

LIFE HISTORY AND POPULATION BIOLOGY OF THE
PADDLE CRAB, *OVALIPES CATHARUS*

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ABSTRACT

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Life history and population biology of paddle crabs, *Ovalipes catharus* were investigated at two South Island localities, Pegasus Bay and Tasman Bay between 1984 and 1986. In Pegasus Bay, crab distributions are related to moulting and breeding cycles. Males and females aggregate in sheltered bays and harbours during winter and mate there at the time of the female moult. After moulting, females move to spawning grounds which are probably offshore in deeper water whereas males move to open sandy beaches to feed.

Growth rates of captive crabs kept at the Edward Percival Field Station, Kaikoura declined with increasing size as a result of lower moult frequency and percentage moult increment. Three recognizable phases of growth corresponded to juvenile, subadult and adult stages of the life cycle. Variation in individual moult increments resulted in increasing variation around mean instar size in successive juvenile instars. However, after sexual maturity was first attained, variation in instar sizes decreased. A simple population model based on the observed growth patterns of individuals, predicted that 13 instars would be discernible in a natural population.

Thirteen post-larval instars were identified by size-frequency analysis of crabs from Pegasus and Tasman Bays. The interpretation of size-frequency data was supported by laboratory growth studies and tag-recapture data. During the first year of life, growth of *O. catharus* was influenced by the rate of accumulation of day-degrees above 5°C. Tasman Bay crabs grew faster than those from Pegasus Bay (on average 3°C cooler) but adults ultimately reached a similar maximum size. Maximum size (130 mm CW for males and 115 mm CW for females) was attained in Pegasus Bay in about 4 years and in Tasman Bay in 3-3.5

years. *O. catharus* is relatively long-lived and slow growing compared to other warm temperate and tropical portunids but is large and fast growing compared to other species of *Ovalipes*.

In Pegasus Bay, females attained sexual maturity in the year of settlement at a mean size of 65 mm CW as shown by gonad development, evidence of copulation and changes in abdomen shape. The number of eggs per brood was related to female size and ranged between 1×10^5 and 1×10^6 eggs. Two or three broods are likely to be produced per year and up to 9 or 10 in a lifetime. In Tasman Bay, higher water temperature prolonged the breeding season and enhanced growth rates of crabs which in turn resulted in sexual maturity being attained sooner and at a smaller size (mean 50 mm CW). Higher temperature and greater food availability also may have been responsible for enhanced survival of large crabs in Tasman Bay and a predicted increase in number of broods produced annually. The net result of differences in life history traits between the two populations was that reproductive potential of females in Tasman Bay may have been up to three times greater than that in Pegasus Bay.

GENERAL INTRODUCTION

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The paddle crab, *Ovalipes catharus* (White, 1843), has gained a notorious reputation in recent years for being a voracious and mobile predator feeding in all levels of the water column and whose numbers are increasing throughout New Zealand's coastal waters. Paddle crabs can burrow actively in soft sediments to obtain food and to hide from predators (McLay and Osborne, 1985) and they can swim faster than many of the fish upon which they prey using their paddle-like rear legs (Stead, 1984b). Some crabs have even been seen chasing flatfish on the sea bed and using their legs as a dragnet to catch surface-dwelling species (Stead, 1984b). They have also been observed opening toheroas and tuatuas (Wear, 1982) which are large commercial shellfish.

In recent years, commercial fishermen and some fisheries biologists have expressed concern that their increasing abundance may be accelerating the decline of other commercial fish and shellfish stocks either through direct predation upon the adults and juveniles of some species or by competing with others for food. A seemingly logical solution to this apparent ecological imbalance may be the rapid expansion of a viable crab fishery. Commercial catch data and information from other sources (Stephenson, 1972; Wear, 1982; Stead, 1984a) show that paddle crabs occur off most sandy beaches and in estuaries from Northland to Stewart Island and the Chatham Islands. The total length of beach coastline round New Zealand suggests that the paddle crab resource could be very large.

O. catharus has been taken in set nets, beach seines, trawls and pots for many years but little commercial interest was shown in the species until 1977 when Napier fishermen took some good catches using baited,

open-top pots (Stead, 1983b). Since 1981, significant landings have been recorded in New Zealand, with a total catch of 110 tonnes in 1983 and over 240 tonnes in 1984. The bulk of the catch has come from Tauranga and Napier on the east of the North Island, and Motueka in the north of the South Island, but many other ports have recorded small annual catches. Most crabs are being sold whole in New Zealand or Japan and there have been some attempts to extract and market crab meat. In 1987, a trial paddle crab farm began operation at Lake Grassmere in the northeast of the South Island with the aim of producing soft-shelled crabs for markets in the U.S.A.

Portunid crab fisheries have become established overseas, possibly the largest being the blue crab (*Callinectes sapidus*) fishery on the Atlantic coast of the United States. *O. catharus* compares favourably in meat yield with blue crabs, i.e. about 25-35% of total body weight, and the meat flavour and texture is considered to be very good (Stead, 1983a). In Australia, there is a thriving fishery based on the blue swimming crab, *Portunus pelagicus*, and the mud crab *Scylla serrata* is an important commercial species in New South Wales, Queensland and the Indo-West Pacific region. Surf crabs, *Ovalipes australiensis*, are widely distributed round the Tasmanian coast and are now being fished commercially.

Although six other species of Portunidae inhabit New Zealand waters, none has the commercial potential of *O. catharus*. *Portunus pelagicus* is known from a solitary record in Hauraki Gulf (Dell, 1964a), *Ovalipes mollerii* and *Scylla serrata* have very limited distributions in northern New Zealand (Dell, 1964b; Dawson and Yaldwyn, 1974), and three other portunids have been reported off the South Island. They are the dwarf swimming crab, *Macropipus corrugatus* (Bennett, 1964) and two deep-water species *Nectocarcinus antarcticus* and *N. bennetti* (Main, 1974).

There is a reasonable amount of published information on aspects of

the biology of *O. catharus*, perhaps not surprisingly considering its importance as a predator in marine, soft-bottom communities and the recent developments towards a crab fishery. Feeding ecology and behaviour have been investigated by Wear (1984), Davidson (1986), Haddon and Wear (1987) Haddon et al. (1987), Wear and Haddon (1987), larval life history by Wear and Fielder (1985), burrowing behaviour by McLay and Osborne (1985) and relative growth by Davidson and Marsden (1987). Very little is known about the general life history and population biology of *O. catharus* however, except for a few brief reports in the N.Z. Catch magazine (Wear, 1982; Stead, 1983b; 1984a; Armstrong, 1986). Unpublished studies of *O. catharus* include H.T. Kung's MSc thesis (1973) on selected aspects of general morphology, reproduction and development in Wellington, and J.H. Armstrong's MSc thesis (1985) on population biology, growth and reproduction in Otago.

Although there is a paucity of information on the population biology of New Zealand's most important commercial crab species, numerous studies have been made on commercially important crabs in other countries. For example, various aspects of the life history, population biology and fishery potential of the portunid, *Callinectes sapidus*, have been investigated by Hay (1904), Churchill (1919), Van Engel (1958), Haefner and Shuster (1964), Tagatz (1968), Leffler (1972), Dudley and Judy (1973) and Hines et al. (1987). Similarly, growth, movements and reproduction of the edible crabs *Cancer pagurus* and *Cancer magister* have received considerable attention from MacKay and Weymouth (1935), MacKay (1943), Cleaver (1949), Butler (1960, 1961), Edwards (1965, 1978), Hancock and Edwards (1967), Bennett (1974), and Howard (1982).

I have discerned from these and other studies, the preliminary biological knowledge that is most necessary for the successful management of an exploited species, and in the present study have tried to fill some

of the more obvious gaps in our current understanding of the life history and population biology of *O. catharus*. In particular, I have been concerned with how to obtain reliable estimates of growth rates and reproductive potential of crabs and crab populations and how environmental factors affect these traits. However, as science is not wholly governed by commerce, I have directed part of my investigation towards more fundamental issues of current interest in crustacean biology especially variability in growth (Hartnoll, 1982; Botsford, 1985) and the nature of the relationship between growth and reproduction (Hartnoll, 1985).

The thesis is presented as a collection of papers which are being prepared for publication. Each chapter builds on the previous ones and the individual topics are introduced in the context of the overall study. Inevitably, this format has resulted in a certain amount of unavoidable repetition, but I have attempted to keep this to a minimum.

CHAPTER 1

CHAPTER 1

Growth of the New Zealand paddle crab Ovalipes catharus (Decapoda, Portunidae). I. Laboratory growth and population model.

INTRODUCTION

Early statistical and mathematical descriptions of crustacean growth concentrated on growth in independent moult periods, i.e without consideration of previous growth history of individuals. They consisted of descriptions of the size increment at individual moults and sometimes included a description of the time interval between moults (Butler, 1961; Kurata, 1962; Hancock and Edwards, 1967; Bennett, 1974). These two components of crustacean growth were combined to obtain a single average growth curve for the species under study. Hartnoll (1983) stated that although growth curves generated in this way are highly simplified as they ignore seasonal influences and the effects of sexual maturity, they are adequate to indicate the maximum size attainable by a species and the mechanism by which growth in size is limited, i.e. determinate or indeterminate growth pattern.

In other, particularly more recent studies, much attention has been paid to the proper form of line to be fitted to the relationships of growth components (size increment and moult frequency) to size (Hiatt, 1948; Mauchline, 1976; 1977; Somerton, 1980) but gradually more attention was paid to the concept of variability in growth through non-independent moults and its effects on the eventual size distribution of a species

(McCaughran and Powell, 1977; Hartnoll, 1978; Hartnoll and Dalley, 1981; Botsford, 1985). Botsford (1985) pointed out that in the past, variation about single line descriptions had been more or less ignored as 'noise' or measurement error. However, the amount of growth at any one moult probably depends on the amount of growth at the preceding moults and, therefore, the nature of the relationship between 'errors' at each moult can have a profound effect on growth.

The present paper describes laboratory studies on growth of *Ovalipes catharus* (White, 1848) and is part of a larger study on the population biology and life history of the species in Pegasus Bay, New Zealand. *O. catharus* is a portunid crab living subtidally on sandy shores throughout New Zealand and in east and south Australia (Wear and Fielder, 1985). Relative growth of *O. catharus* in Pegasus Bay has been studied previously by Davidson and Marsden (1987). The purpose of the present study was to examine (1) differing phases of somatic growth in relation to reproductive maturity; (2) seasonal patterns of growth with reference to timing of larval development; and (3) the mechanism of variability in individual moult increments and its effects on overall size distribution. The latter in particular requires a study of growth of individuals over successive moults and is best obtained in the laboratory. The fact that both moult increment and intermoult duration vary with changes in environmental conditions (Hartnoll, 1982) means that observations of growth in captivity may not be applied indiscriminately to natural populations. Therefore, the growth model generated in this study was tested in a subsequent study of a natural population of *O. catharus* (Chapter 2).

METHODS

Between December 1983 and February 1985, paddle crabs of all sizes were collected using a small beam trawl and baited lift pots (see Chapters 2 and 4) from the sandy beaches around the Canterbury and Kaikoura coasts of the South Island, New Zealand and transported to the Edward Percival Field Station, Kaikoura. Crabs were kept in one of either five 160-l or two 540-l wooden aquaria containing a 40-50 mm layer of sand and fresh running seawater. Each of the two larger aquaria contained 18 circular cages (diameter 240 mm and depth 60 mm) made of strong plastic netting (mesh size 17 mm). The five smaller aquaria also contained 18 cages 180 mm in diameter and 30 mm deep. Two sets of the smaller cages were made with plastic net of 6 mm mesh size. These finer meshed cages were used for the smallest crabs but because the fine mesh reduced water flow through them, they had to be flushed with fresh seawater at regular intervals. It was necessary to keep the crabs in cages for individual identification and to prevent predation on newly moulted, soft-shelled individuals. Each crab was fed half a freshly opened mussel every second day. Uneaten food remained attached to the mussel shell and was removed the next day to prevent fouling the sand in the cages. Cages were inspected daily for moult shells and at least once a month each crab was removed and its maximum carapace width (CW) was measured with Vernier calipers to the nearest 0.1 mm. The temperature of seawater in aquaria followed the natural cycle for the Kaikoura region (Ottaway, 1976), and ranged from 8 to 17°C.

All records of moult increment and duration of intermoult period were stored on a Burroughs computer at the University of Canterbury. Mean increment, percentage increment and intermoult duration of each 5 mm CW size class were calculated using the data managing program

BMDP9D. Regressions and analyses of covariance of \log_{10} percentage increment and \log_{10} intermoult duration on size were performed using the regression program BMDP1R.

