

# Natural diet of the crab *Ovalipes catharus* (Crustacea, Portunidae) around central and northern New Zealand

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**ABSTRACT:** Foregut contents were examined of 4324 *Ovalipes catharus* (White 1843) collected from 11 locations in central and northern New Zealand, from November 1984 to September 1985. Of these 2572 foreguts contained recognizable food items, and a total of 72 species were identified in the diet. No significant differences were found in the relative proportions of foregut contents between males and females. Sand was an important component of the foregut contents, but was not considered part of the diet. When measured in terms of frequency of occurrence and estimated volumes (points method), Mollusca dominated the diet at 6 locations and Crustacea at 5. At all localities almost all the Mollusca eaten were small juvenile bivalves, mainly from the commercially and recreationally important genus *Paphies*. *Callianassa filholi*, *O. catharus*, isopods, and amphipods were important Crustacea in the diet at different localities. The diet at all localities differed significantly in the proportions of 14 dietary categories, but when 6 generalized dietary categories were considered similarities were found. *O. catharus* is a versatile and opportunistic predator. The possible impact of this predator on commercially important shellfish species is discussed.

## INTRODUCTION

The paddle crab *Ovalipes catharus* (White 1843) occurs on sandy coastlines throughout New Zealand, the Chatham Islands, and in east and south Australia (Wear & Fielder 1985). New Zealand coastlines extend 13000 km, 57 % of which is sand-dominated (0.063 to 200 mm) (J. G. Gibb, N. Z. Min. Works & Devel., pers. comm.). Because of its abundance and large size (up to 140 mm carapace width) *O. catharus* is possibly the most significant invertebrate predator from the intertidal zone to about 100 m depth. It is also becoming increasingly important as a fishing resource (King 1985).

Along with recent increases of fishing effort and catches (with no perceptible decline in the resource), there is abundant anecdotal evidence of *Ovalipes catharus* biomass increasing throughout New Zealand (Wear 1982, Stead 1983). Its role as a predator may thus be changing.

To assess how sandy-coast communities may be influenced by *Ovalipes catharus*, its natural diet was investigated. No previous analyses of the foregut contents of *O. catharus* have been published.

Commercial shellfisheries in Europe and North America are claimed to suffer serious damage through predation by the shore crab *Carcinus maenas* (Ropes 1968, Walne & Dean 1972, Elner 1981, Dare et al. 1983). Shellfisheries of economic or recreational value at risk to predation by *Ovalipes catharus* in New Zealand are the 3 fisheries of the bivalve genus *Paphies*: pipi *P. australis*; tuatua *P. subtriangulata*; and toheroa *P. ventricosa* (Redfearn 1974, Wear 1984). Thus, a particular aspect of this present work was to assess the relative status of the 3 *Paphies* species and other bivalves of commercial and ecological importance in the natural diet of *Ovalipes catharus*.

## MATERIALS AND METHODS

A total of 4324 crab foreguts from 11 sandy beach localities in central and northern New Zealand was examined (Fig. 1). Most crabs (2959) were from Raumati South, near Wellington.

**Sampling methods.** All crabs were collected using a 30 m, heavily weighted seine net of 80 mm knot-to-knot mesh, dragged by hand parallel to the shore in

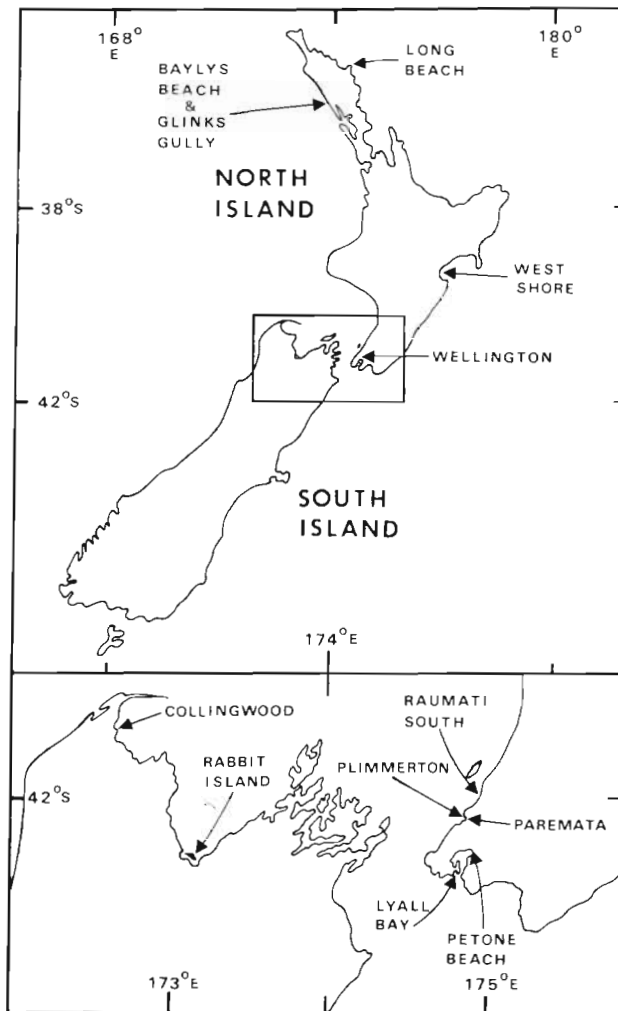


Fig. 1. Map of New Zealand with details of the Wellington area, showing the 11 sampling sites. Two sites (Glinks Gully and Baylys Beach) are located 15 km apart on Dargaville Beach

water 1.0 to 1.5 m deep. An exception was the Collingwood sample, which was made using a 110 mm knot-to-knot mesh net. All samples were taken over low tide except for Raumati South, where in 10 of 12 sample sets, individual nettings at 6 h intervals over 24 h yielded approximately equal numbers of crabs over both low and high tides. Sea conditions were calm or relatively calm, except during the Glinks Gully, Baylys Beach and West Shore samples, and for 9 of 43 separate nettings from Raumati South, for which wave heights were  $\geq 1.0$  m.

