Morphology of the Feeding Apparatus Of *Cancer novaezelandiae* in Relation to Diet and Predatory Behavior[1]

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ABSTRACT: Morphology of the mouthparts, gastric mill, and chelae of the New Zealand cancer crab, *Cancer novaezelandiae* Jacquinot, 1853, was investigated in relation to dietary composition and predatory behavior. Mouthparts and gastric mill were typical of those of other large, predatory brachyurans, with similar structure for male and female, small (60–70 mm) and large (120–130 mm carapace width) crabs. The third maxilliped had large crista dentata, and the inner margin of the mandible was rounded, with a sharp, cutting edge. The large, robust chelae were homeochelous with respect to structure and dental pattern. A large diastema was present and both chela exhibited high mechanical advantage (0.36 and 0.37 for left and right chela, respectively). Relative growth of the propodus was positively allometric, which remained constant throughout crab growth. Morphological features of the feeding apparatus suggested adaptations for macerating coarse, particulate material. This was supported by foregut analysis showing a predominance of sessile and slow-moving macroinvertebrates in the diet. Bivalve and gastropod molluscs followed by crustaceans dominated the diet; fish, sponges, coelenterates, and plant matter occurred less frequently. Little variation in dietary composition was evident with crab sex, size, or season. *Cancer novaezelandiae* adopted five distinct techniques to open bivalve shells and three techniques to open gastropod shells. These include direct, umbone and posterior crushing, umbone splitting, posterior chipping, and aperture breakage and spire removal. The success of these techniques was dependent upon crab size and prey size and shape. Large crabs were able to use direct crushing over a wider size range of prey than smaller crabs. The structural and behavioral adaptations permit *C. novaezelandiae* to specialize on mollusc prey and may explain its migrations into areas dominated by molluscan species.

BRACHYURAN CRABS EXHIBIT WIDE dietary tendencies, feeding on sediment, algae, and mobile and sedentary prey. The chelae are the main manipulatory structures in crabs that feed predominantly on molluscs, but these differ greatly in morphology within the portunid, xanthid, and cancrid crabs (Brown et al. 1979). Differences in cheliped form, structure, and robustness, however, may reflect habitat adaptations, display behavior, aggres-sion, or mating, rather than diet. The functional relationships of the feeding apparatus are therefore best explained by examination of not only the chelae, but also the structure of the mouthparts and gastric mill. The morphology of such structures is regarded as similar in carnivorous crabs, although clearly the type of prey consumed can vary considerably from polychaetes to bivalve molluscs (Warner 1977).

This study investigates the morphology of the feeding apparatus and feeding behavior of *Cancer novaezelandiae*, relating it to the natural diet of crabs collected from its habitat. *Cancer novaezelandiae* is a species endemic to New Zealand commonly found in harbors, estuaries, and open rocky coastlines (Bennett

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1964, McLay 1988). Its depth range is between 0 and 60 m, where it can be found buried in fine sediment, under rocks, stones, and among seaweeds (Bennett 1964). Juveniles are found in shallow rocky areas living among seaweeds. Because there was no detailed information on the feeding apparatus of *C. novaezelandiae*, we examined the chelae, mouthparts, and gastric mill of a wide size range of crabs. The aim was to examine structure of the feeding apparatus, including growth of the chelae, in relation to dietary composition. We also examined the ability of *C. novaezelandiae* in the laboratory to open selected species of bivalve and gastropod prey found in the habitat.

MATERIALS AND METHODS

Natural Diet

Cancer novaezelandiae was collected bimonthly between June 1985 and April 1987 from shallow subtidal sites within Lyttelton Harbour (43° 38' S, 172° 44' E). Traps were set at Diamond Harbour wharf 1–2 hr after sunset to coincide with time of maximum feeding activity. Traps 1 m² (10-mm wire mesh) baited with fish enclosed in nylon (0.1-mm mesh) bags were lowered to depths of between 1.0 and 4.5 m and left for a period of 15 min. Crabs were also collected by 10-min trawls at a depth between 3.0 and 6.0 m using 1.5-m beam trawl (10-mm mesh net and 2-mm mesh cod-end) from a channel between Quail Island and Diamond Harbour. Trawls were taken between 0900 and 1200 hours.

All crabs were killed immediately by piercing the dorsocardiac region and placed into 10% formalin. In the laboratory, sex and carapace width of each crab were recorded. The gastric mill (proventriculus) was extracted and its contents examined under a binocular microscope.

Diet was assessed for abundance and volume using both the percentage occurrence and the points methods. These methods have been used previously to describe stomach contents of brachyurans (Paul 1981, Williams 1981, Choy 1986, Wear and Haddon 1987).

Where possible, individual food items were identified to species level. However, for the analysis of results, they were grouped into one of 10 taxonomic categories. These were bivalve and gastropod, cephalopod, amphipod and isopod, crab, shrimp, fish, sponge, coelenterate, and plant. Amorphous material was grouped as unidentified matter.

Frequency of occurrence of each food category was recorded for each crab on a presence or absence basis. The relative contribution of each food category to the overall abundance and volume within the stomach was assessed using a points method (see Elner 1981). A high correlation was found between the two methods of diet estimation (male, $r = 0.89$; female, $r = 0.99$; $n = 10$). Frequency of occurrence was therefore subsequently used to compare statistically the effects of crab size, sex, and season on crab diet. Data were expressed in percentage terms based on total number of food items found in those stomachs containing food. Empty stomachs were not included in the analysis.

Crabs were divided into three size groups: small (40.0–60.0 mm), medium (61.0–100.0 mm), and large (101.0–160.0 mm carapace width). Seasonal variation in diet was examined for spring (Sept.–Nov.), summer (Dec.–Feb.), autumn (Mar.–May), and winter (June–Aug.) using 1986 data only. Results were compared using chi square goodness-of-fit tests on frequency of occurrence data using 5% level of significance.

Structure of the Feeding Apparatus

The mouthparts (third maxilliped and mandibles), gastric mill, and chela were removed from five male and female specimens of two size classes (60.0–70.0 mm and 120.0–130.0 mm carapace width). These were drawn under a stereomicroscope using a camera lucida. The relationship between mouthpart size and crab size was investigated using length/width ratio of basi-ischium and endopod of the third maxilliped.

The mechanical advantage (MA) of the chelipeds is defined as the ratio of distance from the pivot to the tip of the dactylus (L2), and the distance between pivot and point of
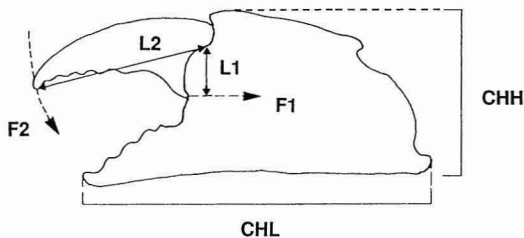
FIGURE 1. Dimensions used in measurements of the chela. CHH, propodus height; CHL, propodus length; L_1/L_2, mechanical advantage. Dotted arrows indicate the directions through which forces F1 and F2 act.

insertion of the dactylus of the closer muscle apodeme (L1) (Figure 1) (see Warner and Jones 1976, Brown et al. 1979). The force produced by this system increases with an increasing L1/L2 ratio, and thus MA is regarded as a good indication of the stress applied by the chela.

