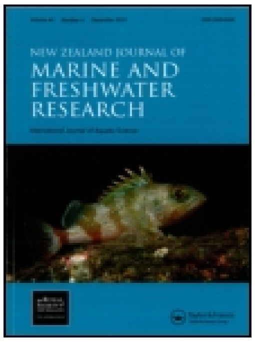

New Zealand Journal of Marine and Freshwater Research

ISSN: 0028-8330 (Print) 1175-8805 (Online) Journal homepage: http://www.tandfonline.com/loi/tnzm20

Seasonal incidence of egg-bearing in the New Zealand paddle crab Ovalipes catharus (Crustacea: Brachyura), and its production of multiple egg batches

Malcolm Haddon & Robert G. Wear

To cite this article: Malcolm Haddon & Robert G. Wear (1993) Seasonal incidence of egg-bearing in the New Zealand paddle crab Ovalipes catharus (Crustacea: Brachyura), and its production of multiple egg batches, New Zealand Journal of Marine and Freshwater Research, 27:3, 287-293, DOI: 10.1080/00288330.1993.9516569

To link to this article: http://dx.doi.org/10.1080/00288330.1993.9516569

Published online: 21 Sep 2010.

New Zealand Journal of Marine and Freshwater Research, 1993: Vol. 27: 287–293
0028–8330/93/2703–0287 $2.50/0

Seasonal incidence of egg-bearing in the New Zealand paddle crab *Ovalipes catharus* (Crustacea: Brachyura), and its production of multiple egg batches

MALCOLM HADDON
ROBERT G. WEAR
Marine Laboratory Island Bay
School of Biological Sciences
Victoria University of Wellington
P.O. Box 600, Wellington, New Zealand

Abstract The annual reproductive cycle of *Ovalipes catharus* (White) was investigated by determining the proportion of mature females carrying eggs, in samples of crabs taken at dusk every 4 or 5 weeks for 22 months from Plimmerton Beach, near Wellington, New Zealand. Three peaks of egg-bearing were found over each breeding season: the first during August, the second through late November and early December, and the last during early January into early April. The average carapace width (CW) of crabs carrying eggs was 84.6 ± 9.65 mm and this average did not alter significantly during the year. Smaller female crabs (41–60 mm CW) were found carrying eggs predominantly during January and February. Captive *O. catharus* were able to produce a maximum of five batches of eggs during one intermoult period, from a single insemination. The average number of egg batches produced increased with crab size. Crabs < 50 mm CW produced only one egg batch before moulting, whereas those > 90 mm CW produced an average of three batches. Overall, the mean number produced was 2.6 batches. The period of incubation and the inter-batch period for captive females each became as short as 2.5 weeks during December and January. This was about half the time taken at the beginning and end of the egg-bearing season. No evidence was found for retention of sperm between moults.

M89007
Received 15 February 1989; accepted 27 July 1993

Keywords Crustacea; Portunidae; *Ovalipes catharus;* reproductive cycle; multi-ovipositions; incubation period

INTRODUCTION

The New Zealand paddle crab, *Ovalipes catharus* (White, 1843) is of local importance as an inshore fishery in New Zealand, with the total catch growing from 0.775 tonnes in 1977 to 200 t in 1986 (King 1985; Ministry of Agriculture and Fisheries, unpubl. data). Over the same period, there was anecdotal evidence pointing to an increase in numbers and biomass of the paddle crab (Wear 1982; Stead 1983). The great abundance and large size of *O. catharus* (up to 140 mm carapace width, CW) makes this species possibly the most important invertebrate predator and scavenger on sandy coastlines in New Zealand (Haddon & Wear 1987; Wear & Haddon 1987). Despite this, little has been published about the reproductive biology of the species. Wear & Fielder (1985) gave details relating to the larval development of *O. catharus* whereas Armstrong (1988) analysed the seasonality of oocyte production in Otago paddle crabs. The present work considers field or external evidence for the occurrence of reproductive cycles in *O. catharus*.

The seasonality of egg bearing was investigated to elucidate the reproductive cycle of the paddle crab in central New Zealand. It was considered possible that different-sized crabs were producing egg batches at different times of the year. If this were the case, the mean size of ovigerous females would vary on a seasonal basis and so the average size of egg-bearing females was also determined.