An experiment to determine variation in moult increments between individuals and the effect of season on growth rate involved monitoring the growth of two groups of small crabs. Between May 1984 and May 1985, 12 crabs in post-larval instars 3 or 4 were grown to instars 9 or 10. Between January 1985 and June 1985, 26 first post-larval instar crabs were grown to instar 9. The latter were caught as megalopae during January and February. For the two groups of crabs, mean moult increment and intermoult duration were calculated for each instar in order to determine whether there were differences in growth rate between autumn recruits and summer recruits. The pattern of within instar size variation in successive instars was examined by calculating the coefficient of variation (CV) of the mean for each instar. The sequence of instars was long enough to investigate mechanisms controlling variability in the growth of individuals. Botsford (1985) suggested that variability in growth could be caused by (1) a distribution of intrinsic growth rates among individuals or (2) all individuals inherently identical but variation in moult duration and increments correlated in one or more of the following ways: (i) sequential size increments correlated; (ii) sequential intermoult periods correlated; and (iii) intermoult period correlated with moult increment. Each of these possibilities was tested by examining successive moult increments and intermoult durations of individual crabs.

The relationships between increment, intermoult duration and CV of mean instar size to body size were used to predict a total population size structure for *O. catharus* using the model described by Hartnoll (1978).

RESULTS

During the course of the study 445 moults were recorded from 176 captive crabs. Each individual moulted at least once and some up to eight times. Most moult records came from crabs less than 75 mm CW. Above this size mortality increased and sample size decreased because it was difficult to provide adequate laboratory space for such large mobile animals.

Components of growth

The first component of growth in crustaceans is the increase in size after each moult, ie. the moult increment. In *O. catharus*, absolute moult increment increased as premoult size increased (Fig. 1) up to about 55 mm

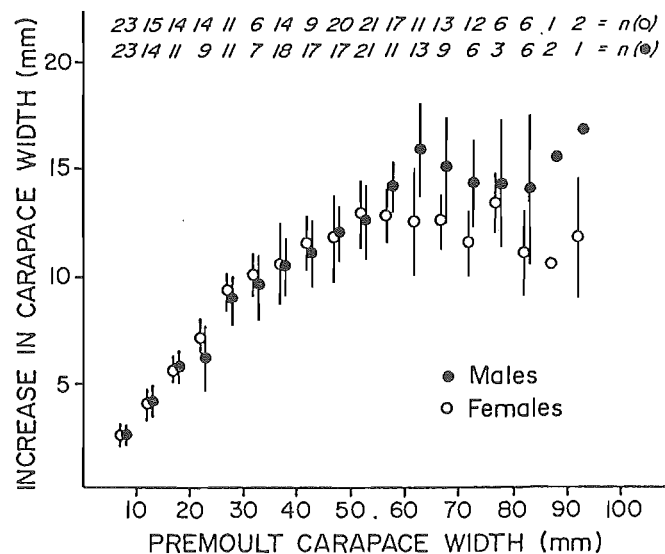


Fig. 1. *Ovalipes catharus*. Mean moult increments of 5 mm size classes of crabs reared in the laboratory. Vertical bars are ± 1 standard deviation. Number of male and female crabs in each size class given at top.

CW but the relationship was not linear. At larger sizes the increments of similarly sized males and females differed. The moult increment of adult males levelled off at about 15 mm. A significant negative slope for moult increment on size was a characteristic of adult females (>55 mm CW; $P < 0.05$) and the size at which growth rate of females first departed from that of males was probably a result of the onset of maturity.

The relationship between absolute moult increment and premoult size has limited usefulness because it does not allow comparisons between species of different size ranges, and it is not easily described by a single linear equation. Instead, moult increment can be explained in relative terms by expressing it as a percentage of premoult size (Fig. 2). In *O. catharus*, percentage increment decreased linearly as premoult size increased; this is an almost universal pattern in crustaceans (Hartnoll, 1982).

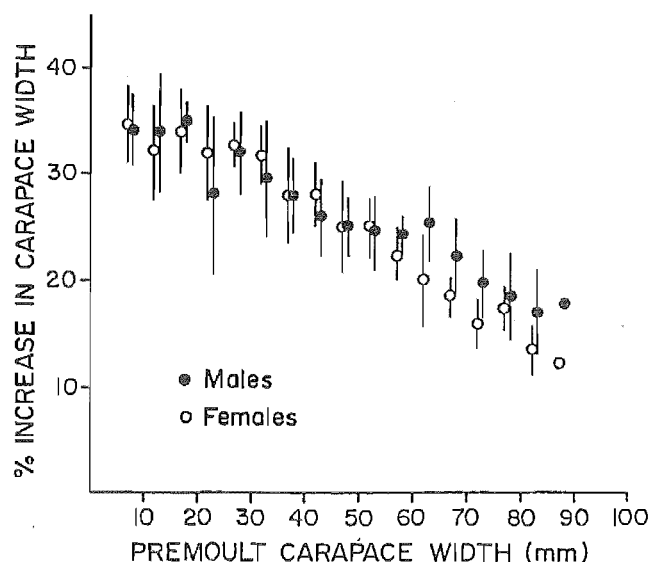


Fig. 2. *Ovalipes catharus*. Mean percentage moult increments of 5 mm size classes of crabs reared in the laboratory. Vertical bars are ± 1 standard deviation. Number of crabs in each size class same as Fig. 1.

An even more consistent pattern of crustacean growth concerns the second component of growth - intermoult duration, sometimes also described as moult frequency. In *O. catharus* (Fig. 3), as well as many other crustaceans, intermoult duration increased with increasing premoult size. The relationship between intermoult duration and carapace width was clearly not linear and after about 55 mm CW the duration of female intermoult was greater than that of males.

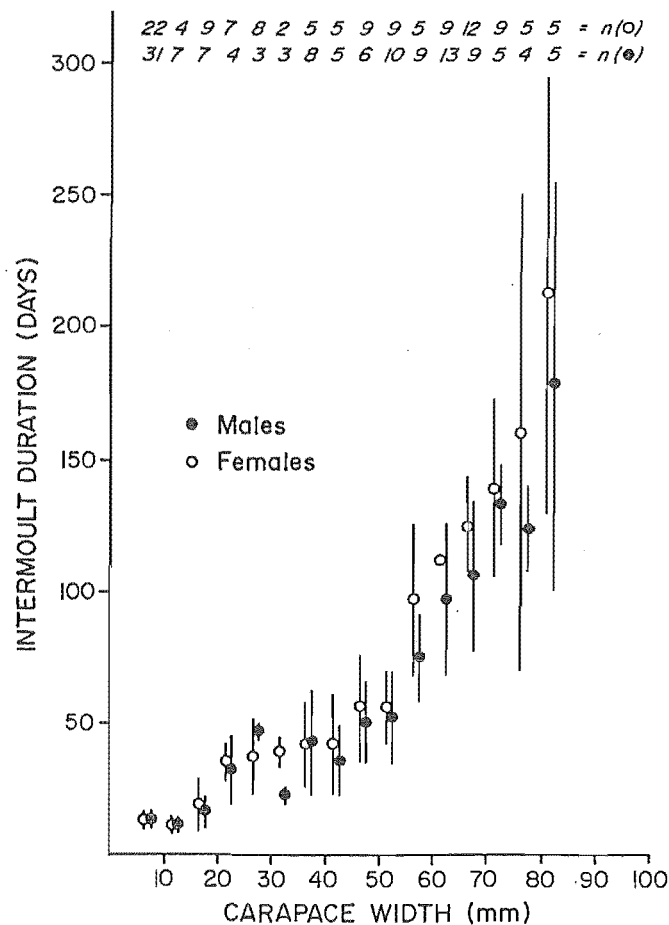


Fig. 3. *Ovalipes catharus*. Mean intermoult duration of 5 mm size classes of crabs reared in the laboratory. Vertical bars are ± 1 standard deviation. Number of male and female crabs in each size class given at top.

The Growth Curve

The relationship between the two components of growth and premoult size was best described by linear regressions of log percentage increment and log intermoult duration on carapace width. The relationship between each of the growth components and premoult size could be divided into four separate regression lines (Fig. 4) representing three phases of growth in *O. catharus*. For convenience the three growth phases were termed juvenile, subadult and adult. Pairwise comparisons of these lines (Table 1) showed that all were significantly different except for the subadult and adult male lines of log intermoult duration on size (Fig. 4B).

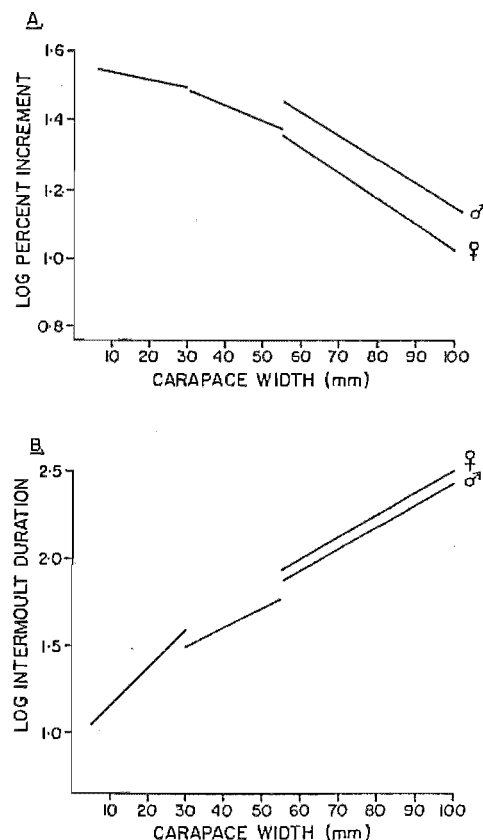


Fig. 4. *Ovalipes catharus*. Regressions of (A) log percentage increment and (B) log intermoult duration on carapace width for juvenile, subadult, adult male and adult female crabs reared in the laboratory. Regression equations and coefficients in Table 1.

Table 1. *Ovalipes catharus*. Regression equations and tests of covariance of percentage increment and intermoult duration on size for each growth phase.

Regression of percentage increment on premoult size			
regression equations	correlation coefficient	pairwise comparisons	probability level
M $\log Y = 1.83 - 0.007X$	$r = 0.65$	M:F	$P < 0.001$
F $\log Y = 1.75 - 0.007X$	$r = 0.63$	M:S	$P = 0.010$
S $\log Y = 1.60 - 0.004X$	$r = 0.37$	F:S	$P = 0.032$
J $\log Y = 1.55 - 0.002X$	$r = 0.23$	S:J	$P = 0.043$
		FS:MS	$P = 0.901$ n.s.
Regression of intermoult duration on size			
M $\log Y = 1.20 + 0.012X$	$r = 0.68$	M:F	$P = 0.047$
F $\log Y = 1.22 + 0.013X$	$r = 0.62$	M:S	$P = 0.135$ n.s.
S $\log Y = 1.17 + 0.011X$	$r = 0.37$	F:S	$P = 0.021$
J $\log Y = 0.94 + 0.022X$	$r = 0.75$	S:J	$P = 0.001$
		FS:MS	$P = 0.656$ n.s.

M = male, F = female, S = subadult, J = juvenile.

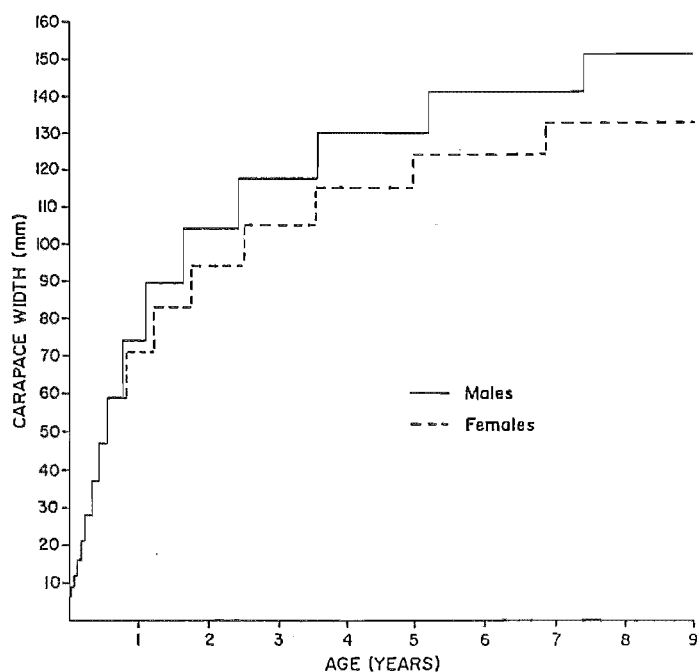


Fig. 5. *Ovalipes catharus*. A generalised scheme of growth for laboratory reared crabs.