Correlations of the left and right MA and crab size were obtained. Comparisons of mean MA between left and right chela and sex were made with Student t tests using a 5% level of significance.

Morphometrics of the Chela

Crabs collected during the sampling program for dietary composition were used to examine the morphometrics and relative growth of the chela. Individuals with missing or regenerated appendages were excluded. In the laboratory, the following measurements were made to the nearest 0.1 mm using vernier calipers: carapace width (CW), measured at the widest part; chela propodus height (CHH), from tip of the large dorsal spine to base of the chela; and chela propodus length (CHL), from base to tip of the propodus along the ventral margin (Figure 1). Carapace width was used as the reference dimension.

Relative growth of the chela was examined mathematically using the allometric growth equation

$$Y = aX^b$$

where Y and X are morphological dimensions and a and b are growth constants.

This method has been used extensively in previous studies of brachyuran growth patterns (Huxley 1932, Hartnoll 1974, 1978, Davidson and Marsden 1987). Regression lines were fitted using least squares regression (model 1) procedure following the natural logarithmic transformations. Student t tests were used to compare the slope and y intercepts of regression lines for left and right chela and between male and female crabs. Differences were accepted or rejected using a 5% level of significance. All slopes were tested against a value of 1.0 using t tests. A slope of $b < 1$ indicated negative allometry, while a slope of $b > 1$ indicated positive allometry. Where the slope of the line did not differ significantly from 1, there was isometry, and both structures grew at the same rate.

Predatory Behavior on Molluscs

Behavior experiments were undertaken using four crabs from each of three size groups: large (105.0–115.0 mm), medium (80.0–90.0 mm), and small (55.0–65.0 mm carapace width). Crabs were maintained individually in seawater (salinity 36‰) in large glass aquaria (36 × 20 × 38 cm) at 16–18° C under fluorescent lights on a 12 light/12 dark hour regime. Only male crabs were used in all experiments to reduce variability caused by possible sexual differences in morphology and predatory behavior. Crabs with lost or regenerated chelipeds or walking legs were not used.

Four prey species were presented individually to crabs. Prey used were blue mussel, *Mytilus edulis aoteanus* Powell, collected from the upper midtidal zone of North Brighton beach, Christchurch (43° 29′ S, 172° 43′ E); cockle, *Austrovenus stutchburyi* Wood, collected from the low intertidal zone of Avon-Heathcote Estuary, Christchurch (43° 33′ S, 172° 44′ E); spotted whelk, *Cominella maculosa* Martyn, and catseye, *Turbo smaragdus* Gmelin, both collected from midtidal levels of Lab Rocks and Wairepo Flats, Kaikoura (42° 25′ S, 173° 42′ E). Collections were made regularly and only undamaged individuals in good condition were used as prey items. Bivalve length was measured along the longest axis of the shell; gastropod height was

TABLE 1

LIST OF ORGANISMS AND THEIR IDENTIFYING FEATURES REMOVED FROM FOREGUTS OF 186 MALE AND FEMALE CRABS FROM LYTTELTON HARBOUR BETWEEN JUNE 1985 AND APRIL 1987.

FOOD TYPES	TYPES OF FRAGMENTS
Mollusc	
Bivalve / Gastropod	Shell fragments, tissue,
Mytilus edulis aoteanus	gill filaments, perio-
Austrovenus stutchburyi	stracum chips
Venerupis largillieriti	
Paphies australis	
Cominella maculosa	
Cephalopod	Chromatophore-covered
Octopus maorum	flesh
Crustacea	
Amphipod / Isopod	Exoskeleton fragments,
Isocladus armatus	including appendages
	(i.e., limbs, thoracic
	plates, antennae, spines,
	eyestalks)
Crab / Shrimp	Fragmented exoskeleton,
Cancer novaezelandiae	including carapace and
Nectocarcinus antarcticus	leg fragments: gills,
Callianasa filholi	eyestalks, gastric mill
Halicarcinus whitei	ossicles, mouthparts
Hemigrapsus edwardsii	(including maxil-
Upogebia hirtifrons	lipeds, maxillae, and
	mandibles)
Teleost	
Pleuronectidae	Muscle and fibers, scales,
	skeletal fragments, jaw,
	teeth, fin rays
Porifera	Spicules, spores
Coelenterata	
Hydroids	Mass of tentacles, stalk
Sea anemone	
Anthopleura aureoradiata	
Plant	
Green algae	Small pieces of frond,
Brown algae	groupings of cells
Red algae	

measured from spire tip to posterior tip of the siphonal canal.

Crabs were presented with an individual prey item of a particular species, chosen at random from a wide size range. The behavioral responses of each attack sequence were recorded. The cheliped used to open prey (left or right) was also noted. Once prey had been opened, consumed, or rejected, another prey item of a different size was presented imme-diately. Approximately 60 trials were performed for each prey species and each size group of crab. Each crab was used in no more than 15 trials, with a maximum of three trials per day. All trials were performed under natural daylight conditions because initial experiments revealed no differences in feeding behavior between day and night. At the beginning of all experiments crabs were starved for 24 hr to standardize hunger level.

RESULTS

Natural Diet

From a total of 547 crabs collected between June 1985 and April 1987, only 186 (34%) contained ingested material in the foregut. They consisted of 120 (64.2%) males and 66 (35.8%) females ranging in size from 40.0 mm to 135.0 mm carapace width.

Fourteen species were identified from stomach remains (Table 1). Phyla represented included Mollusca (bivalves, gastropods, and cephalopods), Crustacea (amphipods, isopods, crabs, and shrimps), Porifera (sponges), Coelenterata (sea anemones and hydroids), Chordata (fish), and Algae (Phaeophyceae, Chlorophyceae, and Rhodophyceae). Diet was composed of two main categories: Mollusca and Crustacea (Figure 2). Molluscs composed one-third of all food items found, with bivalves and gastropods constituting the major dietary components. Crustacea were the second most important food category, composing one-fifth of the diet. Fish, sponges, coelenterates, and algae were infrequently encountered. Dietary composition of male and female crabs consisted of the same food types in relatively similar proportions (χ^2 = 8.447, df = 8, NS).