Ovalipes catharus can only copulate when the female is soft-shelled, and does so for up to 4 or 5 days following the moult (pers. obs.). Many species of crab have been found capable of increasing their reproductive potential by producing more than one batch of eggs between moults (Boolootian et al. 1959; Hines 1982; Morgan et al. 1983). If *O. catharus* had similar capabilities this would imply multiple egg

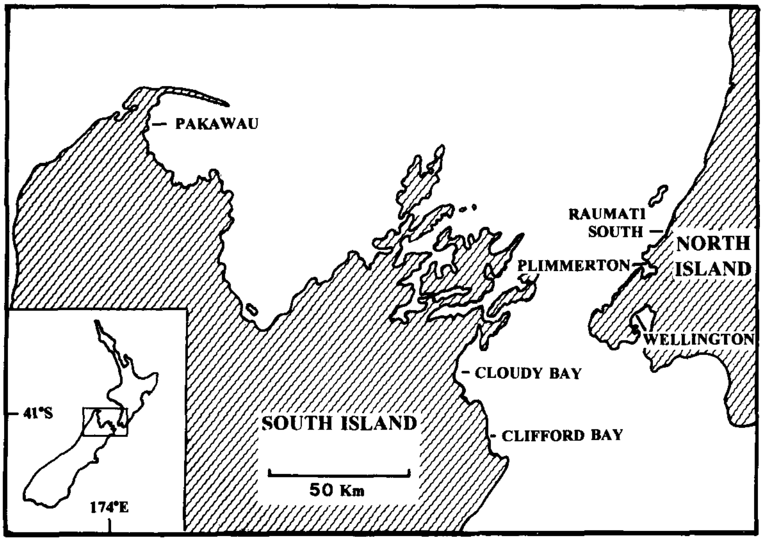

Fig. 1 Map of central New Zealand showing the sampling sites. Seasonal incidence of egg bearing was primarily investigated at Plimmerton.

batches from a single copulation and also the ability to store viable sperm. The number of batches of eggs that isolated females can produce was, therefore, investigated. This also provided information in relation to whether *O. catharus* is capable of retaining viable spermatozoa through a moult, an ability known from other crab species (Cheng 1968).

METHODS

Seasonality of egg production

To determine the seasonality of egg bearing in *O. catharus,* samples of crabs were taken every 4–5 weeks from 22 November 1985 to 10 September 1987. Crabs were taken from approximately the same location in Plimmerton Bay, on the west coast north of Wellington, New Zealand (Fig. 1), using a 60 m baited set net (105 mm knot to knot). The net was always set close to dusk as the crabs are generally most active at that time. The net was retrieved after 1–1.5 h. The crabs were transported to the laboratory, removed from the net, and placed in aerated circulating sea water overnight; soft and vulnerable crabs were kept apart from hard-shell crabs to prevent cannibalism. For all crabs the maximum carapace width was measured to the nearest mm and details of maturity and egg-carrying recorded. The proportion of mature females carrying eggs was then calculated. Corresponding 95% confidence limits of the proportion were also calculated using an estimate of standard error derived from the binomial distribution (Snedecor & Cochran 1967). These data were plotted to illustrate any recurrent trends.

The sizes of females bearing eggs at different times of the year was compared statistically using a one-way ANOVA (with date of sample as the treatment), and visually by plotting the mean size flanked by the ranges of each of the samples.

Spot samples of crabs taken from Raumati South, Clifford Bay, Cloudy Bay, and Pakawau (Fig. 1) were compared with the more extended Plimmerton data set to ascertain whether the reproductive cycle was in phase in all areas. A few spot samples were also taken from Plimmerton in years subsequent to the regular sampling.

Number of egg batches between each moult

To determine how many batches of eggs can be produced from a single insemination, a selection of newly moulted female crabs were maintained in individual tanks with running sea water, ambient sea water temperatures, natural photoperiod, and feeding to excess every 1 or 2 days. These were checked, usually at daily intervals, to monitor the dates of egg laying, incubation period, and inter-batch period. For these purposes a total of 30 newly moulted crabs (females between 34 and 103 mm CW, with soft shells, either with or without eggs) were caught at Plimmerton in August 1986, November 1987, and January 1988, and held until they moulted again or died. The data were summarised by grouping the crabs into different size classes to determine their relative productivity.