Information on intermoult duration and moult increment can be combined to provide a description of average growth in relation to age. Fig. 5 shows the growth model derived by combining the equations in Table 1. Juvenile growth was characterised by a very rapid increase in size (Fig. 5) which was achieved by maintaining a high percentage increment at each moult (Fig. 4A) and a short intermoult duration. This rapid growth phase continued until a CW of about 30 mm was reached.

Subadult growth was slower than that of juveniles probably because in subadults the reproductive system began to compete with somatic growth for energy resources. The subadult was a short phase which lasted for about two intermoult periods (Fig. 4). As maturity was reached, the growth of female crabs slowed markedly compared with that of males. Adult females had slightly longer intermoult durations and smaller percentage increments than males. These differences may be associated with egg bearing in females and the greater energetic requirements for egg rather than sperm production.

Decreasing percentage increment and increasing intermoult duration with body size resulted in an ever decreasing growth rate which effectively placed a limit on the maximum size attained by *O. catharus* (Fig. 5). Moulting is predicted to continue indefinitely for as long as individuals survive and on this basis *O. catharus* is defined as an indeterminate grower (Hartnoll, 1983). The maximum size of *O. catharus* collected in Pegasus Bay was about 130 mm CW for males and 115 mm CW for females (see Chapter 2) and given that the instar sizes in (Fig. 5) are means, the present model predicts that maximum sized crabs would be in instar 13 (mean size 118 mm for males and 105 mm for females) and 3-4 years old. The difference between the maximum size observed and that predicted (about 160-170 mm, Fig. 5) suggests that further information is required on the moulting and growth of large *O. catharus*.

before they can be definitely classed as indeterminate growers.

Variation in growth rates

Newly recruited juvenile crabs were present in Pegasus Bay mainly between January and May, and in the laboratory the early (January) recruits grew at a much faster rate over at least the first eight instars (Fig. 6). The slower growth rate of autumn recruits was the result of longer intermoult durations and no significant difference was found between the percentage moult increments of the two groups ($P > 0.05$, ANCOVA). Therefore, it can be concluded that rate of growth over the first year was influenced by the timing of larval settlement and could not be described by a simple curve such as that in Fig. 5.

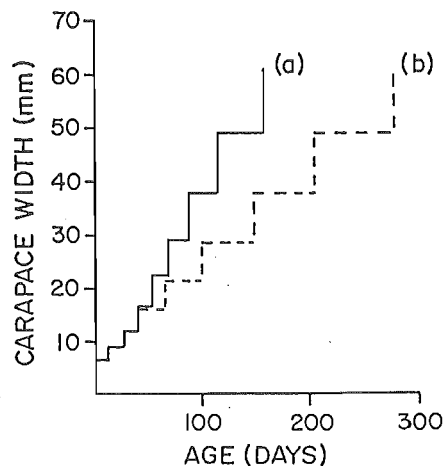


Fig. 6. *Ovalipes catharus*. A generalised scheme of growth for (a) summer recruits and (b) autumn recruits reared in the laboratory. Age of autumn recruits at size first captured (start of dashed line) was unknown so for convenience this was assumed to be the same as that for similar sized summer recruits.

Sexual maturity of *O. catharus* is generally reached during the first spring or summer after recruitment (Chapter 3) which means that different growth rates within a year class will affect the time that individuals take to reach maturity and the size attained at that time.

A feature of crustacean growth that is not shown in Figs. 5 and 6 is that of individual variation in growth. Calculation of coefficients of variation (CV) for each instar of the summer and autumn recruits permitted comparisons to be made of within instar size variation independent of the value of the mean (Fig. 7). CV tended to increase over the first seven instars and may have resulted from either an accumulation of successive random fluctuations in moult increment, or the presence of intrinsically fast and slow growers within each group. Over the range of instars in which sexual maturity was attained by *O. catharus*

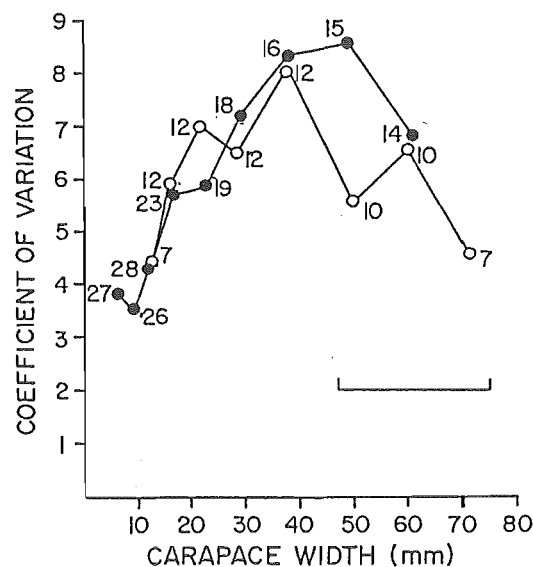


Fig. 7. *Ovalipes catharus*. Coefficient of variation of mean size of instars 1 to 9 for summer recruits (●) and instars 3 to 10 for autumn recruits (○). Numbers next to points are sample size for each mean. (—) indicates size range in which pubertal moults occur in natural population in Pegasus Bay.

(instars 8-10; Chapter 3), CV declined suggesting that the diversion of some energy from somatic growth to gonad development acted to decrease the variability of moult increments within maturing instars.

To investigate the mechanism accounting for variability in growth increments, the successive moults of each crab were ranked according to whether the crab was above or below the average size for that instar and whether its moult increment to the next instar was above or below the average increment between the two instar means. A moult which tended to bring a crab closer to the mean size of the instar was termed a compensatory moult. The proportion of compensatory moults was generally high throughout the sequence of instars (Table 2) despite the fact that size variation increased rapidly between instars 3 and 7. Only 3 of the 38 crabs did not undergo a compensatory moult at some stage in the instar sequence and they could be considered intrinsically slow growers. All the other crabs showed no consistent pattern in their growth rates, having above average increments between some instars and below

Table 2. *Ovalipes catharus*. Number of crabs observed moulting to each instar in the laboratory and the percentage of compensatory moults (see text) by summer and autumn recruits.

	Post-moulting instar								
	2	3	4	5	6	7	8	9	10
Summer recruits									
total no. of moults	26	26	23	19	18	16	15	14	
compensatory moults (%)	50	46	48	21	44	19	33	50	
Autumn recruits									
total no. of moults			7	12	12	12	10	10	7
compensatory moults (%)			86	67	50	8	40	0	72

average increments between others. There was no consistent pattern of correlation between successive moult increments or intermoult durations nor was there any correlation between moult increment and intermoult duration within the same instar.

Size distribution model

Hartnoll (1978) evaluated the effect of measured variability in instar size on the population size structure of *Rhithropanopeus harrisii* assuming constant recruitment. By using mean estimates of moult increment and moult duration, estimates of individual variation in moult increment and estimates of mortality within each instar, he was able to predict the shape of the overall population size structure. Hartnoll also applied his model to similar data for *Carcinus maenas* and *Cancer anthonyi*. The predicted size distributions for the three species reflected interspecific differences in the relationship between increment and intermoult to body size, but they all had one common feature, the fact that only the first few instars could be discriminated. All three species showed steadily increasing CV in all successive instars in contrast to *O. catharus* in which the CV declined at maturity.

In order to apply Hartnoll's model to *O. catharus*, I used the estimates of mean size increment and mean intermoult duration shown in Fig. 5 for instars 1 to 13. The standard deviations in mean size of instars 1 to 9 (Fig. 7) were averaged for the two recruitment groups. Standard deviation of subsequent instars was assumed to increase at a constant 6% of the mean and hence would be represented in Fig. 7 as a horizontal line at CV=6. If recruitment is assumed to be constant, the relative proportion of the total population in a particular instar will be the product of survival to that instar and the duration of that instar. In

the absence of any information on natural mortality, a constant rate of 10% mortality per instar was assumed as in the rock lobster population models of Annala (1977) and Campbell (1985).

Application of Hartnoll's (1978) model to *O. catharus* resulted in the size distribution shown in Fig. 8. Two important predictions of the model are: (1) size-frequency analysis of a natural population should permit the discrimination of all 13 instars, and (2) crabs in the 13th instar (110-130 mm CW) should be the most abundant in a natural unexploited population.

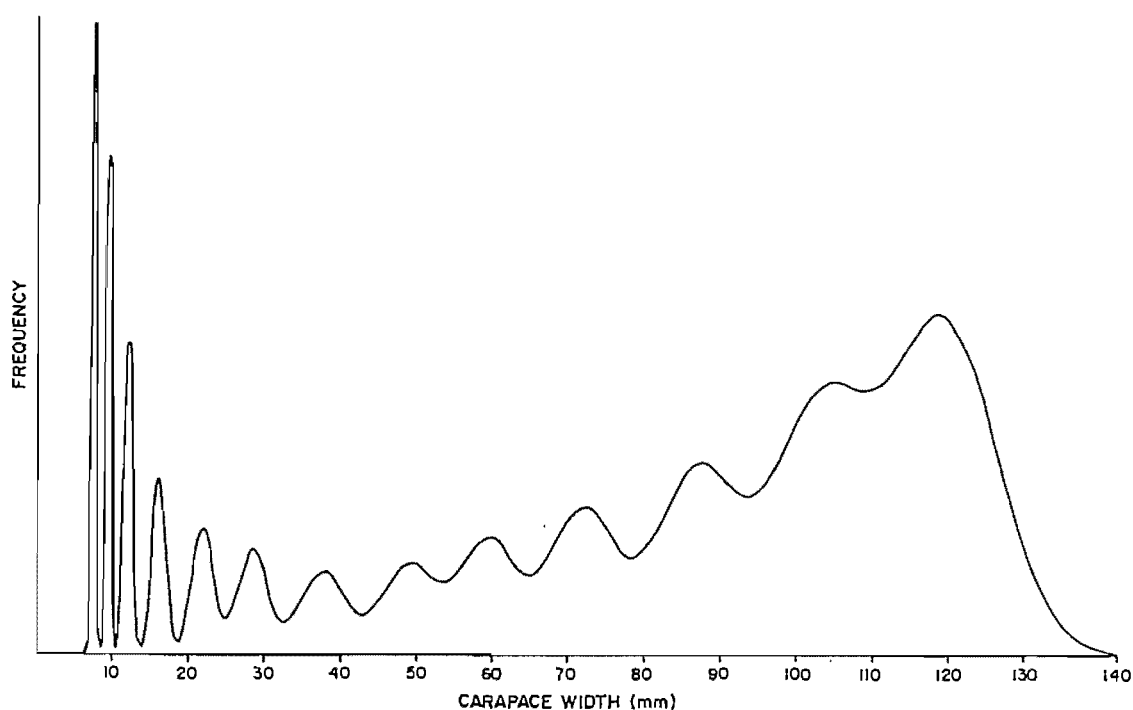


Fig. 8. *Ovalipes catharus*. Size-frequency model based on data from laboratory rearing experiments.

DISCUSSION

Components of growth

A decrease in the percentage growth increment at moulting with size is a common phenomenon in Crustacea (Hartnoll, 1982). The slope of the regression of percentage moult increment on size defines the rate at which the increment changes with size. Hartnoll (1983) believed that the slope of this regression has a major bearing on the size that a species can attain, such that species in which the regression has a shallow slope can reach a larger maximum size and vice versa. The slope of the regression of \log_{10} percentage increment on size over the entire size range of *O. catharus* (-0.004) was slightly steeper than those described (-0.002) for the larger cancrid crabs *Cancer magister* (max size 200 mm CW; Butler, 1961) and *Cancer pagurus* (max size 200 mm CW; Mauchline, 1977). However, it is not as steep as that for two smaller species, *Pachygrapsus crassipes* (-0.019, max size 50 mm CW; Mauchline, 1976) and *Rhithropanopeus harrisii* (-0.14, max size 10 mm CW; Hartnoll, 1978). In some other portunid crabs for which this type of data is available (*Carcinus maenas*, *Carcinus mediterraneus* and *Callinectes sapidus*) percentage increment showed little tendency to decrease as size of crab increased (Hartnoll, 1983). The latter condition is characteristic of species with determinate growth whereby maximum size is controlled by the termination of moulting.

A more consistent characteristic of crustacean growth even amongst determinate growers, is that of increasing intermoult duration with size (Hartnoll, 1982). The slope of the regression of intermoult duration on size has been correlated with the maximum size attained by a species such that small species generally have steep slopes and large species have more

gradual slopes (Hartnoll, 1983). The slope of the regression of \log_{10} intermoult duration on size over the entire size range of *O. catharus* (0.015) is steeper than that for the larger *Callinectes sapidus* (0.005, max size approx 240 mm CW; Tagatz, 1968) but not as steep as for the smaller *Cancer anthonyi* (0.023, max size 110 mm CW; Anderson and Ford, 1976) and *Carcinus maenas* (0.04, max size 70 mm CW; Klein Breteler, 1975b).