With respect to crab size, no significant differences in dietary composition were observed between the three size groups of crabs between 40 and 160 mm carapace width (χ^2 = 25.9, df = 18, NS). All crabs contained molluscs as the principal prey type; however, crabs of 40–60 mm carapace width consumed considerably a greater proportion of amphipods and isopods. Crab, fish, and algal
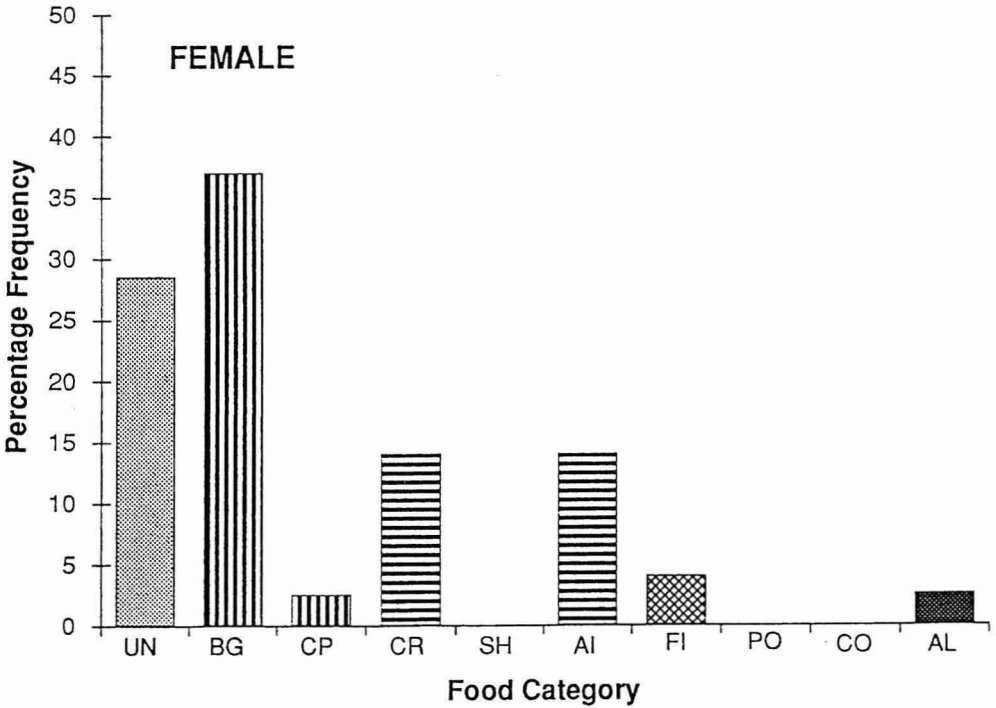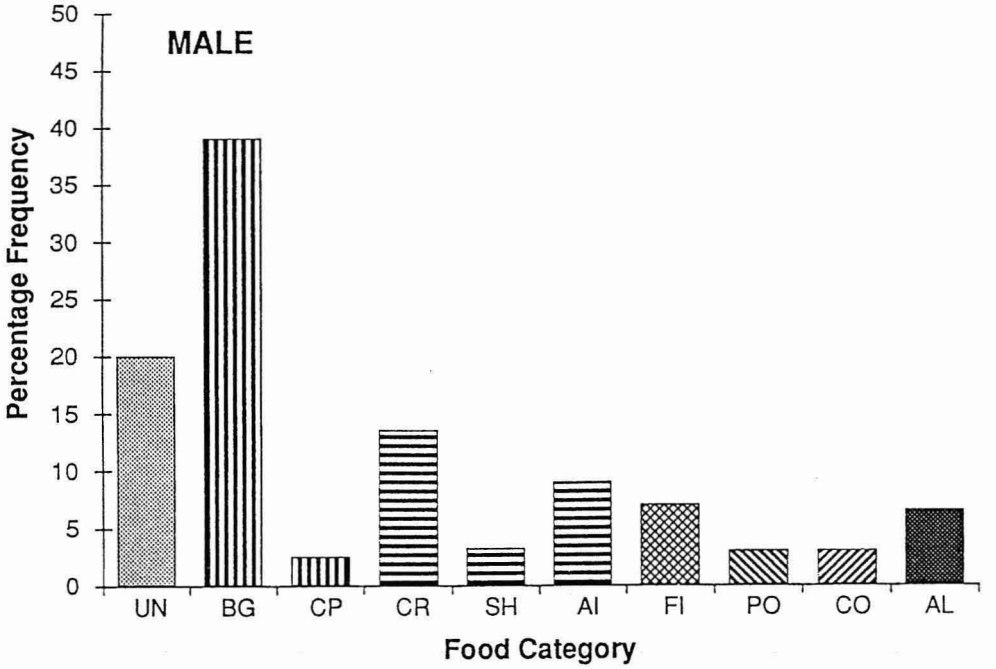
FIGURE 2. Percentage frequency of occurrence of dietary composition for male ($n = 120$) and female ($n = 66$) crabs collected between June 1985 and April 1987. Key: UN, unidentified material; BG, bivalves and gastropods; CP, cephalopods; CR, crabs; SH, shrimps; AI, amphipods and isopods; FI, fish; PO, porifera; CO, coelenterates; AL, algae.

remains were found only in stomachs of larger crabs.

No clear seasonal pattern in dietary composition was evident during 1986 ($\chi^2 = 32.06$, df = 24, NS). Molluscs, followed by crustaceans, dominated all seasons.

Structure of the Feeding Apparatus

THIRD MAXILLIPED AND MANDIBLES. Apart from the size differences, there were no obvious differences in shape between the same mouthparts from large (120.0–130.0 mm) and small (60.0–70.0 mm carapace width) crabs. Also, no differences in basi-ischium and endopod length/width ratios of the third maxilliped between large and small crabs were observed (2.45 and 4.12 for basi-ischium and endopod, respectively).

The structure of the third maxilliped is shown in Figure 3. The basi- and ischium of the third maxilliped endopod are flattened dorsoventrally and fused to form a platelike structure. The medial margin of the basi-ischium is fringed by a dense row of short setae and bears numerous blunt, rounded teeth, the crista dentata. The distal portion of the meropodite is also flattened and articulates distally with the carpopodite. The three distal segments, particularly the terminal dactylopodite, articulate freely and are sparsely covered with setae. The basal segment of the exopodite distal to the coxopodite interlocks with the basi-ischiopodal and meropodal sections of the endopod when in a resting position. The flexible terminal segment of the exopodite is held posterior to the endopodal meropodite, which is covered extensively with long setae.

The mandible is heavily chitinized; the main portion is elongate and divided into two parts, an inner part, which acts as a jaw, and an outer apophysis for the attachment of the mandibular muscles. The inner region of the mandible is rounded, lacking teeth, with a sharp margin to the incisor process. The mandibular palp arises dorsally from the apophysis of each mandible, with the palpal segment uniformly covered with setae around the periphery.