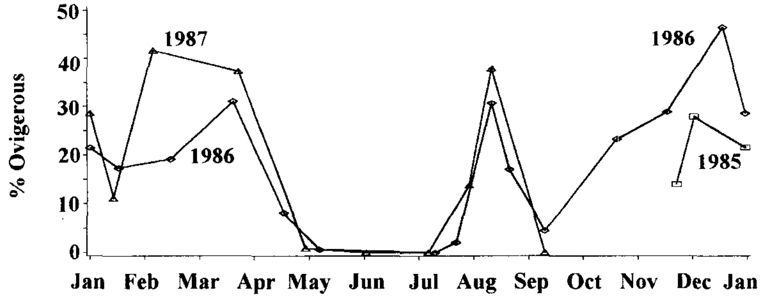

Fig. 2 Three peaks in the proportion of ovigerous female *Ovalipes catharus* caught at Plimmerton over the period November 1985 through to September 1987.

RESULTS

Seasonality of egg bearing

A total of 5142 crabs were caught in Plimmerton over the 22-month period of sampling. 3004 (58.4%) of these were mature females, and 498 (16.6%) of these females were carrying eggs. The proportions of ovigerous females, the confidence limits, the sex ratios, and details of each particular sample are presented in Table 1. Ovigerous females were found at Plimmerton from the start of August through to early May, during which time there were three peaks of egg production (Fig. 2). The first peak is isolated and occurs in August, followed by two more connected peaks between November and April. These two peaks were thought to illustrate a decrease in egg batch production during late December and early January. This decline was tested using a χ^2 comparison of the numbers of ovigerous females versus the non-ovigerous at different dates. The differences between the troughs of production and the peaks was highly significant for both summers ($\chi^2 = 12.047$, $P < 0.005$,

Table 1 Catch statistics of *Ovalipes catharus* at Plimmerton. Mean carapace width and standard deviation (CW ± SD, in mm), are of ovigerous females. The number, percentage, and 95% confidence limits are also of ovigerous females.

Date	Total caught	Total males	Mature females	Number ovigerous	Percentage ovigerous	95% limits	CW ± SD
22 Nov 85	91	19	72	10	13.9	5.9–21.9	86.7 ± 8.62
2 Dec 85	386	120	265	74	27.9	22.5–33.3	87.5 ± 7.92
17 Jan 86	948	284	664	115	17.3	14.4–20.2	87.4 ± 9.65
14 Feb 86	342	81	261	50	19.2	14.4–23.9	82.5 ± 11.44
20 Mar 86	245	68	177	55	31.1	24.3–37.9	83.7 ± 11.63
17 Apr 86	314	94	220	18	8.2	4.6–11.8	90.9 ± 10.83
7 May 86	247	92	155	1	0.7	0.0– 1.9	79.0 ± –
10 Jul 86	126	64	62	0	0.0	0.0– 0.0	– ± –
22 Jul 86	81	30	47	1	2.1	0.0– 6.3	79.0 ± –
11 Aug 86	154	92	62	19	30.7	19.2–42.1	82.3 ± 10.45
21 Aug 86	103	56	47	8	17.0	6.3–27.8	78.1 ± 8.73
10 Sep 86	272	94	176	8	4.6	1.5– 7.6	82.5 ± 8.83
20 Oct 86	143	53	90	21	23.3	14.6–32.1	84.1 ± 6.89
17 Nov 86	138	92	45	13	28.9	15.7–42.1	84.4 ± 8.35
18 Dec 86	86	55	28	13	46.4	28.0–64.9	84.5 ± 12.89
14 Jan 87	72	36	36	4	11.1	0.9–21.4	79.3 ± 12.29
5 Feb 87	177	88	84	35	41.7	31.1–52.2	86.1 ± 12.07
23 Mar 87	170	93	75	28	37.3	26.4–48.3	88.8 ± 9.15
29 Apr 87	145	34	111	1	0.9	0.0– 2.7	97.0 ± –
2 May 87	155	44	110	0	0.0	0.0– 0.0	– ± –
6 Jun 87	178	123	49	0	0.0	0.0– 0.0	– ± –
29 Jul 87	323	242	73	10	13.7	5.8–21.6	81.9 ± 10.57
11 Aug 87	95	55	37	14	37.8	22.2–53.5	86.7 ± 6.68
10 Sep 87	151	89	58	0	0.0	0.0– 0.0	– ± –
All samples	5142	2098	3004	498	16.6	15.3–17.9	84.6 ± 9.65