The present study supports the observations of Hartnoll (1983) that increasing intermoult duration and decreasing percentage growth increment with size interact to produce a decreasing growth rate. This effectively limits the maximum size attained by crustaceans and the rate of increase and decline of growth components with body size influences the maximum size attainable.

Growth phases

Many authors have reported a decline in growth rate after maturity has been reached and have shown that as in *O. catharus* the decline is usually greater in females than males (Hartnoll, 1985). Competition for energy resources between growth and reproduction is the most likely explanation for this decline and the greater cost of production of eggs than sperm could account for female growth being slower than that of males. *O. catharus* exhibits two separate growth phases prior to maturity. Initially, rapid growth in size may enable juveniles to quickly reach a size refuge from predation as predation pressure is likely to be highest on small individuals. Small *O. catharus* have been observed in the stomachs of skate, *Raja nasuta* and red cod, *Pseudophycis bacchus* (pers obs), sole, *Pelotretis flavilatus* and flounder, *Rhombosolea plebeia* (McLay, pers obs) and larger *O. catharus* (Wear and Haddon, 1987) which together make up most of the predatory bottom feeders on sandy shores in Pegasus Bay.

Predators of large *O. catharus*, particularly during periods of moulting when the crabs are soft-shelled, are likely to be mainly the bottom feeding sharks, *Mustelus lenticulatus* (pers obs) and probably *Galeorhinus australis* and *Squalus acanthias*. Intuitively, it would seem to be advantageous for *O. catharus* to grow quickly to a size beyond the limits of the feeding capabilities of many of its predators. This should be particularly so in shallow waters occupied by many *O. catharus* where large predators would be less abundant, and smaller predators may be more abundant.

The slower subadult growth phase lasts for about two instars (30-55 mm CW) and seems to correspond to the size range when gonads first appear (Chapter 3). The adult growth phase starts at about 55 mm CW, the size at which mating first begins and at which gonads are developing towards maturity (Chapter 3).

If the growth phases observed for *O. catharus* are the consequence of differing rates of growth of the carapace in relation to other body parts, then a study of relative growth of other structures, particularly secondary sexual characteristics should illustrate these growth phases too. Davidson and Marsden (1987) found only two phases of abdomen growth in female *O. catharus* which they interpreted as being characteristic of immature and mature crabs. The transition occurred at 30-40 mm CW, a size which corresponds closely to the transition from juvenile to subadult growth phases observed in my study. I observed an additional phase of female abdomen growth (Chapter 3) not previously reported by Davidson and Marsden (1987) which started in the size range 50-70 mm CW. That this third phase was characteristic of mature females was supported by evidence of copulation and gonad maturity. Hartnoll (1982) found that relative growth in post-larval Brachyura typically consisted of one or more immature growth phases and one mature phase. Two phases of

abdominal growth prior to maturity and a third phase after maturity have been found in females of *Ocypode ceratophthalmus* (Haley, 1973), *Dissodactylus primitivus* (Pohle and Telford, 1982) and *Ovalipes stephensoni* (Haefner, 1985). Males of *Eriocheir sinensis* (Hoestlandt, 1948) showed three phases of abdominal growth but only two were evident in females. Both male and female *Maja squinado* showed three phases of growth in chela length (Teissier, 1935).

Overall, it seems that changes in the growth rate of the carapace of female *O. catharus* are paralleled by changes in relative growth of the abdomen and changes in the stage of ovarian development. Similar parallels were not found in males in which the gonad development was not studied and distinct phases of relative growth of secondary sexual characteristics were not observed (Davidson and Marsden, 1987).

One of Hartnoll's (1982) criticisms of the procedure of generating growth curves from single regressions of growth components on size, is that too often they are based on limited observations over a narrow size range and therefore ignore the effects of sexual maturity and other intrinsic factors on the pattern of growth of individuals. By combining the separate regressions of percentage increment and intermoult duration on size for each of the three growth phases covering the entire size range of *O. catharus*, it was possible to create an average growth curve for the species which incorporated the effects of sexual maturity.

Variation in growth rates

Differences in growth rate of first year crabs depending on the timing of larval settlement (summer or autumn) were probably attributable to differences in water temperature, as found by Astthorsson and Ralph (1984) for the mysid *Neomysis integer*. Increasing water temperature

invariably causes a decrease in intermoult duration in Crustacea but it is not uncommon for moult increment to be unaffected within the natural range of temperatures experienced by the species (Hartnoll, 1982). A reasonably long season of larval settlement and differential growth of crabs settling early or late in the season result in the presence of maturing crabs of a wide range of sizes at the beginning of the first reproductive season. This is consistent with my observations that pubertal moults occurred in crabs of a wide size range (Chapter 3).

An important factor often overlooked in studies of crustacean growth is the degree to which moult increment varies between individuals undergoing the same moult. Such variations result in a range of sizes within each instar, and affect the degree to which successive instars can be discriminated in a size-frequency distribution. Although a number of published reports describe change in mean size through a sequence of crustacean instars, very few enable size variation within each instar to be assessed. If the variability of moult increments is random, then the coefficient of variation should increase with successive instars as found in *Rhithropanopeus harrisi* (Hartnoll, 1978), *Carcinus maenas* (Klein Breteler, 1975b) and juvenile *O. catharus* (this study). However, a few authors have found different patterns of changing CV with size which may indicate non-randomness in individual growth. Anderson et al. (1937) found a steady decline in CV through a sequence of 20 instars in *Daphnia pulex*, whereas studies of size variation in *Cyprinotus* sp. and *Cambaroides japonicus* (Kurata, 1962), *Cycloleberis zealandica* (Fenwick, 1983) and *Palaemon elegans* (Hartnoll and Dalley, 1981) demonstrated a decrease in CV only at certain stages of the life cycle. Both *Cancer magister* (MacKay and Weymouth, 1935) and *Palaemon elegans* (Hartnoll and Dalley, 1981) tended to have less size variation in either the last larval or first post-larval instar than in earlier ones. The portunid,

Portunus sanguinolentus had a lower CV in mature instars than in the last juvenile instar (Ryan, 1967b) and I found a decline in CV over the range of instars of *O. catharus* in which sexual maturity was first attained.

For CV to remain constant or to decrease in the face of variation in the moult increment, a negative feedback mechanism must be operating whereby individuals which are large for a given instar undergo a smaller increment than individuals which are small for that instar (Hartnoll, 1982). MacKay and Weymouth (1935) termed this compensatory growth and implied that in some crustaceans there is an adaptive advantage in being within a certain size range at particular stages of ontogeny, for example at the end of larval life or at the onset of sexual maturity. The compensatory affect may be aided by differential mortality if it eliminates both the largest and smallest individuals within an instar as found by Kunisch and Anger (1984) in a study of juvenile spider crabs, *Hyas araneus*.

The reasons for the observed pattern of variability in individual growth for *O. catharus* are elusive. The mechanisms suggested by Botsford (1985) (see methods) were tested in laboratory experiments but there were no correlations between size increments or intermoult periods in sequential moults, and no correlation between size increment and intermoult period in the same moult. Instead, growth occurred by a series of random moult increments checked at intervals by compensatory moults which tended to decrease instar size variation particularly during the time of gonad maturation.

Size distribution model

Application of Hartnoll's model, which assumes constant recruitment,

to a species for which recruitment is seasonal, will have the effect of overestimating the proportional representation of the smaller instars which do not occur in the population all year around. The model therefore is of limited value in predicting the size structure of a natural population of *O. catharus* in which recruitment is seasonal. The proportional representation of each instar in a population also will be affected by mortality which probably varies between instars and between populations. Further work is currently underway to estimate mortality rates within instars of two natural populations of *O. catharus* in the South Island of New Zealand and this hopefully will provide a better understanding of the effects of mortality upon population structure. Despite the inadequacies of the present model, it did enable all (13) post-larval instars of *O. catharus* to be distinguished on the basis of size. This is rare in large decapod crustaceans (Hartnoll, 1982) and is a consequence of the low variation in instar sizes. In contrast, only the first six instars could be distinguished on the basis of size in *Carcinus maenas* (out of a total of 18 instars), *Cancer anthonyi* (total of 14 instars) and *Rithropanopeus harrisii* (total of 9 instars) since all three of these species had increasing CV of size in successive instars (Hartnoll, 1978).

The hypothesis that *O. catharus* has relatively low variability in instar sizes and therefore easily discernible instars within a total size-frequency distribution is tested and discussed in more detail in a study of natural population structure of *O. catharus* in Pegasus Bay (Chapter 2).

CHAPTER 2

CHAPTER 2

Growth of the New Zealand paddle crab Ovalipes catharus (Decapoda, Portunidae). II. Studies of age and growth in a natural population

INTRODUCTION

In a previous study of growth under laboratory conditions (Chapter 1), the paddle crab *Ovalipes catharus* (White, 1843) was shown to exhibit indeterminate growth, moulting 13 times after settlement of megalopae before reaching maximum size in 3-4 years. Growth in captivity may not be representative of growth in the wild, however, and for this reason a study of growth in a natural population of *O. catharus* was undertaken to test the predictions based on laboratory experiments.

The methods available to study growth of crustaceans in natural populations are very limited because all calcified structures are lost at each moult. Therefore, determination of age by examination of annual rings in persistent skeletal material is not possible. The only methods available for studying crustacean growth which do not involve keeping specimens captive are to observe moulting in the wild, record moulting of tagged individuals, and observe changes in size-frequency distributions in repeated samples of a population. The first two of these methods are difficult to use for a variety of logistic reasons and the third is generally thought to be useful only in the early stages of growth or in species with a limited number of instars (Hartnoll, 1982).

Nevertheless, my laboratory studies predicted that size frequency

analysis could be an appropriate method for determining growth in a natural population of *O. catharus* (Chapter 1) and the large size of the species suggested that these crabs might be suitable for tagging. Therefore, I employed both size-frequency analysis and tagging in an attempt to measure growth rate in a population of *O. catharus* in Pegasus Bay, New Zealand.

MATERIALS AND METHODS

Two populations of paddle crabs were sampled regularly in Pegasus Bay to obtain data on growth rates. Little Akaloa (Fig. 1) was chosen as the site to conduct a tagging experiment and a 2-year sampling program. Between January 1984 and December 1985 the crab population at Little Akaloa was sampled monthly mainly with baited lift pots described in Chapter 4. Crabs <30 mm CW rarely entered pots and instead were caught using a 2 m wide beam trawl with a mesh size of 10 mm.

The second sampling program was conducted at Brighton where according to local fishermen, paddle crabs were abundant and large in size. At Brighton, where crab densities were lower and sea conditions were rougher than at Little Akaloa, samples were taken by towing an otter trawl from a 6 m boat. The cod end of the otter trawl had a mesh size of 25 mm and only crabs larger than 30 mm CW were caught. Nine samples were obtained at this location between June 1984 and May 1985.

All crabs were sexed and carapace width (CW) was measured with calipers to the nearest 0.1 mm. Between January 1984 and January 1985 crabs caught at Little Akaloa that were >60 mm CW, active, and with no more than two missing limbs were measured and tagged with numbered, 10 mm long, Floy FD67 anchor tags inserted with a Dennison tagging gun

into a muscle at the junction of carapace and abdomen (Fig. 2). The tag was inserted slightly off centre to avoid any part of the exoskeleton associated with the abdomen or leg sockets, and to prevent damaging the dorsal abdominal artery. The old exoskeleton splits along the junction of carapace and abdomen (termed the suture line) when moulting, and placing the tag on the suture line minimizes the chance of tag loss during the moult. All crabs were measured and tagged and returned to the sea within one hour of capture. Recaptures of tagged crabs were made during normal sampling and tagging excursions as well as by local amateur fishermen in response to a poster advertising the experiment.

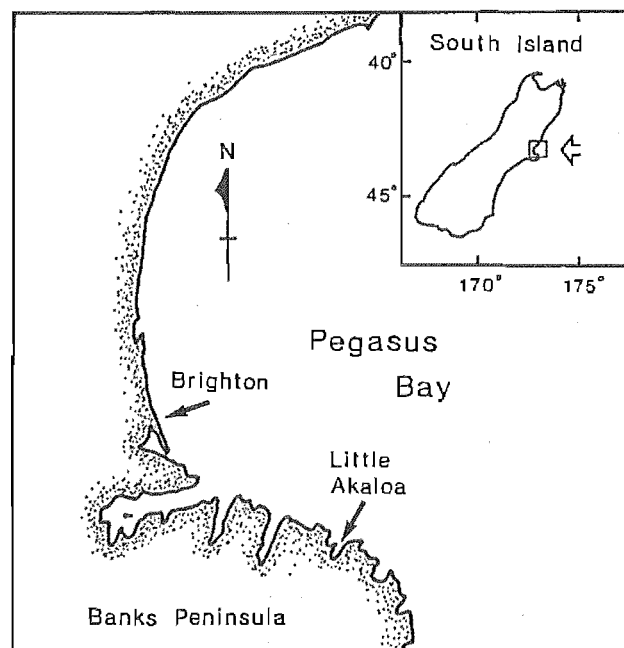


Fig. 1. Map of Pegasus Bay showing sampling sites at Little Akaloa and Brighton.