GASTRIC MILL. The cardiac-stomach is a large, spherical, dorsoventrally flattened sac. Parts of the membranous wall are thick and calcified, forming three major ossicles. The single urocardiac ossicle on the dorsal wall bears a single tooth; on the lateral wall, a pair of zygocardiac ossicles also bear single teeth. The lateral teeth consist of denticular processes and 15–20 small transverse ridges (Figure 4). In addition, smaller supportive ossicles (mesocardiac, pterocardiac, exocardiac, and pre-pectineal ossicles) are present. A row of dense setae was present within the gastric mill lying immediately behind the urocardiac ossicle.

Although the size of the cardiac-stomach increased with crab size, the structure of the gastric mill remained relatively unchanged. However, the number of transverse ridges of the lateral tooth appeared to increase with crab size. In addition, no structural differences between the sexes were observed.

CHELAE. Male and female chelae showed monomorphism or homeochely, with the left and right chelipeds being similar in size and structure. No differences were observed with respect to chelal dental pattern between males and females and different-sized crabs (Figure 5). The occlusive surfaces of the chela bear 4–5 discrete, blunt, molariform teeth on both
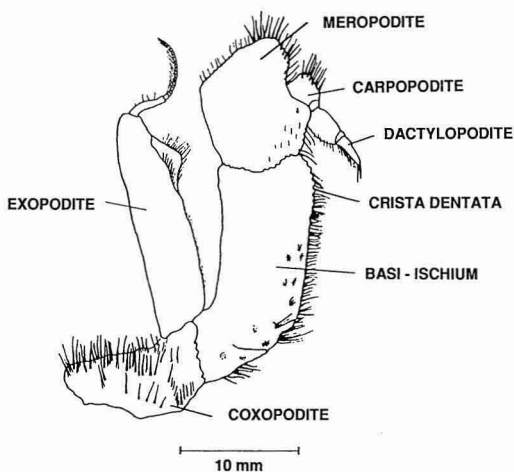

FIGURE 3. Third maxilliped of *C. novaezelandiae*. Removed from 91-mm carapace width male crab. Left side, oral view.
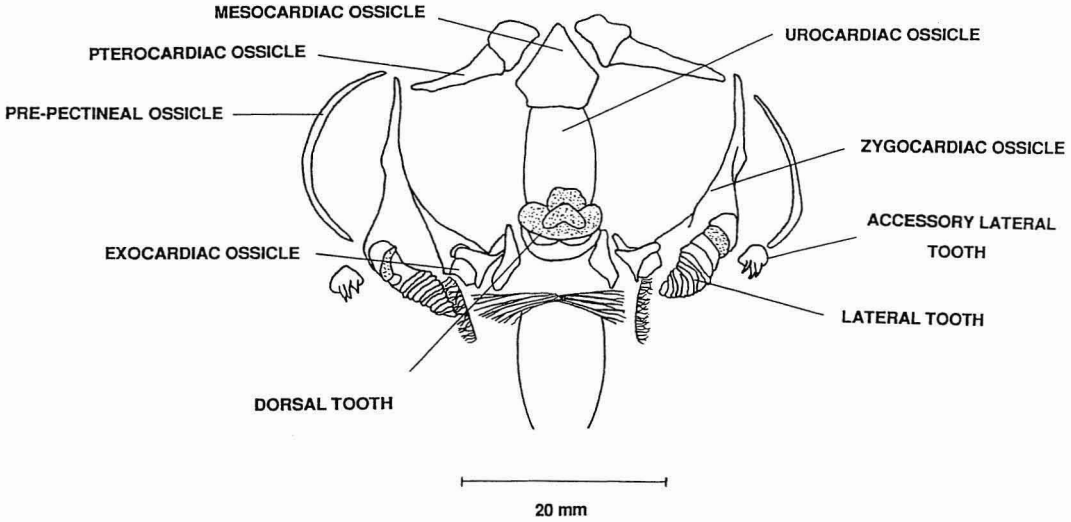
FIGURE 4. Gastric mill of *C. novaezelandiae*. Ventral view of dorsal surface of the cardiac-stomach. Lateral walls spread out.
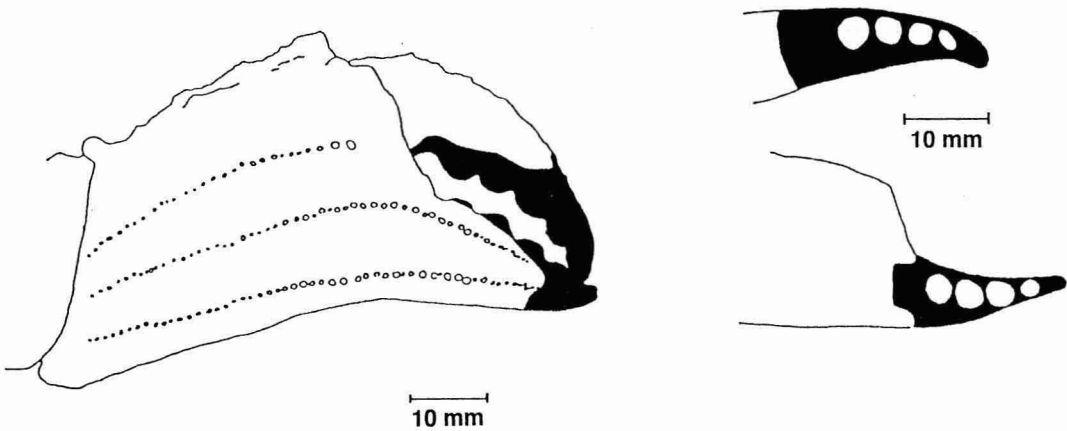

FIGURE 5. Lateral view of right chela of male (122 mm carapace width) (*left*) with occlusive surfaces of the dactyl (*right, top*) and propodus (*bottom*).

the dactylus and propodus. Adjacent to the molar teeth lies a sharp distal tooth on both fingers. When the chela is closed, these distal tips come into contact; however, no contact is made between the molar teeth of the dactylus and propodus. Hence during claw closure there is a relatively large gap.