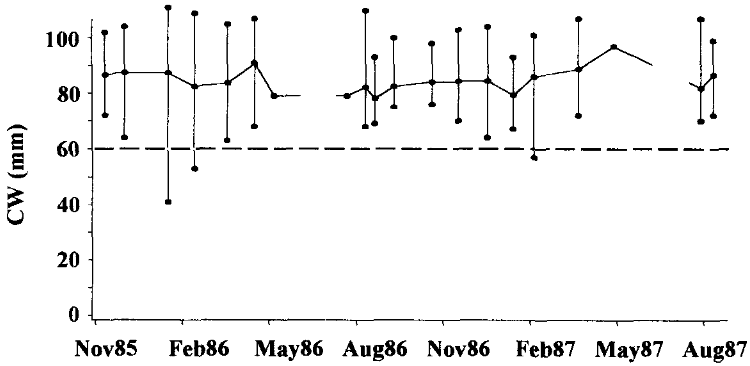

Fig. 3 Mean carapace width and size range of ovigerous female *Ovalipes catharus* caught at Plimmerton. The single points represent samples where only one ovigerous female was caught. The breaks in the line represent periods when no ovigerous females were found. The dashed line at 60 mm is to illustrate when small (< 60 mm CW) ovigerous females occur.

and $\chi^2 = 23.795$, $P < 0.005$ for 1986/87 and 1985/86, respectively; 2 degrees of freedom for each year). The qualitative pattern of three peaks of production was repeated twice over the complete sampling period (Fig. 2). Three subsequent samples were taken during February 1988, 1991, and 1992. These had a high proportion of ovigerous females as expected for the start of the third peak (Table 2).

The proportion of ovigerous females in occasional samples from other regions within Central New Zealand are consistent with the expectations of the three peaks found at Plimmerton (Tables 1 and 2). The precise timing of the peaks of egg production appears to be influenced by location. No ovigerous females were found at Plimmerton on 6 July 1987 (Table 1) whereas on 7 July 1987 up to 15% of females were carrying eggs at the northern end of Cloudy Bay (Mike Tait, MAF Fisheries, Wellington, pers. comm.; Table 2). At Pakawau, on the north coast of the South Island (Fig. 1, Table 2), the first egg laying of the season started at least 2 weeks earlier than at Plimmerton (Table 1).

Table 2 Frequency and proportions of ovigerous female *Ovalipes catharus* caught in four different locations around central New Zealand, 1986–87, including extra samples taken at Plimmerton, February 1988, 1991, and 1992, which were not part of the original series of samples.

Location	Date	Ovigerous females	Mature females	% Ovigerous
Raumati South	18 Nov 86	12	24	50.0
	16 Dec 86	42	99	42.4
Clifford Bay	8 Dec 86	25	91	27.5
Pakawau	13 Mar 87	10	170	5.9
	15 May 87	0	57	0.0
	17 Jun 87	0	75	0.0
	15 Jul 87	5	34	14.7
	15 Aug 87	33	49	67.4
Cloudy Bay	7 Jul 87	–	–	15
Plimmerton	5 Feb 88	50	138	36.2
	3 Feb 91	41	120	34.2
	10 Feb 92	23	58	39.7

Size of ovigerous females throughout the year

The mean (± SD) size of ovigerous females caught at Plimmerton was 84.6 ± 9.65 mm CW, and does not change in any regular manner through the year (Table 1, Fig. 3). This was confirmed by a one-way ANOVA (omitting samples with zero or only one ovigerous female) which indicated that there was no statistically significant difference in mean size of ovigerous females through the year ($F_{15,472} = 2.060$, $P \geq 0.05$). Despite this a consideration of the ranges indicates that crabs of 41–60 mm CW tend to bear eggs (if mature) only during January-February (Fig. 3).