Fig. 2. Ovalipes catharus. Tag inserted at the juncture of the carapace and abdomen.

An experiment to determine the comparative growth rate of tagged and untagged crabs was conducted at the Edward Percival Field Station, Kaikoura. Crabs were collected using baited lift pots from beaches around Kaikoura, and 36 between 60 and 85 mm CW were selected for the laboratory experiment. They were kept in individual cages in two, 160-l wooden aquaria under conditions described previously (Chapter 1). Each of the two aquaria contained nine tagged and nine control (untagged) crabs. The experiment was conducted between June and November 1984.

Growth rate of crabs in Pegasus Bay was estimated from tag-recovery data and polymodal analysis of size-frequency distributions using the maximum likelihood program of MacDonald and Pitcher (1979) run on a Prime computer at the University of Canterbury.

RESULTS

Instar sizes and moult increment

Size records of all crabs caught in monthly samples from Brighton and Little Akaloa were combined into size-frequency histograms for Pegasus Bay (Figs. 3 and 4). On the assumption that instar sizes are normally distributed about a mean size, a set of normal curves was fitted to the size-frequency histograms for small (<30 mm CW) and large (>30 mm CW) crabs. Five instars were identified in the size distribution of small crabs (Fig. 3), the first of which corresponded to the second post-larval instar (Chapter 1). The set of normal curves shown in Fig. 3 describes a distribution not significantly different from that observed ($P > 0.10$, Chi-square test).

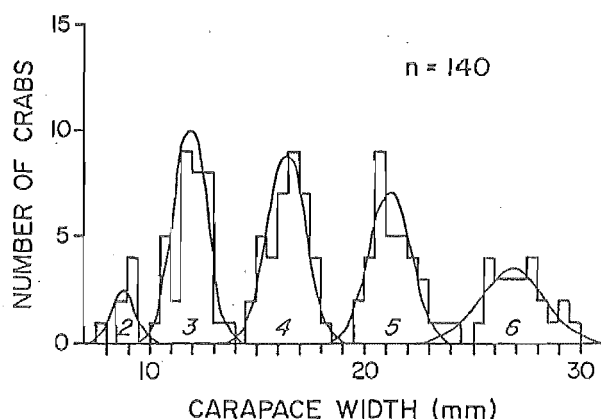


Fig. 3 *Ovalipes catharus*. Size-frequency and fitted instar distributions of juvenile crabs from Little Akaloa, 1984-1985.

Separate size-frequency distributions for male and female crabs larger than 30 mm CW showed clear modes representing instars 7 to 10 (Fig. 4). The magnitude of size increments between instars, estimated from a study of growth of captive crabs (Chapter 1), suggested that three more instars should be present after instar 10. Therefore, the set of seven normal curves that best described the observed size distributions of males and females were calculated using MacDonald and Pitcher's (1979) method of polymodal analysis. The calculated distributions for male and female crabs were not significantly different from the observed distributions ($P > 0.10$, Chi-square test).

The means and standard deviations calculated for each instar are given in Table 1. The parameters of the normal curves representing the last four instars were constrained when necessary as indicated in Table 1, to give results that were reasonable biologically as well as statistically. The conclusion from the above analysis is that individuals of *O. catharus* in Pegasus Bay attain maximum size in the 13th post-larval instar.

The average increase in size of crabs moulting from one instar to the

next is shown in Table 1. Moults increment as a percentage of body size declined as size increased and after instar 8, was smaller for females than males resulting in a smaller maximum size of females. These results are in accordance with previous observations on growth of captive *O. catharus* (Chapter 1).

Mean size of instars might be expected to vary from year to year and perhaps between the two sampling locations in response to different environmental conditions. However, if instar sizes varied appreciably, then modes would not be recognizable when size records from different years and locations were combined as in Figs. 3 and 4. The instar modes visible in the separate size frequency distributions for each year and locality (Fig. 5) vary slightly, but the expected distributions based on the

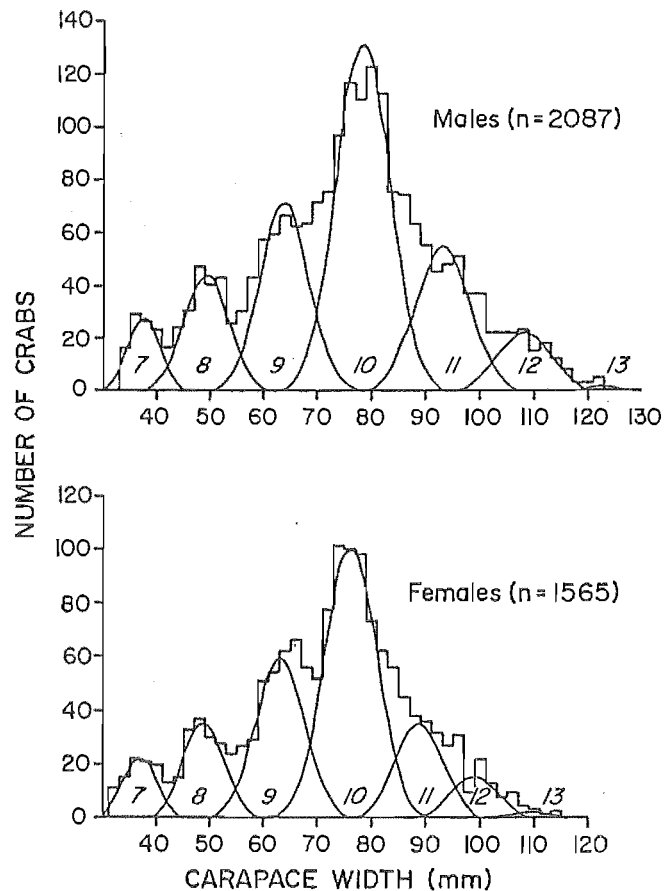


Fig. 4 *Ovalipes catharus*. Size-frequency and fitted instar distributions of male and female crabs from Brighton and Little Akaloa, 1984-1985.

Table 1. *Ovalipes catharus*. Instar parameters, size increment between instars and increment as percentage of premoult size for crabs from Little Akaloa and Brighton. Size and increment measurements in mm CW. Tests of significance were performed on differences between fitted and observed distributions (see Fig. 2). (*) means value was constrained.

	2	3	4	5	6	7	Instar 8	9	10	11	12	13
Juveniles \bar{x}	8.8	11.9	16.4	21.2	26.9							
S.D.	0.58	0.78	0.88	0.94	1.47							
increment	3.1	4.5	4.8	5.7	-							
% increment	35.2	37.8	29.3	26.9	-							
Goodness of fit	$\chi^2 = 27.907$, df = 30, P > 0.10											
Males \bar{x}						37.6	49.4	63.8	78.4	93.2	108.1	*122.0
S.D.						3.03	4.27	4.52	*5.0	*5.0	*5.0	*5.0
increment					10.7	11.8	14.4	14.6	14.8	14.9	13.9	-
% increment					39.8	31.4	29.1	22.9	18.9	16.0	12.9	-
Goodness of fit	$\chi^2 = 42.2377$, df = 35, P > 0.10											
Females \bar{x}						36.8	48.8	63.1	76.3	88.8	99.1	109.4
S.D.						3.27	3.90	4.56	4.83	*4.50	*4.50	4.55
increment					9.9	12.0	14.3	13.2	12.5	10.3	10.3	-
% increment					36.8	32.6	29.3	20.9	16.4	11.6	10.4	-
Goodness of fit	$\chi^2 = 21.2497$, df = 25, P > 0.10											

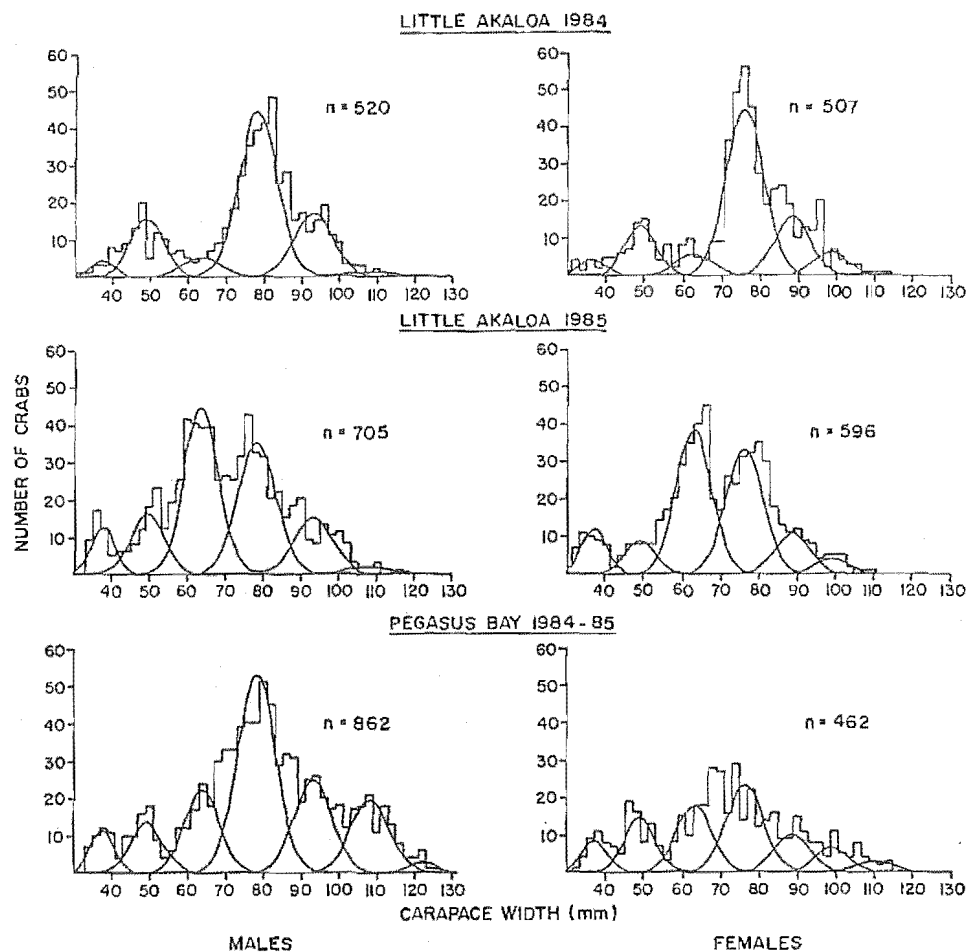


Fig. 5 *Ovalipes catharus*. Size-frequency and fitted instar distributions of male and female crabs separated into yearly periods for each location. Parameters for the fitted instar distributions are the same for the three cases and are given in Table 1.

instar parameters given in Table 1 gave an adequate description for most of the observed distributions. In four cases, no significant differences were found between observed and expected distributions (Table 2) and in the two cases where differences were significant, sample sizes were small. Therefore, differences in instar sizes from year to year and between localities were small and polymodal analysis of the combined data gave average estimates of instar mean sizes and moult increments of *O. catharus* in Pegasus Bay.

Tagging experiment and moult frequency

Results of the 170-day laboratory tagging experiment are shown in Table 3. Mortality among tagged crabs (22%) was not significantly different from untagged crab mortality (11%; $P > 0.05$; Chi-square test). During the experiment, all surviving crabs moulted at least once, with two of 14 tagged crabs losing their tags while moulting. Two untagged crabs but no tagged crabs moulted twice which suggests that tagged crabs may have a lower moult frequency than untagged crabs. However, the mean

Table 2. *Ovalipes catharus*. Tests of significance performed on differences between fitted and observed size frequency distributions (see Fig. 3). (*) indicates significant difference.

	χ^2	Males df	P	χ^2	Females df	P
Little Akaloa 1985	49.9	36	>0.05	32.1	34	>0.10
Little Akaloa 1984	33.0	35	>0.10	64.2	35	$* < 0.01$
Pegasus Bay	46.3	40	>0.10	59.4	35	$* < 0.01$

Table 3. *Ovalipes catharus*. Data obtained from tagged and control crabs used in laboratory tagging experiment.

	Died during intermoult (% mortality)	No. of crabs moulting at least once (% retaining tag)	No. of crabs moulting twice	Mean CW (S.D.)	Mean no. days to first moult (S.D.)	Mean size increment at moult (S.D.)
Tagged (N = 18)	4 (22%)	14 (86%)	0	67.7 (5.2)	76.9 (29.3)	13.4 (2.01)
Untagged (N = 18)	2 (11%)	16	2	68.7 (4.5)	70.1 (40.8)	13.9 (2.19)

number of days between the initiation of the experiment and the first moult of tagged crabs (76.9 days) was not significantly different from that for untagged crabs (70.1 days; $P>0.05$; t-test). The mean increase in size during a moult did not differ significantly between tagged crabs (13.4 mm) and untagged crabs (13.9 mm; $P>0.05$; t-test).