All crabs sampled were picked from the net and their carapaces torn free from the body posteriorly to allow 10% formalin (in seawater) to penetrate immediately to the foregut. All crabs were preserved within 15 min of beaching. After a minimum 48 h fixation, each crab was sexed and carapace width was measured to the nearest 1.0 mm. All crab foreguts were removed, their

relative degree of fullness determined and each individually labelled and preserved for later analysis of contents.

**Analysis of foregut contents.** Relative degree of fullness was assessed visually and each foregut was placed in one of 6 ordered classes as follows: 100% full foreguts, designated Class 5; 75% (<100% but >65% full), Class 4; 50% (<65% but >35% full), Class 3; 25% (<35% but >5% full), Class 2; <5% full or only a trace of food, Class 1; and empty foreguts, Class 0. Foreguts 100% full were distinguishable as those in which the whole foregut was distended and the foregut wall tightly stretched. All foreguts were subsequently opened and any designated Class 1 (<5%) found to be empty or to contain only liquid were recategorized as Class 0. Any foreguts initially classed as empty and found to contain traces of food (occasionally caught in the gastric mill) were reclassified into Class 1.

The use of only 6 classes of foregut fullness permitted different workers to classify separate collections of foreguts consistently. Visual assessment of fullness was made possible by the foregut of *Ovalipes catharus* being a thin-walled translucent bag, except for the gastric mill apparatus.

Five stages of digestion were determined under a dissecting microscope: (1) Identifiable soft and hard parts not separated; soft material retaining natural colours. (2) Some soft material still adhering to identifiable hard parts. (3) Traces of identifiable soft material not attached to identifiable hard parts. (4) Unidentifiable, or no soft material, plus hard parts not readily identifiable. (5) Empty, or non-organic material, or containing only fluid. Only guts in Digestion Stages 1 to 3 were used in our analyses of foregut contents.

Foregut contents were identified to the lowest possible taxonomic level (Table 1), but for analysis contents were separated into 15 major categories ranging from the level of phylum to species (Tables 2a, b). Sand was included as a foregut content category but was not considered as a prey or a dietary category. Organic material included algal and terrestrial plant fragments and unidentifiable organic material. Major prey categories listed as species were the burrowing thalassinid shrimp *Callinassa filholi*, *Ovalipes catharus* (i.e. cannibalism), and the 3 bivalve molluscs *Paphies australis*, *P. subtriangulata*, and *P. ventricosa*. The 3 *Paphies* spp. were separated by shell texture and by hinge characteristics. The category 'Other Bivalves' includes identifiable bivalve species other than those of the genus *Paphies*, and also unidentifiable bivalve remains (which may therefore include any of the above species). Similarly, the category 'Other Crustacea' includes those which were obviously not amphipods, isopods, or mysids, identifiable species other than

those specified above, and also unidentifiable crustacean remains.

**Points method.** The relative contribution of the 15 foregut content categories, when present, to the total content of each foregut was subjectively assessed on a 5 step scale of points: A category representing 95 to 100 % of foregut contents was given 100 points; 75 % (<95 % and >65 %), 75 points; 50 % (<65 % and >35 %), 50 points; 25 % (<35 % and >5 %), 25 points; 5 % or less, 2.5 points. The number of points each category received was weighted according to the fullness of the foregut in which they were found. This weighting consisted of multiplying the number of points by a value dependent on the class of fullness: Class 5 = 1.0; Class 4 = 0.75; Class 3 = 0.5; Class 2 = 0.25; Class 1 = 0.02. Thus, the maximum weighted points a single category in a single foregut could obtain would be 100 (100 × 1.0, i.e. only one category in a completely full foregut). The minimum possible would be 0.05 (2.5 × 0.02, i.e. the category makes up <5 % of foregut contents where the gut is <5 % full).

Where data are expressed as percent frequency of occurrence these are based on the number of foreguts which contained food in Digestion Stages 1 to 3, and not on the total number of foreguts examined from a sample. Percent points was the proportion of the total number of points in the sample. Thus, the percent frequency of occurrence of any dietary category is independent of sand, but the percent points for a given category is dependent on whether sand is being considered.

**Statistical analyses.** To test for differences in the proportional constitution of foregut contents of the 2 sexes, at each of the 11 sampling localities, chi-squared tests were performed on the frequency of occurrence of the 15 foregut content categories. These were combined when necessary to maintain expected frequencies greater than one.

To compare the proportional composition of the diets of crabs from the different sampling localities, chi-squared tests, at the 5 % level of significance, were performed on the frequency of occurrence of 6 generalized dietary categories. In the context of this work the 3 *Paphies* species were amalgamated into the first generalized category. The remaining 5 generalized categories for comparison were Crustacea, Mollusca, Organic Material, Fish, and Polychaeta. The general category Mollusca included all *Paphies* species, other bivalves, and all gastropods.

To obtain information on relative similarity of diet a multi-variate cluster analysis was performed on all 11 locations. To ensure that sample size had no influence on the clustering, the percent points of all the dietary categories were used as location properties. The 3 *Paphies* species were again considered together. Clus-

tering was performed by the CLUSTER procedure from SAS using the average linkage criterion on the squared Euclidean distances (SAS Institute Inc. 1982).

To obtain a measure of how variable the diets from different locations were, the Shannon-Weiner diversity index of the diet category points was calculated using base 10 logarithms (Zar 1974) for each sampling locality.

## RESULTS

From the total of 4324 foreguts examined 1094 (25.3 %) were empty, and of the 3230 (74.7 %) foreguts with contents, 2572 (59.5 %) contained material in Digestion Stages 1 to 3. When all sampling localities were considered 72 different species were identified in the diet of *Ovalipes catharus* (Table 1).

No differences were found in the relative proportions of the foregut contents between males and females at any of the 11 sampling locations (all comparisons  $p > 0.1$ ). In the following analyses the data for both sexes are therefore combined.

### Frequency of occurrence and points

Frequency of occurrence and total points for the 14 dietary categories, plus sand, for the 5 Wellington area sample locations, are given in Table 2a. Those for the 6 remaining sampling locations are given in Table 2b. The relative proportions of the diet components, in terms of points (all categories except sand), are illustrated in Fig. 2 & 3. Although sand was not considered part of the diet, it was, nevertheless, an important component of the foregut contents and contributed more than 20 % to the total points at 6 locations (Tables 2a, b): Plimmerton (51.7 %); Paremata (24.4 %); Rabbit Island (30.9 %); Glinks Gully (44.5 %); Baylys Beach (62.1 %); and West Shore (41.8 %).