Number of egg batches between each moult

The number of egg batches produced by the 30 captive female crabs ranged from one to five (Table 3). The overall mean number of batches produced per female was 2.6. A single female survived in captivity for 469 days without moulting and gave rise to four batches of eggs during the 1986/87 summer and, after the

Table 3 Number of egg batches produced by captive female *Ovalipes catharus* held at the Marine Laboratory from 11 August 1986 to 21 November 1987.

Batches produced	Number of females
5	1
4	7
3	6
2	11
1	5

winter, produced a further batch in October 1987. Where females lived through egg bearing, viable larvae hatched from all batches of eggs. The average number of egg batches produced increased with increasing size of mature crab (Table 4). All captive crabs < 50 mm CW produced only 1 batch before moulting. For crabs > 100 mm CW the average number of egg batches appears to be fewer than for crabs 91–100 mm CW. This is, however, only a reflection of the fact that the larger crabs died more quickly in captivity than animals < 100 mm CW. Three large crabs died when only part way through the season and all were found to have well-developed ovaries. It is therefore assumed that they would have produced at least one further batch of eggs.

By summing the laboratory information from different months it is possible to produce estimates of the incubation period and the time between batches (Table 5). There was no inter-batch period for August, because during that period no crabs hatched their eggs and laid a second batch. Similarly, for the incubation period in September, no females hatched their eggs in September. By January the incubation period was reduced to about 29% of its August duration, and the inter-batch period was about 24% of its September level (Table 5).

Retention of sperm through the moult

A single female which had spawned and then moulted (in the absense of a male) went on to produce another small batch of eggs. However, most of this post-moult egg production did not attach to the pleopod setae and the very few which were retained turned black after only 2 days and were lost. None of the eggs showed any signs of being fertilised or viable.

DISCUSSION

Reproductive cycle

Usually when the reproductive cycles of crustaceans are investigated, either some index relating to the state of gonad development through time is used (determined by weighing or histology, e.g., Armstrong 1988) or the proportion of ovigerous females in a population is monitored (Boolootian et al. 1959; Giese 1959). Working on the reproductive cycle of *Ovalipes punctatus*, Du Preez & McLachlan (1984) used an index of gonad development. Although their results relating to the index were highly variable, taken in conjunction with data on the occurrence of gravid females in both laboratory and field conditions, they concluded that *O. punctatus* breeds almost throughout the year, with single peaks in summer and winter, the main breeding period in South Africa being in winter from April to September (Du Preez & McLachlan 1984).

Although *O. catharus* is similar to *O. punctatus*, in having peaks of egg-bearing during its reproductive season, differences do occur. Armstrong (1988) studied the ovarian cycle of a population of *O. catharus* in Otago and found no evidence for more than one peak of egg production. He stated: "From oocyte size-frequency analysis it appeared that one clutch of oocytes was developed and spawned completely. No evidence of multiple spawning using sperm from a single copulation was found" (Armstrong 1988). This observation is contrary to the field and laboratory evidence presented in the present study for the existence of multiple spawning in *O. catharus*. This difference is possibly related to the geographical distance between the two study sites. Armstrong's populations were in the colder waters of

Table 4 Number of egg batches produced by different size classes of paddle crab. Crabs in the smallest size class tended only to have time for one batch of eggs before moulting. All of the largest size class died before extruding their last batch of eggs (they all contained ripe ovaries); if these had been laid then the mean number of batches would have been 3.33.

CW (mm)	Total batches	Total crabs	Average batches
< 65	6	5	1.2
66–80	14	7	2.0
81–90	22	9	2.44
9–100	18	6	3.0
> 100	7	3	2.33

Table 5 Mean Incubation and inter-batch periods in days. The incubation period for each month is the mean time taken for batches laid in that month to hatch. The inter-batch period for each month is the mean time taken from the hatching of an egg batch in a particular month to the laying of a subsequent batch of eggs.

Month	Incubation period	No. of crabs	Inter-batch period	No. of crabs
August	58.6	10	–	0
September	–	0	72.0	2
October	26.0	5	37.3	3
November	28.0	7	24.8	6
December	18.7	16	19.1	15
January	16.7	8	14.0	10
February	20.0	4	25.5	3
March	29.0	1	26.0	1

southern New Zealand (about 45°45′S) whereas those in the present work are in central New Zealand (approximately 41°S). Whether temperature differences between the two sites would be sufficient to bring about such a major change in reproductive biology would require further investigation.