Since the data indicated that neither growth nor mortality of *O. catharus* were affected significantly by tagging, a field experiment was conducted using the same procedure. In 1984, 2657 crabs were tagged and released at Little Akaloa. At intervals between February 1984 and December 1985, 343 tagged crabs were recaptured. Of these only 14 had moulted between the times of release and recapture. Fig. 6 shows the time elapsed between initial release and recapture of both male and

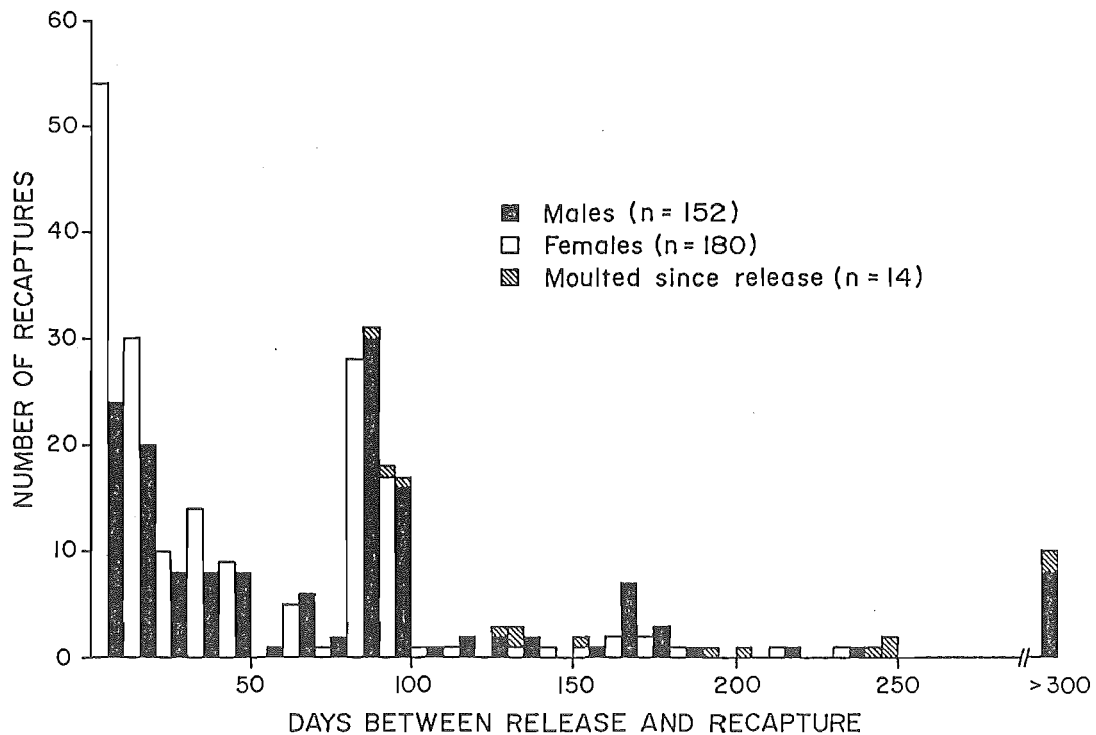


Fig. 6 *Ovalipes catharus*. Number of days elapsed since release of male and female tagged crabs recaptured at Little Akaloa.

female tagged crabs. Most recaptures of both sexes were made shortly after release but some large male crabs were free for over a year before recapture and had still not moulted. The average duration of the intermoult period for tagged crabs must have been greater than 100 days because most of the recaptures were made within 100 days of initial release and only 1% of them had moulted. The fact that far fewer recaptures were made after 100 days may indicate that crabs began moulting after this interval. During the moulting process, crabs are not caught using baited traps because they cease feeding and after moulting most crabs migrate out of Little Akaloa Bay (Chapter 4). Therefore, there is little opportunity to catch crabs after they moult. Of those that were caught more than 100 days after being released, 15% had moulted, and of those that were caught more than 200 days after release, 43% had moulted.

Another way to estimate the frequency of moulting is to examine changes in population size structure with time. Figs. 7 and 8 show the size-frequency of male and female crabs in the population every second month for one year. Samples that were taken within a few days of each other from Little Akaloa and Brighton were combined so that the entire size range of crabs was represented. The previously fitted instar distributions whose parameters are given in Table 1 have been superimposed on the monthly size-frequency histograms to show changes in instar frequency with time. It was assumed that changes in instar frequency could be attributed to growth of a cohort, an assumption that was supported by growth records from the few tagged crabs which had moulted before being recaptured.

Figs. 7 and 8 illustrate that January to March was the main period of recruitment in 1985, and that in 1984, March was probably the only significant recruitment month. Crabs entering the population in January

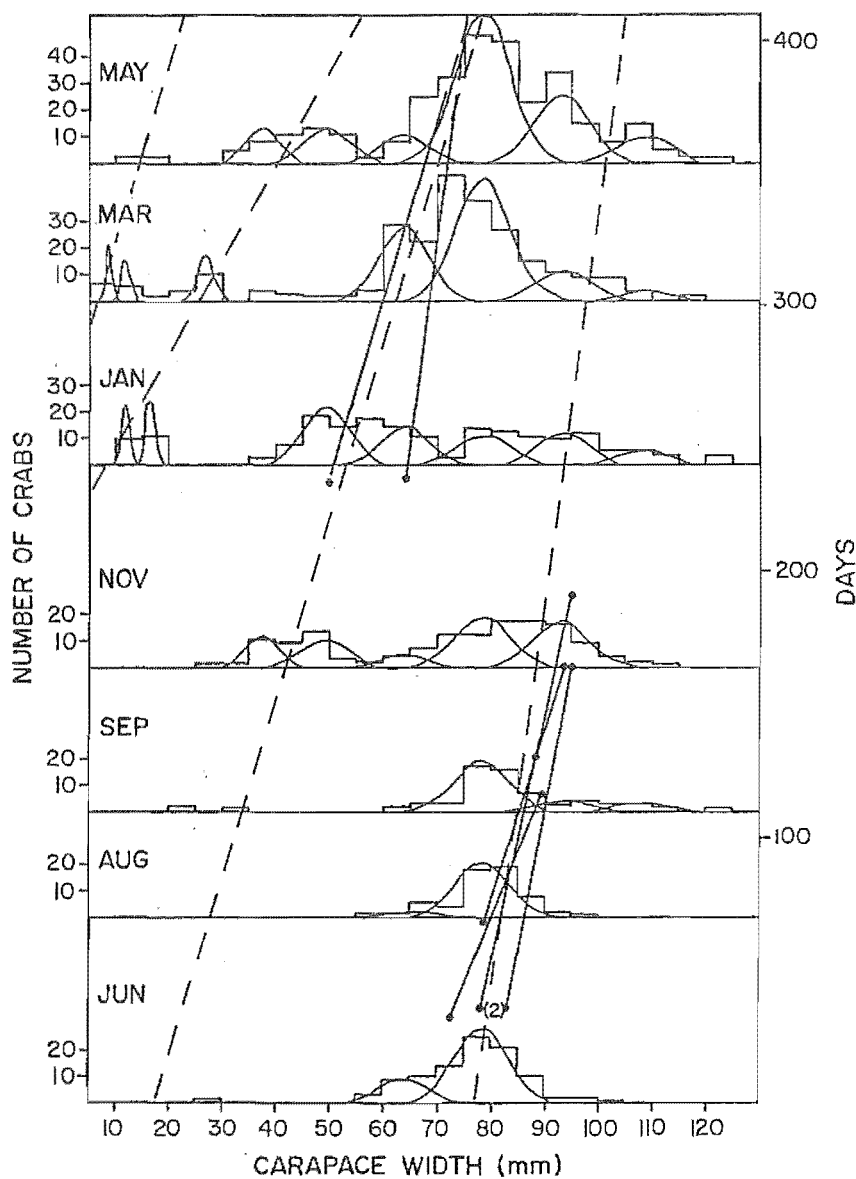


Fig. 7 *Ovalipes catharus*. Bi-monthly size-frequency distributions and fitted instar distributions of male crabs from Brighton and Little Akaloa, June 1984 to May 1985. Parameters of instar distributions are given in Table 1. (—•—) represents time of release and recapture of individual tagged crabs which had moulted and increased in size before recapture. (---) represents approximate instar movement attributed to growth.

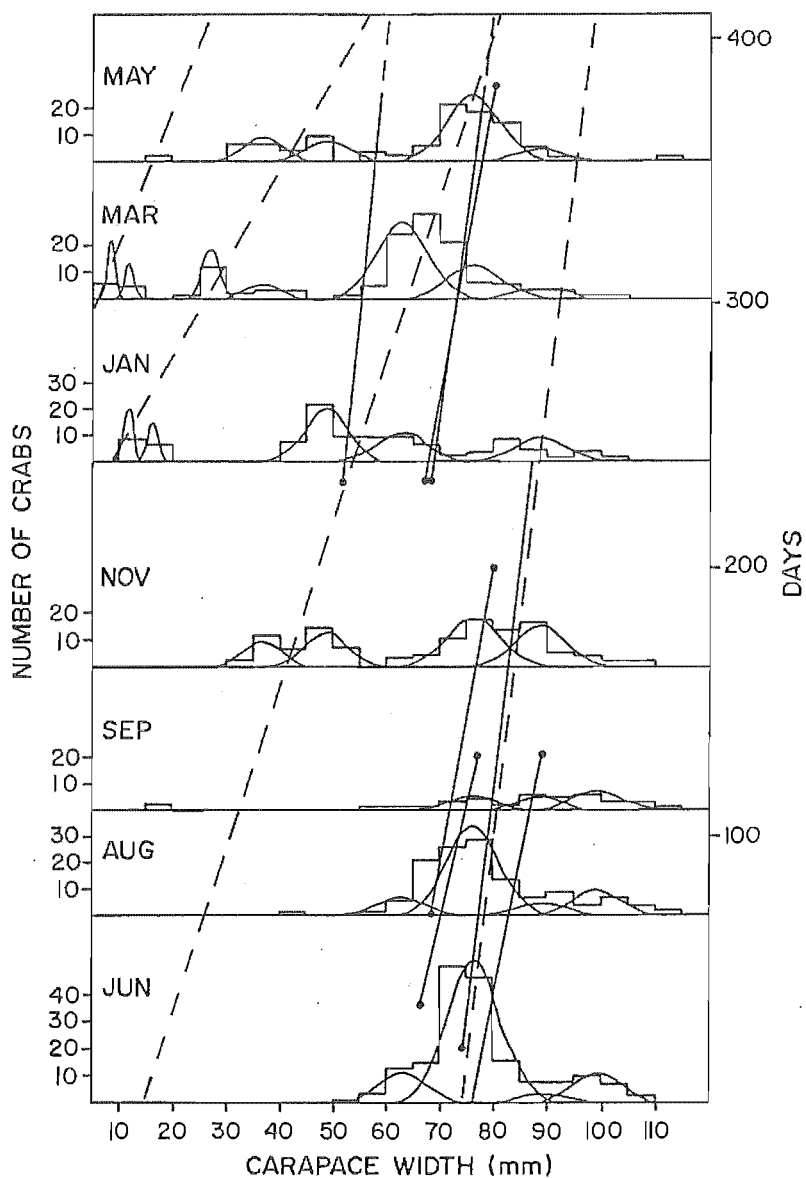


Fig. 8 *Ovalipes catharus*. Bi-monthly size-frequency distributions and fitted instar distributions of female crabs from Brighton and Little Akaloa, June 1984 to May 1985. See legend of Fig. 7 for more details.

1985 grew rapidly during the warmer months and reached instars 7 or 8 by May. Those recruited in March of both years, grew more slowly over the winter and reached instars 7 or 8 by November and instar 10 by the following May. Crabs that were in instar 10 by the beginning of winter 1984 had moulted to instar 11 by January 1985. This indicates an intermoult duration of about 200 days for instar 10, a figure that is in agreement with conclusions drawn from recapture data of tagged crabs (Fig. 6). Moulting to subsequent instars was presumed to occur once during each mating season (Chapter 4).

An average growth curve for *O. catharus* in Pegasus Bay (Fig. 9) was constructed using the calculated instar sizes and durations from the preceding analysis of size-frequency distributions and was supported by returns of tagged crabs. Both summer and autumn recruits reached instar 10 by the end of their first year although growth of summer recruits was slightly faster. The moult to instar 11 occurred in 1+ crabs and if annual moulting continued, the maximum size (instar 13) would be obtained by 3+ crabs.