In terms of points the most important generalized food category was either Crustacea or Mollusca dependent on location (Table 3). Thus, crustaceans were the most important component of the diet at Raumati South, Paremata, Lyall Bay, and Baylys Beach, whilst molluscs were the most important at Plimmerton, Petone, Rabbit Island, Collingwood, Glinks Gully, and West Shore. Long Beach (12 foreguts only) was an exception, with Crustacea, Mollusca, Organic Material, and Polychaeta all being of approximately the same relative importance (Table 2b).

In terms of frequency of occurrence the order of relative importance of Crustacea and Mollusca was the same as that found with the points system except at Paremata and Long Beach (Table 3). At Paremata the order is reversed in that molluscs appear more impor-

Table 1. List of species in the diet of *Ovalipes catharus*. Locality abbreviations: RS, Raumati South; PL, Plimmerton; PA, Paremata; LY, Lyall Bay; PB, Petone Beach; RI, Rabbit Island; CO, Collingwood; DB, Dargaville Beach; WS, West Shore; LB, Long Beach. (Dargaville Beach includes both Baylys Beach and Glinks Gully; the same species were identifiable from both areas)

Taxa	Locations present		Taxa	Locations present	
<b>Annelida</b>					
<b>POLYCHAETA</b>					
Arenicolidae			Cirrolanidae		
<i>Abarenicola</i> sp.	RS	PB	<i>Eurylana arcuata</i> (Hale)	RS	DB LB
Glyceridae			Sphaeromatidae		
<i>Glycera</i> sp.	RS	PB RI	<i>Exosphaeroma obtusum</i> (Dana)	LY	
Nephtyidae			<i>Exosphaeroma chilensis</i> (Dana)	LY	
<i>Algaophamus</i> sp.	RS		Sphaeromatidae (unidentified)		RI DB
Nereididae			<b>AMPHIPODA</b>		
Nereididae (unidentified)			Haustoriidae		
<i>Nereis</i> ? <i>alcaria</i> (Willey)	RS		<i>Haustoria</i> (unidentified)	RS PL	DB
<i>Perinereis</i> ? <i>brevicirris</i> (Grube)		PA	Lysianassidae		
Onuphidae			Lysianassidae (unidentified)	RS	
Onuphidae (unidentified)			Hyalidae		
<i>Onuphis</i> sp.			Hyalidae (unidentified)	RS	
Opheliidae			Isaeidae		
<i>Euzonus otagoensis</i> Probert			Isaeidae (unidentified)	RS	
Orbinidae			Ampeliscidae		
Orbinidae (unidentified)			Ampeliscidae (unidentified)	RS	
Pectinariidae			Phoxocephalidae		
<i>Pectinaria australis</i> Ehlers		PB	Phoxocephalidae (unidentified)	RS	DB
Spionidae			Oedicotidae		
Spionidae (unidentified)			<i>Fatuki</i> cf. <i>breviropodus</i>		DB
<i>Scolecopsis</i> sp.		RI DB	Cooper & Fincham		
<b>Mollusca</b>					
<b>GASTROPODA</b>					
Trochidae			Gammaridae		
Trochidae (unidentified)	RS		Gammaridae (unidentified)	RS	
<i>Cantharidus purpureus</i> (Gmelin)	RS	LY	Talitridae		
<i>Cantharidella tessellata</i> (A. Adams)		LY	<i>Allorchestes novaezealandiae</i> Dana	RS LY	
<i>Microfenchus dilatatus</i> (Sowerby)		LY	<b>DECAPODA; THALASSINIDEA</b>		
Estoniellidae			Callinassidae		
<i>Estoniella</i> sp.		PA LY	<i>Callinassa filholi</i> A. Milne Edwards	RS LY	DB
Calyptaeidae			<b>DECAPODA; ANOMURA</b>		
<i>Zegalerus tenuis</i> (Gray)			Paguridae		
Terebridae			<i>Paguristes barbatus</i> (Heller)	RS PA RI	
<i>Duplicaria (Pervicaria) tristis</i> (Deshayes)	RS		<b>DECAPODA; BRACHYURA</b>		
Pyramidellidae			Portunidae		
<i>Turbonilla (Chemnitzia) sp.</i>	RS		<i>Ovalipes catharus</i> (White)	RS PL PA LY RI	DB WSLB
<b>BIVALVIA</b>					
Nuculidae			Majidae		
<i>Nucula hartvigiana</i> Pfeiffer		PA	<i>Notomithrax ursus</i> (Herbst)		LY
<i>Nucula nitidula</i> A. Adams	RS	PA RI	Pinnotheridae		
Mytilidae			<i>Pinnotheres novaezealandiae</i> Filhol	RS PL PA	
<i>Mytilus edulis aoteanus</i> Powell	RS	LY DB	Hymenosomatidae		
<i>Perna canaliculus</i> (Gmelin)	RS	PA LY DB	<i>Halicarcinus cookii</i> (Filhol)		PA
Macluridae			<i>Halicarcinus whitei</i> (Miers)		PA PB
<i>Mactra discors</i> Gray	RS		<i>Hymenosoma depressum</i> (Jaquinot)	RS	PB
<i>Spisula (Crassula) aequilateralis</i> (Deshayes)	RS	LY RI WS	<i>Neohymenicus pubescens</i> (Dana)		PB
Mesoleptidae			Grapidae		
<i>Paphies (Paphies) australis</i> (Gmelin)	RS PL LY RI CO DB WS		<i>Planes</i> sp.	RS LY	
<i>Paphies (Paphies) subtriangulata</i> (Wood)			<b>Echinodermata</b>		
<i>Paphies (Paphies) ventricosa</i> (Gray)			ECHINOIDEA		
Veneridae			<i>Fellaster zelandiae</i> (Gray)	RS	WS
<i>Dosinia</i> sp.	RS PL RI CO DB WS		<b>OPHUROIDEA</b>		
<i>Tawera spissa</i> (Deshayes)		PA LY	<i>Amphura</i> sp.		PL
<i>Austrovenus stutchburyi</i> (Wood)		PA PB	<b>Pisces</b>		
<b>Crustacea</b>					
<b>COPEPODA</b>					
Thalestridae			Carangidae		
Thalestridae (unidentified)	RS		<i>Pseudocaranx dentex</i> (Bloch & Schneider)	RS	
<b>MYSIDACEA</b>					
Lophogastridae			Clupeidae		
<i>Tenagomysis cf. producta</i> Tattersall	RS		<i>Spattus</i> sp.	RS	
<i>Tenagomysis macropsis</i> Tattersall		RI	Engraulidae		
<i>Tenagomysis cf. novae-zealandiae</i> Thomson	RS		<i>Engraulis australis</i> (White)	RS	
<b>ISOPODA</b>					
Idoteidae			Galaxiidae		
<i>Zenobiana tubicola</i> (Thomson)	RS	LY	<i>Galaxias</i> sp.	RS	
<i>Macrochirodothea urcinata</i> Hurley & Murray			Moridae		
			<i>Pseudophycis barbata</i> (Bloch & Schneider)	RS	
			Leptosomidae		
			<i>Craspedula</i> sp.	RS LY	
			Pleuronectidae		
			<i>Pelthorhynchus novaezealandiae</i> Gunther	RS	
			Tetraodontidae		
			<i>Cantharus richiei</i> (Fremantille)	RS	