The cyclic pattern found in *O. catharus* of one peak of egg bearing in the late winter and two peaks during the summer months is unusual when compared with cycles found in other crabs with two peaks of production (Boolootian et al. 1959; Haley 1972; Du Preez & McLachlan 1984). We have confidence in the existence of three peaks of egg laying, however, because the pattern was repeated over two complete seasons.

The precise timing of the peaks may differ between locations. By comparing the timing of events at Plimmerton (Table 1) with those in Cloudy Bay and Pakawau (Table 2) it is possible to see that the start of egg laying is not the same everywhere. A difference of at least 2 weeks is indicated between different locations and also between different years in the same location. The proportion of ovigerous females found at other locations were, in all instances, consistent with the proportions expected, assuming the three peaks of egg production found at Plimmerton occur throughout central New Zealand.

The decrease in production of extruded eggs during the middle of summer may initially be caused by either an intrinsic factor such as a natural cycle of gonad development, or by some external influence such as temperature (the decrease in production tends to coincide with the peak in summer water temperatures). This could be investigated by a consideration of the internal development of the gonads through the summer period as in the study by Armstrong (1988).

Mean size of ovigerous females

Through the year the mean size of ovigerous females closely reflects the overall mean of 84.6 mm for ovigerous females (Fig. 3). The only deviations from the general trend appear to be in January and February when the smaller mature females (41–60 mm) produce eggs. These small mature females could be the product of eggs laid the previous year in either February/ March or August. If this were so they would be the result of either 10–11 or 5–6 months' growth.

Multiple egg batches

Summing the number of females carrying eggs through time (Fig. 2) indicated that more than 100% of the population carry eggs over the breeding season. The explanation is that *O. catharus*, like many other species of crab (Hines 1982; Morgan et al. 1983), can carry more than one batch of eggs during their intermoult period. The mean number of batches carried by captive mature females increased with increasing size of crab (Table 4). The apparent decrease in brood numbers produced by crabs greater than 100 mm CW (Table 4) was probably a consequence of all the large females dying part way through the egg bearing season. The ovaries of the large females were well developed when they died. Thus, it is likely that the three crabs > 100 mm CW would have produced a total of 10 batches between them, leading to an average of 3.3 (instead of 2.3).

Although the captive crabs were fed regularly (on squid) the diversity of the diet was presumably lower than available in the field (Wear & Haddon 1987) and the balance and quantities may not have been adequate. When fed on squid, the eggs produced were very pale or colourless instead of the more normal orange to dark red. The eggs were nevertheless viable since all hatched successfully. The obvious stresses the animals were under when held in captivity (Haddon et al. 1987) prevent any certainty being attached to the actual number of batches representing what is possible in the field. Nevertheless, the qualitative fact that they were capable of producing multiple batches is clear and the mean number of batches for each size class may be regarded as a minimum estimate. The production of five egg batches by a single female over a 14-month period, implies that the crabs have the ability to retain viable sperm for at least that long. The reproductive potential of individual female crabs would therefore appear to be high.

Problems of confidence arise when we consider the incubation and inter-batch periods. Under laboratory conditions, ovigerous females caught in August incubated their eggs for an average of 58.6 days, assuming that they had laid their eggs within a day before capture (Table 4). The problem with this value is that by early September, 4 weeks after the laboratory crabs were caught, the proportion of mature females with egg batches had strongly declined at Plimmerton (Table 1). This implies that many crabs in the field had hatched their eggs which, in turn, implies that in the field the incubation period, at least for August and September, cannot be as long as 8 weeks. By November, on the other hand, the times for incubation and inter-batch period were reduced to such short periods that they would seem to be a closer reflection of the natural situation. This is presumably a reflection of the warmer seasonal water temperatures. Thus, by December and January the crabs appear capable of producing and hatching a second or third batch of eggs in about 4 or 5 weeks.

Only one female out of those held captive produced eggs, moulted, and without copulation produced eggs again. However, the rapid loss of the small proportion of eggs laid that had been captured on the pleopod setae, and the lack of any sign of fertilisation, provide a strong indication that *O. catharus* cannot retain viable sperm through a moult.