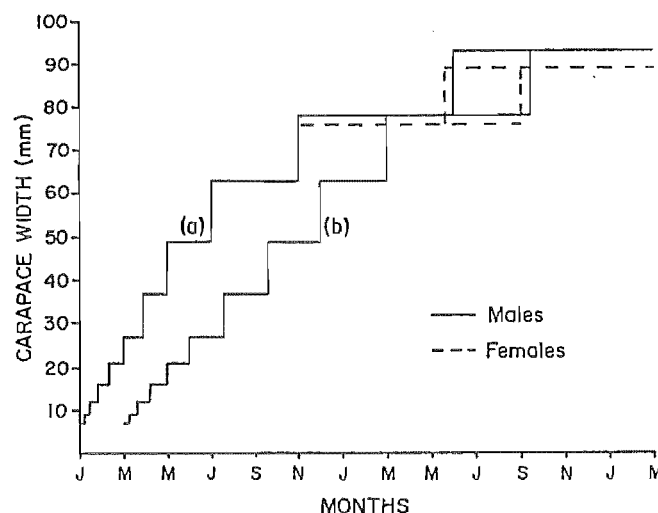


Fig. 9 *Ovalipes catharus*. A generalized scheme of growth for the first 11 instars of male and female crabs in Pegasus Bay. (a) January recruits, (b) March recruits.

DISCUSSION

Estimates of growth rates derived from polymodal analysis of size-frequency distributions often need supporting evidence to ensure that they are biologically reasonable and not just an artifact of the sampling program. The few records of growth of tagged crabs obtained, supported the interpretation of size frequency distributions for *O. catharus* with respect to moulting frequency and size increment during the moult. However, the long term tag returns were not adequate to provide significant information on growth due to the migratory nature of *O. catharus* (Chapter 4) and the lack of a commercial crab fishery in Pegasus Bay to enhance the rate of returns.

An earlier study of growth of *O. catharus* in the laboratory also provided supporting evidence (Chapter 1). Growth rates of *O. catharus* calculated from field and laboratory data were very similar (Fig. 10). Several workers have reported reductions in the growth of laboratory-kept crustaceans compared with natural populations (Hiatt, 1948; Klein Breteler, 1975b; Childress and Price, 1978) whereas others found that laboratory conditions had no apparent affect on growth (Edwards, 1965; Siegel and Wenner, 1985) or even enhanced it (Chittleborough, 1976; Smale, 1978). Clearly the effect varies and will depend on the conditions of maintenance and the suitability of the species for life in captivity.

A prediction from a population model of *O. catharus* based on growth of individuals in captivity (Chapter 1) was that all 13 instars would be discernible in the size-frequency distribution of a natural population. The present study was a test of that prediction and confirmed the notion that size variation within instars of *O. catharus* is relatively small. Several authors have used size-frequency analysis to obtain approximate information on the frequency of moulting of large decapod crustaceans

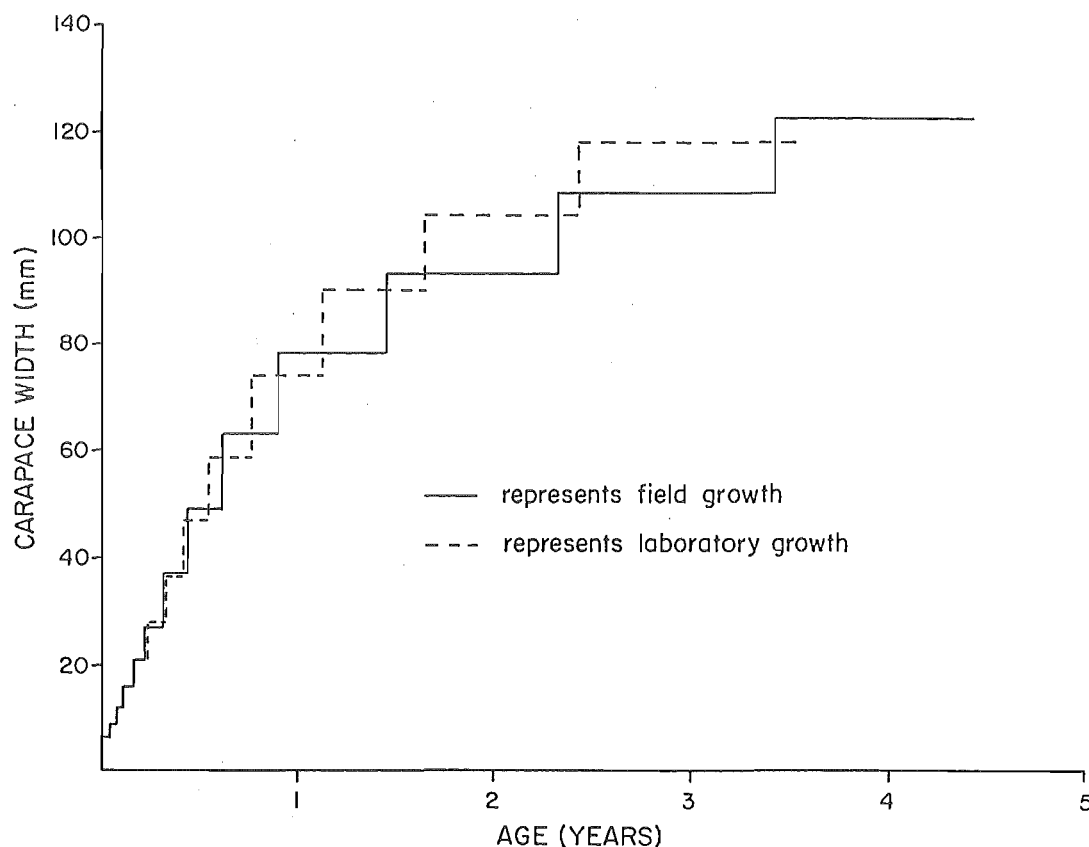


Fig. 10 *Ovalipes catharus*. Comparison of average growth curves for male crabs based on field and laboratory studies.

(Butler, 1961; Poole, 1967; Hill, 1975; Krouse, 1976; Donaldson et al., 1981) but it is not very common for separate instars to be discernible. Hartnoll (1982) considered that only the first few juvenile instars of decapods are generally recognizable by size-frequency analysis. Similarly, Klein Breteler (1975a) found that the first five post-larval instars of *Carcinus maenas* were easy to distinguish whereas larger instars were difficult to identify partly because of small sample sizes in their study. MacKay and Weymouth (1935) identified six post-larval instars of *Cancer magister* under 30 mm CW but did not present data for larger crabs. Butler (1961) collected large numbers of very small *C. magister* and identified three post-larval instars easily. However, when size-frequency data for larger

crabs were presented no analysis of modes was attempted even though many modes were apparent. Donaldson et al. (1981) identified seven post-larval instars of *Chionoecetes bairdi* between 10 and 60 mm CW but did not present size-frequency data for larger crabs.

In only a few studies have larger instars of decapod Crustacea been identified using size-frequency analysis. Bachus (1960) tentatively identified seven instars in lobsters (*Panulirus interruptus*) between 80 and 130 mm carapace length. Poole (1967) identified 13 instars in *Cancer magister* up to 180 mm CW from size-frequency distributions and provided good supporting evidence that the distance between modes was reasonably close to the average size increment at moulting of tagged and captive crabs. In both these studies, modes in size-frequency distributions were distinguished by eye and statistical methods of separation were not used. Sasaki and Kawasaki (1980) used Harding's (1949) probability method of polymodal analysis to distinguish between instars of *Ovalipes punctatus*. They identified six instars in crabs larger than 45 mm CW but their instar separations would have been stronger if supporting evidence on average moult increments had been available.

Part of the reason why instars were easily discernible in the present study of *O. catharus* was because size variation within instars did not continue to increase with increasing size (Chapter 1) as in some other Brachyura (Klein Breteler, 1975b; Hartnoll, 1978) but instead decreased when sexual maturity was reached. Another factor contributing to the successful use of polymodal analysis in evaluating the size distributions of *O. catharus* was that there appeared to be little variation in mean instar sizes between years and locations. Childress and Price (1978) and Donaldson et al. (1981) also found similarities in the mean sizes of crustacean instars between years whereas other authors observed differences in size of individuals within instars between years (Poole,

1967; Bennett, 1974) and seasons (Kurata, 1962; Klein Breteler, 1975a).

These contrasting results could be due to the way in which environmental factors affect each of the growth components (moult increment and intermoult duration) in different species. Factors such as food availability and temperature may affect both components (reviewed in Hartnoll, 1982) but in some species one component may be more sensitive to change. Presumably, species which have relatively constant instar sizes through time also have moult increments that are relatively insensitive to environmental influences (see Chapter 5).

Compared with large portunid species from warm temperate or tropical regions, *O. catharus* is relatively long-lived and slow growing. Maximum size (approx 130 mm CW or 500g) is reached in 4 years whereas *Callinectes sapidus* reaches maximum size in 2 years (240 mm CW, 700g; Van Engel, 1958; Tagatz, 1968), *Portunus pelagicus* grows to 200 mm CW (approx 800g) in 2-3 years (Potter et al., 1983) and *Squilla serrata* reaches 180 mm CW in 3 years (Hill, 1975). Compared to other species of *Ovalipes*, however, *O. catharus* is relatively large and fast growing. Thus, maximum size of *O. trimaculatus* in Argentina (38°S) is 110 mm CW (Fenucci and Boschi, 1975), *O. stephensoni* attains a CW of 90 mm on the east coast of North America (29-34°N) (Haefner, 1985), and in South Africa (34°S), *O. punctatus* reaches only 70 mm CW in about 3 years (Du Preez and McLachlan, 1984). *O. catharus* had a larger maximum size but similar growth rate to that reported for *O. punctatus* in Japan (growth to 100-110 mm CW (300 g) in 2-3 years; Sasaki and Kawasaki, 1980) which was however, at a lower latitude (38°N) and region of warmer water temperature (autumn sea temperature 16-20°C compared with 12-16°C in Pegasus Bay).

In summary, *O. catharus* moults at least 13 times and reaches a maximum size of 130 mm CW in 4 years after settlement of megalopae.

Growth rate was estimated satisfactorily by size-frequency analysis because of the low size variability within instars and because seasonal recruitment meant that cohorts could be distinguished easily and their growth followed through time.

CHAPTER 3

CHAPTER 3

Size at maturity and annual fecundity of female Ovalipes catharus (Decapoda, Portunidae) in Pegasus Bay, New Zealand.

INTRODUCTION

The paddle crab *Ovalipes catharus* supports a developing fishery in New Zealand which as yet is not subject to any management restrictions. Size at maturity and fecundity are important parameters in determining reproductive potential and for managing a crab fishery, but to date little information exists on these aspects of the biology of *O. catharus*. Wear (1982) and Armstrong (1986) have published brief reports on the general biology of *O. catharus* including some aspects of their reproductive biology. Like other portunid crabs, *O. catharus* females mate only after moulting when in a soft-shelled condition. Spermatozoa are stored by the female in paired spermathecae and this makes multiple spawning possible within a single intermoult period. In Brachyura it is likely that all ripe ova are discharged at spawning and that the ovary has to mature again before a further batch of eggs can be laid (Hartnoll, 1985). The fertilized eggs are attached to pleopods on the ventral surface of the abdomen and incubated until they hatch. Annual post-puberty moulting enables females to mate each year prior to the spawning season and to replenish their supply of sperm.

Although egg-bearing by female crabs is an obvious indication of sexual maturity, a previous study indicated that ovigerous females were difficult to locate with the sampling techniques available (Chapter 4). In

the present study, sexual maturity in non-ovigerous females from a population of crabs in Pegasus Bay, New Zealand was estimated by internal examination of the gonads, detecting physical signs of copulation, and measurement of external, secondary sexual characteristics. Two previous estimates of size at maturity have been made for female *O. catharus* from Pegasus Bay. One was based on changes in the pattern of growth in the size range 50-60 mm CW (Chapter 1) and the other was based on a change in allometry of the female abdomen at about 30 mm CW (Davidson and Marsden, 1987). Results obtained in these two studies obviously disagree and one of the aims of the present study was to resolve this problem. Annual fecundity in females is determined by the number of eggs produced per brood and the number of broods produced per year, and both factors are probably size dependent (Hartnoll, 1985; Lipcius, 1985). Information on numbers of eggs per brood, egg development time, length of reproductive season, and potential number of broods produced from a single mating were obtained by combining field and laboratory observations.

METHODS

Mean Size at Maturity

Crabs were collected from two locations in Pegasus Bay, New Zealand. Between March and December 1985, 327 non-ovigerous female *O. catharus* >40 mm CW were collected from Little Akaloa during monthly sampling trips as described in Chapter 2. An additional 25 non-ovigerous females >40 mm CW were collected between December 1985 and February 1986 from gill nets set off Brighton Beach at a depth of 5-10 m.