Table 2. *Ovalipes catharus*. Frequency of occurrence and points (see 'Materials and Methods') for the 15 foregut content categories from (a) the 5 Wellington area sample localities; (b) 6 sample localities outside Wellington area. Restricted to Digestion Stages 1, 2, and 3

(a) Wellington area												
Food category	Raumati South all year		Plimmerton Feb 85		Paremata Feb 85		Lyll Bay Dec 84, Feb 85		Petone Jan 85			
	Freq.	Pts	Freq.	Pts	Freq.	Pts	Freq.	Pts	Freq.	Pts		
Sand	1507	15746.2	58	1642.6	35	645.6	51	294.8	58	359.9		
Organic material	1165	14456.0	14	42.6	6	127.6	30	445.6	10	20.8		
<i>Callianassa filholi</i>	693	23530.0	0	0.0	0	0.0	1	0.1	0	0.0		
<i>Ovalipes catharus</i>	284	8041.0	24	573.3	13	533.5	9	127.5	0	0.0		
Mysidacea	101	728.1	0	0.0	0	0.0	5	12.5	0	0.0		
Isopoda	407	6712.8	0	0.0	0	0.0	26	589.0	0	0.0		
Amphipoda	251	1610.1	1	3.8	0	0.0	15	346.4	0	0.0		
Other Crustacea	408	6609.3	13	67.2	27	677.4	15	329.6	25	152.8		
<i>Paphies subtriangulata</i>	928	16415.0	42	687.6	0	0.0	36	640.5	0	0.0		
<i>P. ventricosa</i>	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0		
<i>P. australis</i>	0	0.0	0	0.0	0	0.0	0	0.0	62	2165.5		
Other bivalves	518	7215.1	16	34.0	42	647.3	7	80.4	14	335.3		
Gastropoda	4	33.8	0	0.0	4	4.0	16	118.6	0	0.0		
Polychaeta	12	219.6	1	0.1	3	9.8	1	25.0	16	66.4		
Fish	266	7088.2	4	128.8	0	0.0	3	65.0	2	3.0		
N/Total	1941	92659.0	63	1537.4	66	1999.6	66	2780.2	67	2743.8		
(b) Other areas												
Food category	Rabbit Is. all year		Collingwood Feb 85		Glinks Jan, Mar 85		Bayllys Jan, Mar 85		West Shore Feb 85		Long Beach Jan 85	
	Freq.	Pts	Freq.	Pts	Freq.	Pts	Freq.	Pts	Freq.	Pts	Freq.	Pts
Sand	122	2173.3	15	90.2	101	2245.7	74	2297.8	24	598.2	10	85.4
Organic material	22	128.9	0	0.0	18	91.2	20	186.3	2	6.3	3	170.0
<i>Callianassa filholi</i>	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
<i>Ovalipes catharus</i>	7	343.8	0	0.0	17	432.0	2	27.5	1	75.0	1	75.0
Mysidacea	2	37.5	0	0.0	0	0.0	0	0.0	1	25.0	0	0.0
Isopoda	2	53.8	0	0.0	9	68.0	11	87.6	0	0.0	4	6.2
Amphipoda	1	12.5	0	0.0	15	88.4	16	235.1	0	0.0	0	0.0
Other Crustacea	60	1387.3	7	162.5	22	211.6	27	315.3	5	78.8	2	56.4
<i>Paphies subtriangulata</i>	73	1665.4	12	261.2	35	620.0	2	10.0	14	446.0	2	3.8
<i>P. ventricosa</i>	0	0.0	0	0.0	14	60.5	27	230.4	0	0.0	0	0.0
<i>P. australis</i>	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Other bivalves	57	1049.8	3	41.3	39	850.7	24	164.0	13	100.9	1	71.3
Gastropoda	1	0.1	0	0.0	1	0.1	4	11.3	0	0.0	1	75.0
Polychaeta	2	6.3	0	0.0	21	372.8	7	127.3	1	100.0	3	146.3
Fish	4	163.8	0	0.0	1	2.5	4	7.1	0	0.0	3	113.5
N/Total	128	4849.2	16	465.0	112	2797.8	76	1401.9	25	832.0	12	717.5

tant than crustaceans, but this reversal is equivocal as Crustacea and Mollusca occur in approximately equal numbers of stomachs (40:43). At Long Beach, in terms of frequency of occurrence, Crustacea are the most important dietary item followed by Mollusca (Table 3).

#### Dietary components

Whilst it was possible to conclude whether Crustacea or Mollusca was more important at different

locations, the specific dietary components which dominated these 2 generalized categories differed in most cases (Tables 2a, b).

