency of occurrence	
	SCUBA transects	*C. oregonensis* in stomachs
Hydrolagus colliei (Ratfish)	N.D.	55%
Sebastes melanops (Black Rockfish)	52%	25%
Hexagrammos stelleri (White Spotted Greenling)	N.D.	too small
Hemilepidotus hemilepidotus (Red Irish Lord)	12%	too small
Scorpaenichthys marmoratus (Cabezon)	9%	too small

[a]From data presented by Miller, Simenstad, and Moulton, 1976.

DISCUSSION

Emlen (1966) said that "... the efficient exploitation of available food is a vital requirement of all animals [therefore] the study of feeding and food preference ... should be of vital importance to the field of ecology."

Examination of the feeding biology of C. oregonensis indicates an efficient exploitation of available food for all habitats sampled. A predator will be the most successful in the process of feeding if all possible food items are eaten when food is scarce, and when food becomes abundant, success depends on increased selectivity of one or more prey species over another (Emlen, 1966). As food density decreases by the presence of competition, the predator is subject to elimination if it cannot widen its feeding preferences or become less specialized in its diet (MacArthur and Pianka, 1966). The concept of optimal use of a foraging territory (or patch) of a predator, aptly described by MacArthur and Pianka (1966), consists of harvesting all prey species possible without a net loss of energy. It is seen in this study that although C. oregonensis will specialize on certain prey, it can become generalized in its feeding habits, thus being able to cope with competition and/or a decreased food supply. The crab's preference for amphipods in the intertidal zone illustrates a very economical choice of food. Utilization of energy in the search, capture, and ingesting of the prey is minimal due to the abundance of the prey. If, per chance, the amphipod prey was not abundant, the crabs could resort to other prey successfully without expanding their foraging territory and losing net energy by increased searching time.

Subtidal crabs living within a patchy environment are another example of optimal utilization of a food supply by exhibiting an adaptability to handling different food items. Special morphological adaptations of the mouth parts and setae allow these crabs to feed on fine bottom detritus, and yet the crabs still retain their ability to prey on other, larger organisms.

Marshall and Orr (1960) pointed out that although discrete methods of feeding are found within the crustaceans, it is not unusual to find a member of the class using two or more of these methods. It is clearly evident from the data and observations that *C. oregonensis* illustrates this diverse ability, which undoubtedly accounts for the success of this species in the San Juan Archipelago.

Consideration of feeding dynamics may also suggest an effect on some or all of the crab's population characteristics. Marshall and Orr (1960) conclude that a good food resource will favorably affect the reproductive activity, giving rise to an increased population size.

Intuitively, one might say a good food supply, as well as the capability to harvest many diverse food items, may give rise to a prolific reproductive capacity. This is evident in *C. oregonensis* which produces a large number of eggs with a rapid increase in the number of eggs that increase with the size of the female. It was also found that females continued to feed even when ovigerous. No evidence of fasting was found in these berried females, as reported by Knudsen (1964).

Mating and courtship behavior for *C. oregonensis* was observed to be consistant with that reported for other cancroid crabs (Butler, 1960; Edwards, 1964; Knudsen, 1964; Scarratt and Lowe, 1972; Snow and Neilsen, 1966). Neither the male nor female crabs involved in mating were observed to feed during courtship and copulation. Although some information is available (Knudsen, 1964), further investigation into the life cycle of these crabs is needed to ascertain the length of courtship and time of egg laying.

Crabs found subtidally do not seem to exhibit diurnal/nocturnal activity preferences. The reason for this may be that very little light (personal observation) is observed at the depth (-20 m and greater) where the crabs are abundant. This "depth-limited light" may eliminate a significant amount of visual predation on *C. oregonensis*. Hence, the crabs would have more foraging time to successfully maintain the population by the predominant subtidal method of feeding (bottom detritus). In shallower water (i.e., the intertidal zone) the crabs definitely show decreased activity diurnally. Visual predation could be considered directly proportional to an increase in the amount of light. With increased danger of predation during daylight, foraging time is essentially limited to the hours of darkness. Therefore, the crabs must utilize a food source which can yield a larger amount of nutrition in a smaller amount of harvesting time. The feeding habits of _C_. _oregonensis_ conform to this model, in that amphipods and polychaetes are the principle food items intertidally for this crab. Since the type of food and the time required to harvest it is directly related to the habitat (i.e., detritus in the "light-limited" subtidal zone and amphipods/polychaetes in the "light-influenced" intertidal zone), it seems reasonable that the main difference in habitats is the increased predator pressure intertidally. It is entirely possible that this increased predator pressure intertidally may affect recruitment success. Data for recruitment presented herein, reflects no significant difference between intertidal and subtidal habitats. Through time however, it is suspected that recruitment would favor the subtidal habitat, due to the intertidal predator pressure. The reason for this favoritism may not be entirely satisfactory, since one could argue that increased foraging (or harvesting) time would also mean increased time for predation by the crab's subtidal predators. The assumption made here is that the periodicity of the predator's activity corresponds to that of the crab's. The fallacy of this assumption is explained by the decreased diurnal activity of the fish, the crab's major subtidal predator, reaffirming a greater predator pressure intertidally.