The left and right chela, respectively, have a mean mechanical advantage of 0.38 ± 0.03 ($n = 61$) and 0.38 ± 0.03 ($n = 56$) for males and 0.37 ± 0.02 ($n = 23$) and 0.37 ± 0.03 ($n = 20$) for females, which were not significantly different ($t = 1.5$, df = 115, NS; $t = 0.506$, df = 41, NS). No differences were found with respect to mean MA for left and right chelae of males and females ($t = 0.296$, df = 82, NS; $t = 0.1723$, df = 74, NS). The relationship of MA and crab size is shown in Figure 6. Correlation analyses suggest that MA remains constant throughout crab growth ($r^2 = 0.74$, $n = 79$; $r^2 = 0.71$, $n = 77$ for left and right chela, respectively).
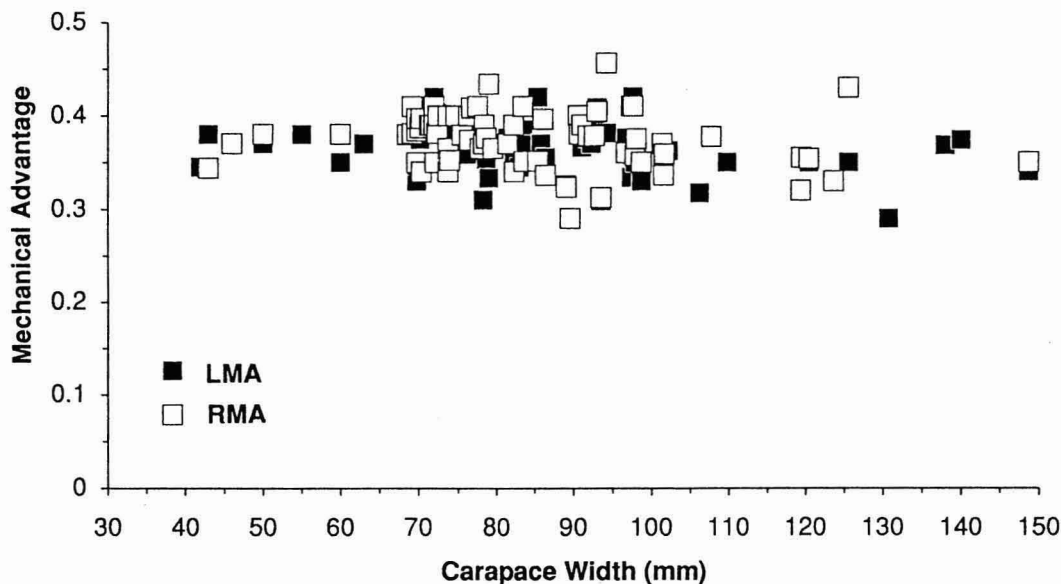
FIGURE 6. Relationship between mechanical advantage and carapace width of left ($n = 79$) and right ($n = 77$) chelae. Sexes combined.

TABLE 2

LINEAR CONSTANTS OF THE REGRESSION EQUATIONS FOR RELATIVE GROWTH OF THE CHELAE IN MALE AND FEMALE CRABS

DIMENSION	a	b	SEM	r^2	n	t	A.S.
Male							
Left propodus height	−2.0019	1.132	0.0117	0.98	166	11.3	+VE
Left propodus length	−1.0987	1.083	0.0085	0.99	165	9.86	+VE
Right propodus height	−2.0623	1.147	0.0094	0.99	160	15.6	+VE
Right propodus length	−1.0780	1.079	0.0077	0.99	159	10.3	+VE
Female							
Left propodus height	−2.0043	1.125	0.0338	0.93	79	3.70	+VE
Left propodus length	−1.0217	1.052	0.0259	0.96	78	2.01	+VE
Right propodus height	−1.9429	1.1128	0.0277	0.96	76	4.07	+VE
Right propodus length	−1.0751	1.0662	0.0261	0.96	77	2.54	+VE

NOTE: $Y = aX^b$, where X = carapace width; Y = chela dimension; a = y intercept; b = slope; SEM = standard error of the mean; r^2 = correlation coefficient; n = sample size; t = slope tested against 1; A.S. = allometric status.

Morphometrics of the Chela

Allometric growth equations of propodus height and length are shown in Table 2. No differences in propodus growth rate were found between male and female crabs of similar size (Table 3). Relative growth of the left and right propodus height and length for male and female crabs was not significantly different (Table 4). Growth of the chelae dimensions was significantly positively allometric. Propodus height increased at a faster rate than propodus length, ultimately conferring a robust, thick-bodied shape. Although chela growth appeared to remain constant with increasing crab size, there was a slight

TABLE 3

COMPARISON OF LINEAR CONSTANTS OF REGRESSION
EQUATIONS OF DIMENSIONS OF THE PROPODUS BETWEEN
MALE AND FEMALE CRABS

DIMENSION	t	df	
Left propodus height			
y intercept	0.015	1	NS
Slope	0.212	1	NS
Left propodus length			
y intercept	0.660	1	NS
Slope	1.150	1	NS
Right propodus height			
y intercept	0.950	1	NS
Slope	1.160	1	NS
Right propodus length			
y intercept	0.029	1	NS
Slope	0.476	1	NS

TABLE 4

COMPARISON OF LINEAR CONSTANTS OF REGRESSION
EQUATIONS OF THE PROPODUS IN MALE AND FEMALE CRABS

DIMENSION	t	df	
Male			
Left vs right propodus height			
y intercept	0.922	1	NS
Slope	0.950	1	NS
Left vs right propodus length			
y intercept	0.410	1	NS
Slope	1.759	1	NS
Female			
Left vs right propodus height			
y intercept	0.327	1	NS
Slope	0.280	1	NS
Left vs right propodus length			
y intercept	0.478	1	NS
Slope	0.546	1	NS

indication of an increase in allometry for male crabs greater than 110.0 mm carapace width.

Predatory Behavior on Molluscs

PREY DETECTION. Large, medium and small *C. novaezelandiae* readily accepted all prey items presented. Approximately 5–120 sec after the introduction of individual prey into the tank, an increase in antennular flickering rate was observed, suggesting that an olfactory response had occurred. The crab then moved quickly in the direction of the prey which was

subsequently located by rapid lateral extensions of both chelipeds. After contact, large prey items (mussels > 35 mm, cockles > 30 mm, whelks > 25 mm, catseyes > 20 mm) were immediately swept under the body and held by the first three pairs of walking legs for between 5 and 10 min. During that time no attempt was made to open prey.

Individual small prey were grasped immediately and crushed by the chela, or pushed into the mouth and readily devoured. Medium and larger prey, however, were extensively manipulated before opening by chelipeds, first and second pairs of walking legs, and third maxillipeds. The chelipeds rotated prey, exposing all regions of the shell to the chelipeds, mouthparts, and walking legs. This behavior may allow the crab to "recognize" prey species and size and, therefore, to assess the feasibility of opening prey.

TECHNIQUES EMPLOYED TO OPEN PREY. Once prey had been accepted by the crab, attempts to open the shell followed immediately. Different techniques were employed to successfully open bivalves and gastropods.