ACKNOWLEDGMENTS

We thank Mr Jeff Forman and Mr Mark Goldman for their regular assistance with the beach sampling, as well as the numerous people who occasionally aided us on the beach. Mr George Grainger's continued technical assistance was greatly appreciated. We thank Dr J. L. McKoy of MAF Fisheries, Wellington, for making available summary catch statistics relating to the paddle crab, and Mr Mike Tait of MAF Fisheries, Wellington, for his observation of ovigerous females in Cloudy Bay. Financial support for the research came from a Regional Development Investigation Grant and from Macdonald Trade Corporation and Dominion Salt Ltd.

REFERENCES

Armstrong, J. H. 1988: Reproduction in the paddle crab *Ovalipes catharus* (Decapoda: Portunidae) from Blueskin Bay, Otago, New Zealand. *New Zealand journal of marine and freshwater research 22*: 529–536.

Boolootian, R. A.; Giese, A. C.; Farmanfarmaian, A.; Tucker, J. 1959: Reproductive cycles of five West Coast crabs. *Physiological zoology 32*: 213–220.

Cheng, T. S. 1968: Trans-molt retention of sperm in the female stone crab, *Menippe mercenaria* (Say). *Crustaceana 15*: 117–120.

Du Preez, H. H.; McLachlan, A. 1984: Biology of the three-spot swimming crab, *Ovalipes punctatus* (De Haan). 3. Reproduction, fecundity and egg development. *Crustaceana 47*: 285–297.

Giese, A. C. 1959: Comparative physiology: annual reproductive cycles of marine invertebrates. *Annual review of physiology 21*: 547–576.

Haddon, M.; Wear, R. G. 1987: Biology of feeding in the New Zealand paddle crab *Ovalipes catharus* (Crustacea, Portunidae). *New Zealand journal of marine and freshwater research 21*: 55–64.

Haddon, M.; Wear, R. G.; Packer, H. A. 1987: Depth and density of burial by the bivalve *Paphies ventricosa* as refuges from predation by the crab *Ovalipes catharus*. *Marine biology 94*: 25–30.

Haefner, P. A. 1985: Morphometry, reproduction, diet, and epizoites of *Ovalipes stephensoni* Williams, 1976 (Decapoda, Brachyura). *Journal of crustacean biology 5*: 658–672.

Haley, S. R. 1972: Reproductive cycling in the ghost crab, *Ocypode quadrata* (Fabr.) (Brachyura, Ocypodidae). *Crustaceana 23*: 1–11.

Hartnoll, R. G. 1968: Reproduction in the burrowing crab, *Corystes cassivelaunus* (Pennant, 1777) (Decapoda, Brachyura). *Crustaceana 15*: 165–170.

Hines, A. H. 1982: Allometric constraints and variables of reproductive effort in Brachyuran crabs. *Marine biology 69*: 309–320.

King, M. R. 1985: Fish and shellfish landings by domestic fishermen, 1974–82. New Zealand Ministry of agriculture and fisheries, research division, *Occasional publication 20*: 1–122.

Knudsen, J. W. 1960: Reproduction, life history and larval ecology of the Californian Xanthidae, the pebble crabs. *Pacific science 14*: 3–17.

Morgan, S. G.; Goy, J. W.; Costlow Jr, J. D. 1983: Multiple ovipositions from single matings in the mud crab *Rhithropanopeus harrisii*. *Journal of crustacean biology 3*: 542–547.

Snedecor, G. W; Cochran, W. G. 1967: Statistical methods, 6th ed. Iowa State University Press. 593 p.

Stead, D. 1983: Paddle crab investigations. *Catch '82 11*: 16–17.

Wear, R. G. 1982: Paddle crabs: a potential industry or a pest? *Shellfishery newsletter 22*, Supplement to *Catch '84 5*: 11–13.

Wear, R. G.; Fielder, D.R. 1985: The marine fauna of New Zealand: Larvae of the Brachyura (Crustacea, Decapoda). *New Zealand Oceanographic Institute memoir 92*: 1–90.

Wear, R. G.; Haddon, M. 1987: Natural diet of the crab *Ovalipes catharus* (Crustacea, Portunidae) around central and northern New Zealand. *Marine ecology—progress series 35*: 39–49.