At all localities except Paremata and Long Beach, a high proportion of the Mollusca eaten were members of the genus *Paphies* (Table 3). The species of *Paphies* eaten, and their relative importance in the diet, reflected availability. Thus, *P. subtriangulata* (tuatua) was common in most samples, but at Glinks Gully, which is close to a large bed of *P. ventricosa* (toheroa), toheroa was more important than tuatua (Table 2b,



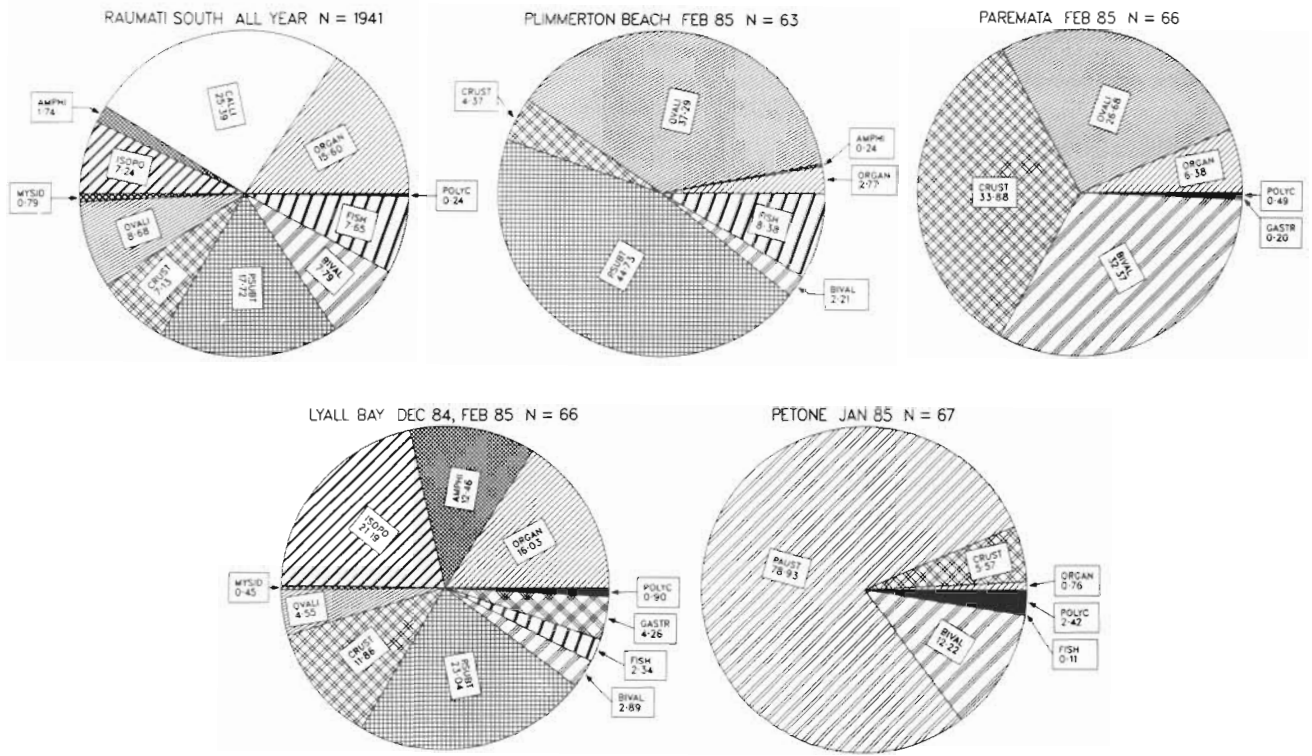


Fig. 2. *Ovalipes catharus*. Percent points of the 14 dietary categories for the 5 Wellington area sampling sites. N: number of foreguts with contents at Digestion Stages 1 to 3

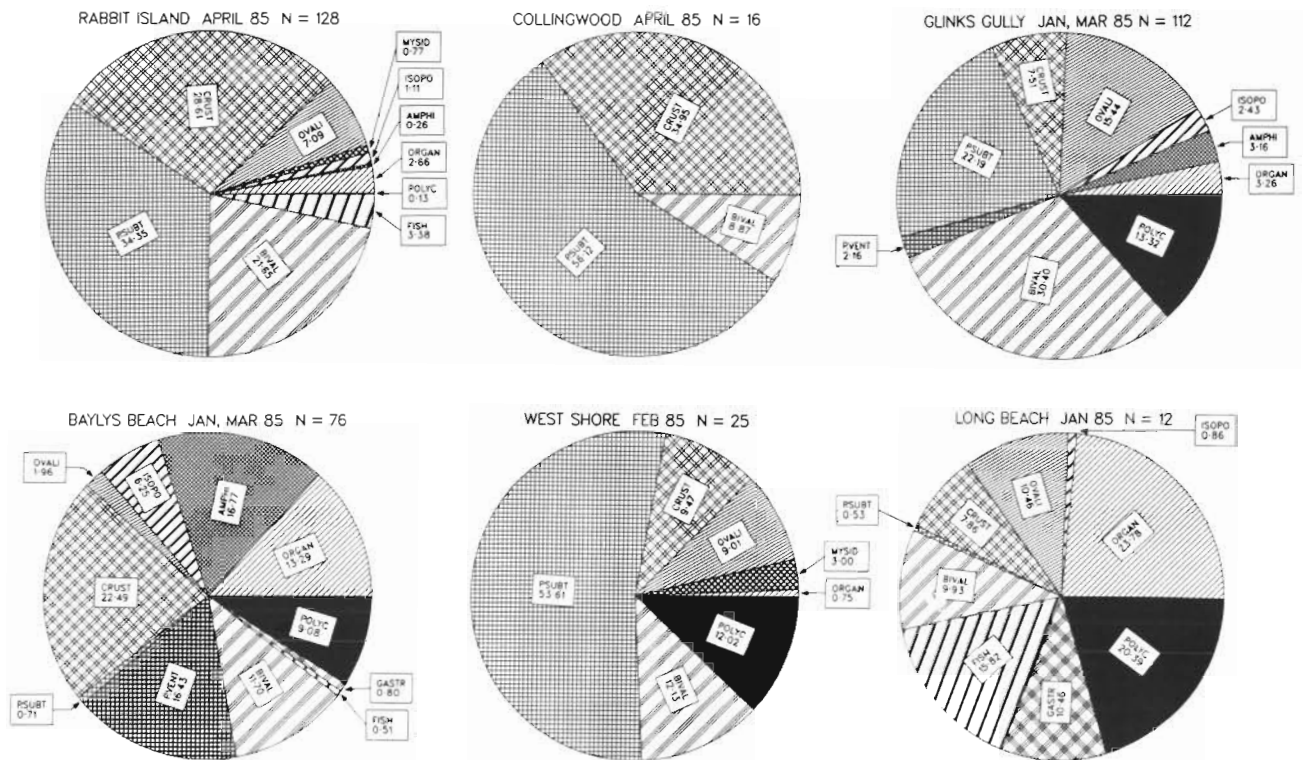


Fig. 3. *Ovalipes catharus*. Percent points of the 14 dietary categories for the 6 sampling sites beyond the Wellington area. N: number of foreguts with contents at Digestion Stages 1 to 3