Mytilus edulis aoteanus and *Austrovenus stutchburyi*: Five distinct techniques were employed to open mussels; four were employed to open cockles. These were as follows:

(1) Direct crushing (DC)

Direct crushing was usually the first technique attempted by *C. novaezelandiae* to open mussels and cockles regardless of shell size. However, this technique was only successful on small and medium-size prey (< 45 mm and 30 mm shell length for mussels and cockles, respectively). Prey was manipulated so that the left, right, or both chela enclosed the shell, with the plane of the hinge line oriented randomly to the lateral crushing action of the chela. Often the umbone tip or posterior edge of the shell was held between the third maxillipeds to provide increased leverage to the crushing chela.

(2) Umbone crushing (UC)

Umbone crushing was used to attack bivalves of all sizes, but was only successful on those of small and medium size (20–60 and 15–40 mm shell length for mussels and

cockles, respectively). The shell was manipulated so that the crushing chela applied pressure directly to the umbone region, with the hinge line perpendicular to the lateral crushing angle of the chela. Usually the non-crushing chela gripped the shell to steady the mussel and provided leverage for the crushing chela.

(3) Umbone splitting (US)

Splitting the umbone (also known as "wedging" [Wear and Haddon 1987]) resulted in the separation of mussel and cockle valves down the hinge line. This technique was employed only after direct and umbone crushing had failed. Umbone splitting was successful in opening large mussels up to 75 mm and cockles up to 50 mm shell length. The shell was manipulated so that the propodus and dactylus of the crushing chela lay directly in plane with the hinge line at the umbone end. Force was then applied, causing the tips of the chela to be inserted between the shell valves. Once a gap had been created, the propodus and dactylus could be inserted before severing of the shell adductor muscle.

(4) Posterior crushing (PC)

Crushing of the posterior region of the shell was the most infrequent attack method used by the crab and was applied only to mussels. During attempts to utilize this attack method, the shell tended to slip away from the chela. The crushing chela enclosed the posterior region of the shell, with the hinge line perpendicular to the leteral crushing action of the chela. Only medium-size mussels (20–30 mm shell length) were opened by this technique.

(5) Posterior chipping (PCH)

Chipping away the posterior shell edge was used after all other methods had failed. In comparison with other methods, chipping was time consuming and was employed only on medium and large shells (29–75 and 15–35 mm shell length for mussels and cockles, respectively). The shell was manipulated to allow the tips of both propodus and dactylus to chip away small fragments of the posterior shell edge. Eventually, continued chipping led to creation of gaps between shell valves. The tip of one finger was then inserted into the

gaps and the shell valves were pried apart in much the same way as umbone splitting.

Cominella maculosa and *Turbo smaragdus*: Three distinct techniques were employed to open gastropods:

(1) Direct crushing (DC)

Direct crushing was the first method employed to open whelks of all sizes; however, it was only successful on small gastropods (< 20 and 25 mm shell height for whelks and catseyes, respectively). The crab grasped the shell using the chela and/or the third maxillipeds while the other chela was used to crush the whelk directly across the body whorl.

(2) Aperture breakage (AB)

This was both the most common technique and the most successful method used by *C. novaezelandiae* to open gastropods that could not be directly crushed. Two variations of this method were evident. In the first method, the dactyl of one chela gripped the columella tightly. The shell was then twisted, fragmenting the lip piece by piece, which resulted in a peeling effect of the aperture lip. In the second method, the dactyls of both chelae were inserted into the aperture, so that the outer lip was grasped firmly by both chelae. They were then twisted in a synchronized fashion so that the force generated from one chela was directed against the other, causing the lip to fracture. After the aperture lip had been peeled back to maximum operculum retraction, the columella was attacked and the flesh was removed.

(3) Spire removal (SR)

Crabs occasionally grasped the columella of the shell with one chela while the other severed the shell spire. Spire removal was only employed on whelks. This technique was rarely successful because the chela tended to slip over the apical shell whorls. Medium and large whelks (25–45 mm shell height) were successfully opened by this technique.

During attempts to open prey species, after considerable effort had been applied by one cheliped, crabs were regularly observed transferring the prey to the opposing cheliped. In all three size groups of crabs, neither the right nor left chela was favored during the

TABLE 5

PERCENTAGE FREQUENCY OF TECHNIQUES EMPLOYED TO OPEN PREY VERSUS PREY SIZE (mm) FOR EACH OF THE FOUR PREY SPECIES TESTED

PREY SPECIES	OPENING TECHNIQUE	PREY SIZE (mm)				
Mytilus edulis aoteanus		5–15	20–30	35–45	50–60	65–75
Large crabs	DC	100.0	50.0	12.5	0.0	0.0
	UC	0.0	36.7	56.3	7.7	0.0
	US	0.0	0.0	31.5	84.6	100.0
	PC	0.0	14.3	0.0	0.0	0.0
	PCH	0.0	0.0	0.0	7.7	0.0
Medium crabs	DC	100.0	26.7	0.0	0.0	0.0
	UC	0.0	53.3	18.7	0.0	0.0
	US	0.0	13.3	75.0	100.0	0.0
	PC	0.0	0.0	0.0	0.0	0.0
	PCH	0.0	6.7	6.3	0.0	100.0
Small crabs	DC	100.0	0.0	0.0	0.0	—
	UC	0.0	50.0	0.0	0.0	—
	US	0.0	50.0	87.5	87.5	—
	PC	0.0	0.0	0.0	0.0	—
	PCH	0.0	0.0	12.5	12.5	—
Austrovenus stutchburyi		10–20	21–30	31–40	41–50	
Large crabs	DC	100.0	70.5	0.0	0.0	
	UC	0.0	16.0	18.2	0.0	
	US	0.0	0.0	73.7	100.0	
	PCH	0.0	13.6	9.1	0.0	
Medium crabs	DC	50.0	13.9	0.0	0.0	
	UC	50.0	36.1	0.0	0.0	
	US	0.0	36.1	100.0	100.0	
	PCH	0.0	13.8	0.0	0.0	
Small crabs	DC	14.3	0.0	0.0	0.0	
	UC	28.6	9.5	0.0	0.0	
	US	42.9	80.9	100.0	100.0	
	PCH	7.1	4.8	0.0	0.0	
Cominella maculosa		5–15	16–25	26–35	36–45	
Large crabs	DC	100.0	100.0	0.0	0.0	
	AB	0.0	0.0	100.0	40.0	
	SR	0.0	0.0	0.0	40.0	
Medium crabs	DC	100.0	36.3	0.0	0.0	
	AB	0.0	63.6	100.0	100.0	
	SR	0.0	0.0	0.0	0.0	
Small crabs	DC	9.1	0.0	0.0	—	
	AB	90.0	91.6	100.0	—	
	SR	0.0	8.3	0.0	—	

TABLE 5 (continued)

PREY SPECIES	OPENING TECHNIQUE	PREY SIZE (mm)				
		5–10	11–15	16–20	21–25	26–30
Turbo smaragdus						
Large	DC	0.0	100.0	50.0	50.0	0.0
crabs	AB	0.0	0.0	50.0	50.0	100.0
Medium	DC	0.0	66.1	10.0	0.0	0.0
crabs	AB	0.0	33.0	90.0	100.0	100.0
Small	DC	100.0	25.0	0.0	—	—
crabs	AB	0.0	75.0	100.0	—	—

Note: Approximately 60 observations were performed for each crab size when crabs were presented with prey species. Key: DC, direct crushing; UC, umbone crushing; US, umbone splitting; PC, posterior crushing; PCH, posterior chipping; AB, aperture breakage; SR, spire removal.