Growth data for C. oregonensis indicated a decreasing amount of growth with increasing size of crab. This trend compares favorably with data presented for other Cancer species (Butler, 1961; Poole, 1965; Scarratt and Lowe, 1972). The reason for the trend is not entertained by these authors, but may be the result of higher energy demands with increasing size.

Another consideration of the growth data suggests a greater increment of growth for females than males of the same size class. This difference may be responsible for the lack of males in the 20 mm size class as disclosed by the sex ratio data. Although an overall sex ratio of 1:1 was found, further investigation by dividing the population into discrete size classes revealed a deviation from the normal Mendelian ratio. A probability curve constructed by the method proposed by Wenner (1972) indicated a low percentage of males in the 20 mm size class and a high percentage of males in the 28 mm, and greater size classes. In Wenner's paper, several possibilities for the lack of males are given to explain this "anomolous" probability curve. Sex reversal and a difference in growth rate between males and females are the more likely reasons for the curve derived for the C. oregonensis population. The most tenuous of these reasons is sex reversal and must be accepted skeptically until further tested. The only evidence that lends credence to the possibility of sex reversal, is that most juveniles sampled were males, especially those of the smallest size class.

Within the framework of predator pressure associated with a specific habitat, C. oregonensis has the ability to utilize various types of food, given an available foraging/harvesting time. This ability, as well as a high reproductive capacity, has allowed C. oregonensis to become the most common Cancer species in the Puget Sound, San Juan Archipelago region.

CONCLUSIONS

Feeding biology and population characteristics for Cancer oregonensis (Dana) Rathbun were examined for types of food and methods of feeding, growth, recruitment, intraspecific associations, reproduction, and predator-prey relationships.

The carapace width ranged from 5.6 mm to 42.5 mm, with a mean of 21 mm. Onset of sexual maturity was 16 mm for both males and females. The overall sex ratio was 1:1, but this varied within size classes, suggesting differential growth rates or sex reversal. Recruitment favored the subtidal habitat over the intertidal habitat, and was most likely attributable to increased predator pressure intertidally.

Mating behavior was similar to other Cancer species. Females ranging in size from 16 mm to 40 mm were ovigerous during the months of March, April, and May. Berried females had an unusually large number of eggs (3,000 to 80,000).

Feeding behavior was a reflection of the types and abundance of food in the habitat. Selective feeding for amphipods in the intertidal zone, polychaetes in the floating dock habitat, and detritus in the subtidal zone, was an effective utilization of food resources for C. oregonensis. Morphological adaptations of the third maxillipeds and setae allowed the exploitation of a diversity of food types in all habitats.

The major predators subtidally were fish, and large *Cancer* species were important predators intertidally.

Cancer oregonensis' success as a population is the result of a high reproductive rate and optimal use of its diet.

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FIGURE LEGENDS

1. Cancer Oregonensis. Dorsal View (above X 1), as Found Subtidally in Balanus Nubilus Shells (below X 0.6).
2. Cancer Oregonensis. Study Sites on and Around San Juan Island. Insert Shows Detailed Description of Cantilever Pier Site.
3. Cancer Oregonensis. Y-Maze Apparatus for Testing Chemoreceptibility (after Castilla and Crisp, 1970). Arrows indicate Flow of Seawater.
4. Cancer Oregonensis. Sex Ratio (above) Expressed as the Percent of Mature Males in the Population for All Data Combined and (below) as the Number of Mature and Immature Individuals Within Each Size Class.
5. Cancer Oregonensis. Histogram Showing the Number of Ovigerous Females in Each Size Class.
6. Cancer Oregonensis. Linear Regression Line for (log) Number of Eggs vs. Carapace Width.
7. Regression Analysis: Third Maxilliped Width vs. Carapace Width for (A) C. Oregonensis, (B) ( ) Hemigrapsus Nudus and ( ) H. Oregonensis, (C) ( ) C. Productus and ( ) C. Magister.
8. Cancer Oregonensis. Third Maxilliped (left) and Setal Types (A) Plumose, Roberts' "Type 5;" (B) Plumose as Found on Antennae; (C) Roberts' "Type 6;" (D) Serrated,

ABSTRACT

Sampling of intertidal and subtidal populations of *Cancer oregonensis* (Dana) Rathbun was carried out over a 3-month period (March, April, May) during 1976. Onset of sexual maturity for both sexes begins at a carapace width of 16 mm. The sex ratio deviated from 1:1 within certain size classes, but conformed to the expected normal distribution overall. As the result of increased predator pressure intertidally, subtidal recruits were more successful. Berried females were found throughout the study (a greater number in March) and carried a large quantity of eggs. Feeding behavior was elicited by the type and abundance of food. Specialized morphological adaptations allowed the exploitation of a diversity of food types. Selective feeding by habitat was found to be amphipods (intertidally), polychaetes (floating docks), and detritus (subtidally). Fish were the dominant predator factor subtidally; large crabs intertidally.

VITA

Gary Lee Child

FEEDING BIOLOGY AND ECOLOGICAL ASPECTS OF A CANCROID CRAB:

CANCER OREGONENSIS (DANA) RATHBUN

(DECAPODA, BRACHYURA)

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COMMITTEE APPROVAL: ______________________