Table 3. Percent points (see 'Materials and Methods') and percent frequency of occurrence of 3 generalized food categories, Crustacea, Mollusca, and the molluscan genus *Paphies*, in the diet of *Ovalipes catharus* from 11 central and northern New Zealand localities

Location	N	Points			Frequency		
		% Crustacea	% Mollusca	% <i>Paphies</i>	% Crustacea	% Mollusca	% <i>Paphies</i>
Raumati South	1941	50.97	25.54	17.72	81.66	61.98	47.81
Plimmerton	63	41.91	46.94	44.72	58.73	82.54	66.67
Paremata	66	60.56	32.57	0.00	60.61	65.15	0.00
Lyll Bay	66	50.54	30.20	23.04	81.82	72.73	54.55
Petone	67	5.57	91.14	78.92	37.31	100.00	92.54
Rabbit Island	128	37.84	55.99	34.34	56.52	81.25	57.03
Collingwood	16	34.95	65.05	56.17	43.75	81.25	75.00
Glinks Gully	112	28.59	54.73	24.32	50.00	66.07	43.75
Baylys Beach	76	47.47	29.65	17.15	63.16	61.84	38.16
West Shore	25	21.49	65.73	53.61	28.00	88.00	56.00
Long Beach	12	19.18	20.92	0.53	50.00	33.33	16.67

Fig. 3). Also, at Petone, a harbour location where only *P. australis* is found, this species was very important in the diet and neither of the other 2 open coast species of *Paphies* occur (Table 2a, Fig. 2). At Long Beach *P. subtriangulata* forms only a very minor part of the diet. Finally, at Paremata, although *P. australis* is present, the genus *Paphies* was not represented in the diet; the bivalve most frequently eaten was *Nucula hartvigiana* (Table 1).

Other than the 3 *Paphies* species, other bivalve species in the diet which are of commercial or recreational value included: blue mussel *Mytilus edulis aoteanus*; green-lipped mussel *Perna canaliculus*; and New Zealand cockle *Austrovenus stutchburyi*. All bivalve species were usually eaten by *Ovalipes catharus* at a very small size. Most shell fragments and hinges derived from bivalves less than 3 to 4 mm shell length. Indeed, crab foreguts packed with shell fragments often contained more than 100 hinges. Gastropoda were important in the diet only at Long Beach where the sample consisted of only 12 crabs (Tables 2a, b). Polychaeta were important at Glinks Gully, Baylys Beach, West Shore, and Long Beach (Table 2b, Fig. 3). Their importance elsewhere was not underestimated since digestion-resistant setae and jaws were present and influenced the frequency of occurrence, which, for Polychaeta, provides the same pattern of relative importance in different places as do points (Table 2a, Fig. 2).

Burrowing ghost shrimp *Callinassa filholi* was the most important crustacean in the diet at Raumati South, but occurred nowhere else except in a single crab from Lyll Bay. *Ovalipes catharus*, however, was present in its own diet at all localities except Petone and Collingwood where only 'Other Crustacea' were present. Further, *O. catharus* was the most important component of Crustacea at Plimmerton, Glinks Gully,

and Long Beach, and the second most important crustacean component at Raumati South, Paremata, Rabbit Island, and West Shore. 'Other Crustacea' was the most important component of Crustacea at Paremata, Rabbit Island, Baylys Beach, and West Shore, and was the only component at Petone and Collingwood. At Petone, 'Other Crustacea' (= Crustacea at this locality) was mostly the small spider crab *Halicarcinus whitei*, although other species did occur (Table 1). At Collingwood, however, all crustacean remains were unidentifiable. Of the remaining 3 major categories of Crustacea, Mysidacea were not important at any locality; Isopoda were relatively important only at Lyll Bay; and Amphipoda were important only at Baylys Beach (Tables 2a, b). Most isopods and amphipods present in the diet are species normally associated with drift algae (G. R. F. Hicks, National Museum of N.Z., pers. comm.). All occurrences of the pea crab *Pinnotheres novaezealandiae*, found at Raumati South, Paremata, and Plimmerton (Table 1), were small, free-living males rather than females which are commensal in bivalve molluscs. This species is thus considered an actual dietary item, rather than a species incidentally ingested with bivalve flesh.

#### Comparison of diet with location

There are 55 comparisons possible when the diet of *Ovalipes catharus* at each location is compared with every other location. The relationships between localities, in terms of the relative proportions of the 6 generalized dietary categories, were very similar to those found by cluster analysis of percent points (Table 4, Fig. 4). The main differences are at Paremata and Long Beach, both of which were significantly different from all other locations (Table 4, Fig. 2 to 4). This is

Table 4. *Ovalipes catharus*. Chi-squared comparisons of the frequency of occurrence of 6 generalized diet categories.  $\chi^2 > 11.07$  indicates significant differences. Only the 9 localities which included non-significant differences are listed

Location	Lyall Bay	Rabbit Island	Collingwood	Glinks Gully	Baylys Beach	West Shore
Raumati South	8.95	69.59	20.52	342.52	88.69	35.14
Plimmerton	8.29	1.39	5.20	16.42	9.54	6.17
Lyall Bay		13.66	11.75	24.45	6.90	15.35
Petone		29.32	6.33	13.73	28.26	4.10
Rabbit Island			4.79	23.21	14.91	5.43
Collingwood				9.00	12.29	3.05
Glinks Gully					10.02	8.30