TABLE 6

Goodness-of-fit Statistics of Techniques Employed to Open Prey and Crab Size

PREY SPECIES	χ^2	df	P^a
Mytilus edulis aoteanus	5.49	6	0.482 NS
Austrovenus stutchburyi	62.18	6	0.001 ***
Cominella maculosa	15.48	4	0.004 **
Turbo smaragdus	1.98	2	0.372 NS

Note: Crab size classes grouped.
^{a}**, $P < 0.01$; ***, $P < 0.001$.

TABLE 7

Goodness-of-fit Statistics of Techniques Employed to Open Prey and Prey Size for Large (105–115 mm Carapace Width), Medium (80–90 mm), and Small (55–65 mm) Crabs

PREY SPECIES	CRAB SIZE	χ^2	df	P^a
Mytilus edulis	Large	66.00	12	0.001***
aoteanus	Medium	85.36	12	0.001***
	Small	73.67	9	0.001***
Austrovenus	Large	61.92	9	0.001***
stutchburyi	Medium	30.80	9	0.001***
	Small	11.37	9	0.498 NS
Cominella maculosa	Large	31.31	6	0.001***
	Medium	23.02	3	0.001***
	Small	2.91	4	0.276 NS
Turbo smaragdus	Large	11.92	4	0.010**
	Medium	8.69	3	0.033*
	Small	8.00	2	0.018*

Note:
^{a}*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

attempt sequence to open prey ($\chi^2 = 0.272$, 0.0204, and 0.1053; df = 1; NS; $n = 40$, 60, and 38 for small, medium, and large crabs, respectively).

INFLUENCE OF CRAB AND PREY SIZE ON OPENING TECHNIQUES. The relative frequency of opening techniques used by small, medium, and large crabs to successfully open a size range of all four prey species is shown in Table 5. Goodness-of-fit tests showing the influence of prey size and crab size on opening techniques are shown in Tables 6 and 7.

The techniques employed to open cockles and whelks were dependent upon crab size. Large crabs were able to successfully employ direct crushing over a wider size range of prey than smaller crabs. However, all crabs, regardless of size, used similar methods to open mussels and catseyes.

When individuals of all four prey species were presented to large and medium crabs, opening techniques were influenced by prey size. For small crabs, prey size was important when attacking mussels and catseyes. As prey size increased, different techniques were progressively employed depending on the success of a previous particular method. However, when small crabs were presented with cockles and whelks, prey size was unimportant. Instead, small crabs employed one technique (usually umbone splitting in cockles and apertural breakage in whelks) regardless of prey size.

DISCUSSION

The morphology of the feeding apparatus of male and female *C. novaezelandiae* is designed to handle a diverse array of food types. This is supported by foregut analysis showing a predominance of sessile and slow-moving benthic macroinvertebrates and in the laboratory a wide repertoire of opening techniques that successfully open molluscs of differing size and geometric shape.

The structure of the mouthparts of *C. novaezelandiae* is typical of that of a number of cancrid and portunid crabs. The third maxillipeds and mandibles are large and are the principal means of food maceration before ingestion. The presence of a strongly developed crista dentata on the third maxillipeds, together with the development of large, incisor-edged mandibles, appears to be a common feature among predatory brachyurans associated with a large, particulate macrophagous diet. They are present in *Carcinus maenas* L. (Borradaile 1922), *Ovalipes guadulpensis* Saussure (Caine 1974), and *Scylla serrata* Forskål (Williams 1978). In *C. novaezelandiae* the crista dentata is adapted both to crush small fragments of shell and to function as a clamp facilitating the tearing of flesh away from shell fragments. The incisor-edged mandibles are also designed to crush and tear shell and flesh before shunting food to the foregut. All surfaces of the mouthparts were particularly setose, and along the medial margins large, stout bristles were present. Setation may serve to hold or bind food to the surfaces of the mouthparts during feeding (Warner 1977), and setae have a chemosensory function in assisting the "tasting" and sorting of food fragments before digestion.

Few previous studies have investigated the relationship between functional morphology of the feeding apparatus and diet of brachyurans. However, differences in third maxilliped and mandible morphology in *Ozius truncatus* Milne Edwards, *Leptograpsus variegatus* Fabricus, and *Ebalia tuberosa* Pennant have been attributed to their differing activities during feeding (Schembri 1982, Skilleter and Anderson 1986). *Cancer novaezelandiae* is most similar to *O. truncatus*, a

species that is also a predator of bivalve and gastropod molluscs. It possesses large third maxillipeds bearing a well-developed crista dentata and large, rounded mandibles. These mouthparts enable the gripping and tearing of large food fragments. In contrast, *L. variegatus* feeds predominantly on algal material, using its chelipeds to pluck and scrape algae off rocks and stones. The third maxillipeds are reduced in size, with a reduced crista dentata composed of 3–4 blunt teeth. The mandibles show a distinct angular process that may act to cut plant material. The mandibles of *E. tuberosa* are similar to those of *O. truncatus*, but the third maxillipeds are more reduced and lack crista dentata (Schembri 1982). These mouthparts are well suited to feed on small soft-bodied animals and detritus that characterize the diet of *E. tuberosa*.

The morphology of the gastric mill of *C. novaezelandiae* reflects a carnivorous diet. The strongly developed urocardiac and zygocardiac ossicles and lack of pointed teeth are similar to features found also in *Callinectes sapidus* Rathbun, where the foregut is well equipped to handle a variety of coarse hard and soft material (Warner 1977). In *C. novaezelandiae* setation within the gastric mill was restricted to small brushes directly posterior to the urocardiac ossicle. This is consistent with the findings of Scharfer (1970), who suggested that the degree of setation increased as diet moved from coarse particular matter toward more finer aqueous material.

The size and structure of the chelipeds, together with their mechanical properties, determine the type and size of prey that can be successfully exploited. *C. novaezelandiae* is homeochelous and therefore is typical of other cancrid crabs; the two chelipeds are morphologically similar in size and shape. Although growth of the chela in male and female crabs was similar, for male crabs greater than 110.0 mm carapace width, a small increase in chela growth was apparent. Such increased relative growth of chela for large crabs (well above the size of puberty) has not been reported previously for other brachyuran species (Hartnoll 1982). However, because this increase was not found in female crabs it is assumed that it is not associated

with feeding, but rather with courtship and mating behaviors.