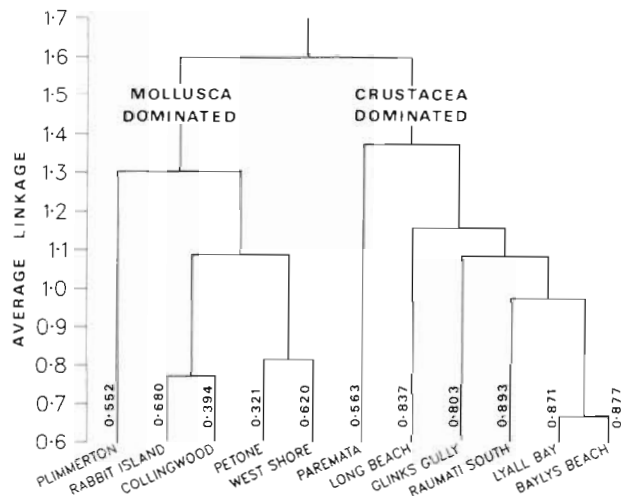


Fig. 4. Cluster diagram expressing the similarity of dietary composition in terms of percent points between locations. The Shannon-Weiner diversity index is given at the root of each branch. Despite the diet at Glinks Gully being dominated by Mollusca, the high diversity associated with the Crustacea dominated localities

reflected in their being the last 2 members to join the right-hand cluster. The diet at Glinks Gully is not significantly different from Baylys Beach but nor is it different from either Collingwood or West Shore. This reflects the fact that the diet at Glinks Gully is dominated by Mollusca. Of the molluscan-dominated diet group, Plimmerton is the only equivocal member in terms of  $\chi^2$ . The analysis shows that Plimmerton is not significantly different from members of both major groupings (Table 4). Its position as the last member of the molluscan grouping reflects this fact.

The cluster analysis (Fig. 4) indicates which locations are similar with respect to proportional make-up of the diet (Fig. 2 & 3). Although the chi-squared analysis of the proportional representation in the diet of the 6 generalized categories is not a test of the

cluster analysis, it does provide corroboration that the clusters are meaningful. The diet of *Ovalipes catharus* at the 5 localities grouped on the left of the dendrogram (Plimmerton, Rabbit Island, Collingwood, Petone, and West Shore) was dominated by Mollusca. Also, the diversities of these 5 samples were less than 0.69. The group on the right of the dendrogram (Paremata, Long Beach, Glinks Gully, Raumati South, Lyall Bay, and Baylys Beach) is more complex. This grouping reflects either a dietary diversity greater than 0.80, or a diet dominated by Crustacea, or both. Thus, Baylys Beach, Lyall Bay, and Raumati South have highly diverse diets dominated by Crustacea. These 3 localities also form the basis of the whole group. In order of addition to this primary group there are: Glinks Gully which has a highly diverse diet (0.8029) dominated by Mollusca; Long Beach which has a diet of high diversity, but where Crustacea are only equal dominant (Fig. 3); and Paremata which has a diet of low diversity but is dominated by Crustacea.

Plimmerton and Raumati South are geographically close (Fig. 1) but are distant on the dendrogram, and Lyall Bay and Baylys Beach are geographically distant but are closely linked on the diagram (Fig. 4). Thus, the groupings in Fig. 4 do not reflect geographical proximity except in the case of Rabbit Island and Collingwood.

In terms of subjective estimates of sampling site exposure, the first 4 sites of the crustacean-dominated grouping were the most exposed of all sites. The least exposed sites amongst this cluster (Long Beach and Paremata) were the last members to be added to the group; the sites with diets dominated by Mollusca were relatively more sheltered. Thus, the degree of exposure to wave action is reflected, to some extent, in dietary composition (Fig. 4).

#### Comparison of biological properties by location

The size range of crabs caught was 18 to 134 mm carapace width (Table 5). In general, the size range of all samples was at least between 30 and 95 mm carapace width except at Collingwood, Glinks Gully, and Baylys Beach. At Collingwood the larger mesh size used to make the collection explains why crabs less than 56 mm carapace width are not represented in the sample. On Dargaville Beach (i.e. Glinks Gully and Baylys Beach sites), however, despite exhaustive sampling, no crabs greater than 79 mm carapace width were caught (Table 5). This may be related to the extreme exposure of this coastline. If rough sea conditions interfere with feeding then crabs on Dargaville Beach would often experience periods of reduced feeding.



The sex ratio varied from 1:12.3 (males:females) at Baylys Beach, to 1:0.47 at Long Beach. However, females predominated at all localities except Long Beach, Rabbit Island, and Collingwood (Table 5). The fishery for crabs is mainly for the larger males which are found offshore in up to 100 m of water. It would appear that male crabs do not spend as much time in shallow beach waters as females and possibly are onshore in numbers only for breeding or when immature. As the diet of the 2 sexes was not found to differ, this partial segregation in space could possibly act to reduce the potential for competition.

## DISCUSSION

Our analysis of foregut contents indicates that, in New Zealand, *Ovalipes catharus* is an opportunistic, generalist predator. At different locations the particular composition of the diet was found to differ but was generally either predominantly Mollusca or Crustacea (Table 3). At all localities except Long Beach, the molluscan component of the diet was almost completely composed of bivalves, most of which were, when available, one of the 3 species of *Paphies* (Tables 2a, b & 3). The diversity of the diet also varied with location, with the highest diversities being found generally in diets dominated by Crustacea (Table 5, Fig. 4). This variability between locations indicates that to characterize the diet of a widespread, active, predatory crab by considering animals caught only at one location or one time period may be misleading.

Although the fauna of New Zealand sandy coasts is documented in general texts (Morton & Miller 1973), details of all the prey species presently available at our 11 sample locations are not known. At Dargaville

Beach, several species noted as dominant or common (Redfearn 1974) occurred in the diet of *Ovalipes catharus*. For example, polychaetes were recorded in dense aggregations just below mid-tide level (Redfearn 1974, authors' obs.) and were found in the diets at both Glinks Gully and Baylys Beach (Fig. 3). The diets from these 2 locations on Dargaville Beach differed in terms of the relative proportions of tuatua *Paphies subtriangulata* and toheroa *P. ventricosa*. At Glinks Gully few toheroa could be found intertidally but there was a dense bed of juvenile tuatua on the upper shore. Conversely, at Baylys Beach toheroa were abundant intertidally and tuatua rare. The proportions of these 2 species in the diet at the 2 localities reflected their relative abundance. The diet of *O. catharus* at other localities also reflected availability of prey species. Thus, at Raumati South both the diet (Fig. 2) and the infauna (pers. obs.) was dominated by burrowing ghost shrimp *Callianassa filholi* and by *P. subtriangulata*. At Paremata, *Nucula hartvigiana* is very common on *Zostera* seagrass flats (Powell 1979), and occurred frequently in the diet; the cockle *Austrovenus stutchburyi* has been reported to reach densities up to 2500 m<sup>-2</sup> (Healy 1980), and may shield deeper burrowing *P. australis* (Fig. 2). At Petone, dense beds of *P. australis* occur whilst cockles are relatively sparse, and this is also reflected in the diet (Fig. 2).

The diverse species composition of the diet (Table 1) demonstrates that *Ovalipes catharus* is extremely versatile in its feeding behaviour. Crabs are able to catch mobile fish, mysid shrimps, amphipods, isopods, and frequently to capture *Callianassa filholi* up to about 50 mm total length. The small degree of trituration, and the relative ease with which we were able to identify newly ingested prey, indicated that most were alive and in good condition when captured. Cannibal-

Table 5. *Ovalipes catharus*. Properties of all crab samples taken from the 11 locations

Location	Total caught	Date	Temp. (°C)	Sex ratio M:F	% Guts empty	% Guts full	% Guts dig. 1-3	Diversity of diet	Size range (mm)
Raumati South	2959	5 Nov 84-30 Sep 85	10-24	1:4.32	19.5	65.6	17.0	0.8930	27-134
Plimmerton	106	22 Feb 85	19	1:2.53	24.5	10.4	60.4	0.5521	34-112
Paremata	126	22 Feb 85	18	1:1	30.2	5.6	52.3	0.5639	33-95
Lyaill Bay	147	3-4 Dec 84	18	1:1.53	42.9	11.6	44.9	0.8712	30-110
Petone	72	23 Jan 85	21	1:1.4	4.2	12.5	93.1	0.3209	45-98
Rabbit Island	330	25-27 Apr 85	13-14.5	1:0.84	46.7	6.7	38.8	0.6803	18-120
Collingwood	82	4 Apr 85	-	1:0.86	52.4	0.0	19.5	0.3936	56-122
Glinks Gully	250	13-14 Jan 85	20-22	1:9.0	37.6	4.4	44.8	0.8029	20-79
Baylys Beach	159	4 Mar 85 13-14 Jan 85	20-22	1:12.3	34.6	9.4	47.8	0.8773	23-75
West Shore	71	26 Feb 85	19	1:2.38	47.9	11.3	35.2	0.6198	27-116
Long Beach	22	9-10 Jan 85	24	1:0.47	31.8	18.2	54.6	0.8370	18-108

ism appeared common in nature, and in the laboratory, crabs of all sizes were vulnerable at ecdysis (pers. obs.; see also Elner 1981). In experiments *O. catharus* could locate and excavate bivalves buried in sand (Haddon et al. 1987). They also use their chelipeds to repeatedly shovel or scoop sand containing very small bivalves into the mouthparts. This latter method of feeding, combined with the importance of small bivalves in the diet (even where Crustacea-dominated), possibly explains the high relative importance of sand in foregut contents (Tables 2a, b).

It is possible that the differences observed between localities are due only to differences of sampling date. However, Glinks Gully and Baylys Beach were sampled either over the same low tide, or 1 d apart, and Plimmerton and Paremata were sampled within 1 h of each other. The Glinks Gully site is approximately 15 km from Baylys Beach but the respective diets, although similar (Fig. 4), are dominated by different species (Table 2b). Plimmerton is only approximately 1 km from Paremata but the diets at these 2 localities were very different from each other. This evidence suggests that geographic location and habitat determine the general availability of potential prey categories, but availability of particular prey species may also vary seasonally.

The natural diet of other crab species, including other species of *Ovalipes*, has been investigated and all have been found to be opportunist predators (Ropes 1968, Caine 1974, Elner 1981, Morales & Antezana 1983, Du Preez 1984, Haefner 1985). The major components of the diet of 144 *O. stephensoni* from the continental shelf (13 to 198 m depth) off the eastern United States were crustaceans (especially amphipods and isopods), bivalve molluscs, and squid (Haefner 1985). Without stating how many foreguts were examined, Caine (1974) found that the diet of *O. guadulphensis* (but see Haefner 1985), on the Florida Gulf coast, was composed mainly of fish, ophiuroids, crustaceans, and annelids, with molluscs being found only occasionally. Again without stating the number of foreguts examined, Du Preez (1984), working in South Africa, found that *O. punctatus* fed mainly on gastropod and bivalve molluscs. Whilst the major items of the diet differ with geographic location, all authors agreed that the *Ovalipes* species they studied were generalist or opportunistic predators. Ropes (1968) and Elner (1981), who both studied large samples of *Carcinus maenas*, found that the diet was dominated by bivalve molluscs and considered that *C. maenas* would therefore be a pest on commercial shellfisheries.

It is probable that *Ovalipes catharus* has little direct impact on established beds of mature shellfish comprising species of commercial or recreational importance in New Zealand. Although we observed large

numbers of bivalve shells chipped in a manner suggesting crab predation (Blundon & Kennedy 1982, Du Preez 1984, Wear 1984) at both Raumat South and Rabbit Island, these may have accumulated over long periods. Adult *Paphies ventricosa* populations are protected to some extent by long periods of exposure during mid to low tides, and by depth of burial and high density acting as refuges from crab predation (Haddon et al. 1987). *P. subtriangulata* and *P. australis* greater than 40 mm shell length are resistant to crushing (Wear 1984), and adult cockles may be protected by their thick and highly inflated shells (Boulding 1984). Natural mussel populations are established on hard substrates where *O. catharus* does not occur in large numbers. However, *O. catharus* may influence recruitment among the bivalves discussed above, and others listed in Table 1, through heavy predation on spat and small individuals, as most foreguts with mollusc contents included large numbers of bivalve spat rather than mollusc flesh attributable to larger bivalves.

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