The predominance of heterochely in molluscivorous brachyurans is attributed to polyfunctionism (Brown et al. 1979, Du Preez 1984): with each cheliped performing different roles during predation. For example, the left chela of portunids is for holding and cutting while the right chela is used to crush prey. However, in homeochelous crabs such as *C. novaezelandiae*, the chelae are large and robust, and when closed they exhibit a permanent diastema. Such morphological features enable the delivery of a strong compressive force along the entire length of the cheliped, and tubular and spherical objects (a characteristic of molluscs) can be held within the diastema. Although the chelae of *C. novaezelandiae* lack specific adaptations for cutting prey, polyfunctionism is exhibited by both chela, with no particular handedness being obvious.

It has been suggested that mechanical advantage reflects chelae function (Vermeij 1976, Warner and Jones 1976). Brachyuran species that exhibit heterochely possess different chelal mechanical properties respective to their crushing, cutting, and holding roles. Homeochelous brachyurans, on the other hand, show similar mechanical properties for both chelae. Previous studies have found that the cheliped mechanical advantage of cancrid crabs ranges between 0.31 and 0.40 (Vermeij 1976). For *Cancer pagurus* L., the mean value of 0.32 ± 0.01 is capable of exerting a mean maximum force of $496 \ kN \cdot m^{-2}$ that can be maintained over a long period of time (Warner and Jones 1976). The large, robust chelae of *C. novaezelandiae* are morphologically similar to those of *C. pagurus*. However, because the New Zealand species has a higher mechanical advantage (0.37 and 0.38 for left and right chelae, respectively), it is probably capable of exerting a greater compressive force. This adaptation is important for predation on sedentary prey such as molluscs, which require considerable strength for crushing rather than great speed for catching.

The dietary composition of *C. novaezelandiae* was similar to that of other cancrid species, with bivalve and gastropod molluscs, followed by amphipods, isopods, and brachyurans dominating the diet. Studies by Feder and Paul (1980) showed that Alaskan Dungeness crab, *Cancer magister* Dana, fed primarily on small bivalves (48% of stomachs), with crustaceans occurring in 30% of stomachs. Similarly, Northern California *C. magister* fed primarily on clams (56.1%) and amphipods/isopods (23.6%) (Gotshall 1977). Other prey items included hydroids, polychaetes, cephalopods, echinoderms, and fish found as minor dietary components.

Differences in dietary composition with crab sex have been demonstrated in some portunid crabs (Ropes 1968, Elner 1980). Choy (1986) showed that for male *Liocarcinus puber* L. molluscs formed a greater proportion of the diet than in female crabs and concluded that this difference reflected cheliped strength, with male crabs possessing larger, stronger chelae than females. Because no morphological differences were found in the feeding apparatus of male and female *C. novaezelandiae*, it is not surprising that diet of male and female crabs was similar. Stevens et al. (1982) also found a lack of variation in diet with sex of crab for *C. magister*.

Differences in dietary composition with crab size have been reported previously (Gotshall 1977, Feder and Paul 1980, Stevens et al. 1982). Estuarine *C. magister* underwent distinct ontogenetic changes in food preferences with age (Stevens et al. 1982), a feature also reported by Gotshall (1977) for the same species. This switching is believed to be a direct result of changed mechanical advantages of the chela with body size. It has been postulated that ontogenetic change may decrease competition for food between age classes that occupy the same territory (Pyke et al. 1977). In the present study no change in diet was found for *C. novaezelandiae* between 40.0 and 135 mm carapace width. The diet of three size classes of postmetamorphic benthic crabs consisted of the same food types in relatively similar proportions.

Laboratory experiments demonstrated that *C. novaezelandiae* readily accepted and consumed a variety of mollusc species. After prey capture, shells were usually manipulated ex-

tensively, with physical contact being the most likely mechanism used to recognize prey species and assess the feasibility of successfully opening the shell.

Once accepted, a large repertoire of opening techniques was demonstrated by *C. novaezelandiae* to open bivalve and gastropod shells in the laboratory. The success of the methods used appeared dependent upon prey size and species and crab size. Similar techniques for opening bivalves and gastropods have been reported for a number of brachyurans, particularly portunids feeding on similar prey species. *Ovalipes catharus* White, when presented with individual *M. edulis aoteanus*, was shown to exhibit five opening techniques and generally utilized a characteristic attack sequence (Davidson 1986). Moreover, techniques employed were dependent on prey size, with small mussels being crushed directly while larger mussels were opened by splitting of the umbone and chipping of the posterior edge. Similar results were also observed by Wear (1984) for *O. catharus*. *Carcinus maenas* used five distinct methods to attack mussels and three methods to attack dogwhelks, *Nucella lapillus* L. (Cunningham and Hughes 1984). The five methods used by *O. catharus* and *C. maenas* are also those observed for *C. novaezelandiae* when presented with identical prey species of a similar size.

Crab size was also an important factor in determining the success of a particular opening technique for both bivalves and gastropods. Larger *C. novaezelandiae* were capable of exerting stronger forces and could crush larger prey than small crabs. Large crabs used more time-consuming techniques (i.e., posterior chipping) only to attack larger, more robust prey.

The similarity in opening techniques observed between portunids and *C. novaezelandiae* in the present study is an interesting feature with respect to hetero- and homeochely morphology and function. Similar methods were used by portunids and *C. novaezelandiae* to open bivalves and gastropods, suggesting that opening techniques for molluscs are general features among large, predatory crabs. Such opening techniques may reflect stereotyped crab behavior patterns and prey size, rather than cheliped morphology.

Few studies have demonstrated the influence of prey shell morphology on opening techniques. Gastropods were more resistant to predation by *C. novaezelandiae* than bivalves. The conical shape of gastropods restricts the regions available for shell attack and penetration to only two planes. In contrast, bivalves exhibit three planes for crushing, providing more scope for developing different opening techniques. Similar findings were shown for *C. pagurus*, *L. puber*, and *O. truncatus* when presented with bivalve and gastropod prey species (ap Rheinallt and Hughes 1985, Lawton and Hughes 1985, Chilton and Bull 1986).

Cancer novaezelandiae, from its dietary composition, feeding apparatus morphology, and predatory behavior, seems specialized for opportunistic feeding on molluscs. Together, the mouthparts, chelae, and gastric mill function effectively to crush and ingest molluscan prey items. This allows *C. novaezelandiae* to inhabit areas such as rocky shores, estuaries, and harbors, which are characteristically dominated by molluscs (Knight 1971, Knox 1983). It may also explain the observed daily intertidal migrations of this crab into rocky habitats (T. Chadderton, pers. comm.) where it is likely to find a wide size range of many different prey species.

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