Samples taken from both localities between January 1984 and February 1986 yielded 42 ovigerous females. All crabs were either frozen within six hours of capture or preserved immediately in 10% seawater formalin for later dissection and measurement. Frozen crabs were thawed and preserved in formalin for 24-48 hours before dissection.

Crabs were dissected to examine gonads and contents of the spermathecae. Gonad stages were distinguished using a modified version of the scheme described by Campbell and Eagles (1983). Because very few *O. catharus* were found with stage 4 ovaries (as defined by Campbell and Eagles), the last two stages (4 and 5) were combined (Table 1). Female *O. catharus* were considered to be sexually mature when ovaries had developed to at least stage 3 since all ovigerous females had stage 3 ovaries. The proportion of sexually mature crabs was calculated by dividing the number of crabs with mature gonads (stages 4 and 4) by the total number of crabs examined in each 1 mm CW size class. The relationship between proportion of crabs with mature gonads (Y) and CW (X) in millimeters for female *O. catharus* was approximated by the logistic function:

$$Y = \frac{a + c}{1 + e^{-b(X-m)}}$$

Spermathecae and vulvae of 394 female *O. catharus* were examined for evidence of copulation. Unmated crabs typically had small slit-like closed vulvae and spermathecae were thin and translucent. Mated crabs had vulvae that were to some degree open and enlarged, and spermathecae that were clearly visible, even when empty. If a crab could not be classified definitely on the grounds of vulva and spermatheca size as having mated or not, the spermatheca was removed and examined microscopically for presence of sperm. The proportion of mated crabs

Table 1. *Ovalipes catharus*. Stages in ovary development.

Stage	Description	Gonad Index		
		n	\bar{x}	Range
1. Undeveloped	Ovaries very thin and translucent	-	-	-
2. Developing	Visible but thin; white-pink	93	0.22	0.02-0.43
3. Mature	Ovaries one third volume of hepatopancreas, lobed; red	120	0.47	0.13-1.06
4. Ripe	Ovaries at least size of hepatopancreas; bright orange	79	6.75	1.12-12.01

was calculated for each 1 mm CW size class and the relationship between proportion mated and CW was estimated by the logistic function as described above.

Sexual maturity was also assessed by measuring abdomen width (maximum width of the 4th abdominal segment) and abdomen length (total length of six abdominal segments plus telson) to the nearest 0.1 mm of 146 unmated (16.0-72.0 mm CW) and 128 mated (53.0-106.0 mm CW) female *O. catharus*. An index of abdominal shape was calculated by dividing abdomen width by abdomen length. The relationship between the abdominal shape index and CW for both mated and unmated crabs was approximated by linear regression. Analysis of covariance was used to compare the slopes and intercepts of the two regression equations.

Determination of Breeding Season

Of all the female crabs caught between March 1985 and February 1986, including those carrying eggs externally, 199 had gonads at developmental stages 3 or 4. These physiologically mature crabs were examined for fullness of the spermathecae and gonad tissue was removed

and weighed for calculation of gonad indices. A full spermatheca was taken to be evidence that moulting and mating of female crabs had occurred since the previous spawning season. The proportion of mature crabs with full spermathecae was calculated for each monthly collection.

Gonad index is a measure of size of gonad tissue in relation to crab size. To calculate gonad index, whole preserved gonads were dissected from each crab, blotted dry and weighed to the nearest gram. Gonad weight was divided by the estimated wet weight of the female crab (W) (predicted from the equation: $\log_{10}W = -3.32 + 2.79\log_{10}CW$; Davidson & Marsden, 1987) and multiplied by 100. Gonad indices were calculated each month for all female crabs with stage 3 and 4 gonads.

Estimation of Annual Fecundity

To estimate numbers of eggs per brood subsamples of 200 eggs were taken from 42 ovigerous females, dried for 24 hours at 60°C and weighed on a CAHN 21 electronic microbalance to the nearest 0.01 mg. The remainder of each egg mass was then scraped from the pleopods, dried to

Table 2. *Ovalipes catharus*. Stages in egg development between spawning and hatching.

Stage	Description	Weight of 200 eggs (mg)		
		n	\bar{x}	Range
1.	Bright orange, no eyespot	11	1.86	1.53-2.27
2.	Dull orange, eye spot and embryo visible	7	1.69	1.55-2.01
3.	Brown, eye spot well formed, yolk half gone	6	1.58	1.00-1.88
4.	Dark brown, nearly all yolk gone	18	1.56	1.15-1.86

constant weight at 60°C and weighed on a Mettler balance to the nearest 0.1 mg. The total number of eggs per brood was calculated by dividing the total weight of the brood by the weight of the subsample and multiplying by 200. Stage of development of eggs in each brood was assessed using the scale shown in Table 2. The relationship between number of eggs per brood (Y) and CW (X) was approximated by the power function $Y = aX^b$. To compare slopes and intercepts of the regression equations, analyses of covariance were performed with the statistical package BMDP.

To estimate the incubation period of a brood of eggs and the number of broods produced per year, adult female *O. catharus* were kept in aquaria at the Edward Percival Field Station under conditions described in Chapter 1. From August 1984 to May 1985, 26 captive female crabs produced egg broods. Of these, 17 were captive for the whole period (one entire reproductive season). From November to February, captive female crabs were examined 2-3 times weekly so that dates of spawning and hatching could be recorded and these were used to calculate the mean incubation period and the mean interval between broods.

RESULTS

Mean Size at Maturity

The size-frequency distributions of female *O. catharus* with ovaries in each of the four stages of development are shown in Fig. 1. A clear relationship was found between stage of ovarian development and female size with 91% of crabs <70 mm CW having immature ovaries (stages 1 and 2) and 88% of crabs >70 mm CW having mature ovaries (stages 3 and

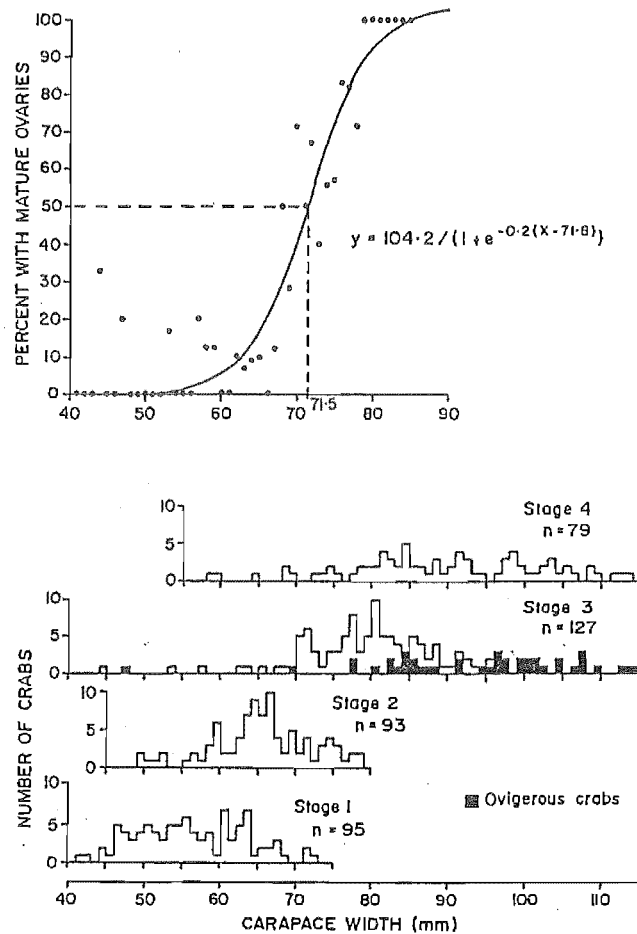


Fig. 1. *Ovalipes catharus*. Size distributions of females with ovaries in each of four stages of development and percent with mature (Stage 3 or 4) ovaries in each 1 mm size class.

4). The smallest female with mature ovaries was 44.7 mm CW and the largest female with immature ovaries was 78.9 mm CW. The relationship between the proportion of crabs with mature gonads and CW was approximated by a logistic curve. The CW at which 50% of females were mature was estimated to be 71.5 mm. The presence of external eggs on females is an obvious indicator of maturity and all ovigerous females had mature ovaries (stage 3; Fig. 1). The smallest ovigerous female caught was 47.8 mm CW although most were >75 mm CW which generally agrees with predictions from the maturity curve based on gonad development.

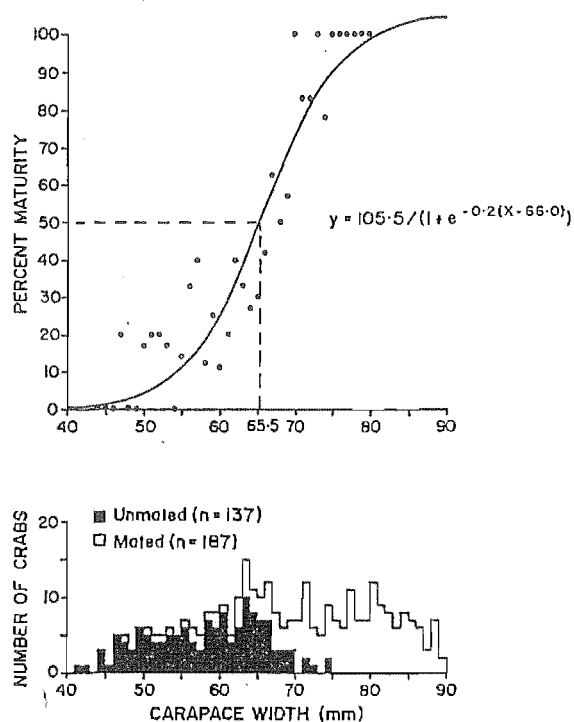


Fig. 2. *Ovalipes catharus*. Size distribution of mated and unmated females and percent mature in each 1 mm size class.

Size at 50% maturity for female *O. catharus*, estimated from the relationship between proportion of crabs mated and CW shown in Fig. 2 was 65.5 mm CW. Mating had occurred in 97% of females >70 mm CW whereas 74% of females <70 mm CW had not mated. The smallest female to show physical signs of copulation (an ovigerous individual) was 47.8 mm CW and the largest female showing no evidence of copulation was 74.3 mm CW.

Abdomen width:abdomen length ratio was calculated for most female crabs collected for gonadal inspection and for a few smaller crabs (Fig. 3). A significant difference was found between the linear regressions describing abdomen shape of mated and unmated crabs ($P < 0.001$; ANCOVA). This indicates that broadening of the abdomen is a female

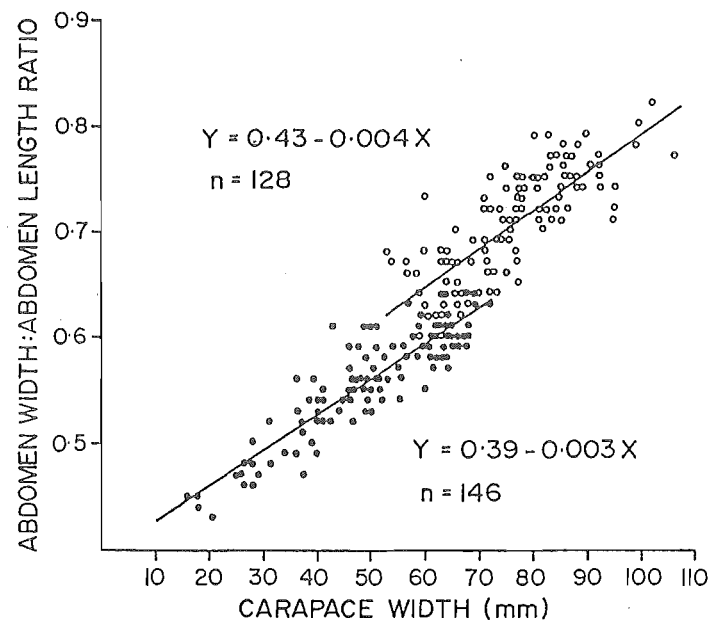


Fig. 3. *Ovalipes catharus*. Relationship of abdomen width : abdomen length ratio to carapace width for mated (open circles) and unmated (closed circles) females.

secondary sexual characteristic. On the basis of abdomen shape, the moult to maturity would be predicted to occur in the 50-70 mm CW size range which is similar to the size range over which mating first occurs (Fig. 2)

Breeding Season

At Little Akaloa during 1985, female moulting and mating occurred during winter and spring (Fig. 4). Females with full spermathecae first appeared in May and increased to a peak in November. Mating activity was followed by a period of gonad maturation from October to February (Fig. 5). After mating, sperm is stored while the ovaries ripen and subsequently spawning and fertilization occur. The main spawning and egg-bearing season in 1985-86 was probably November to March (Figs. 4

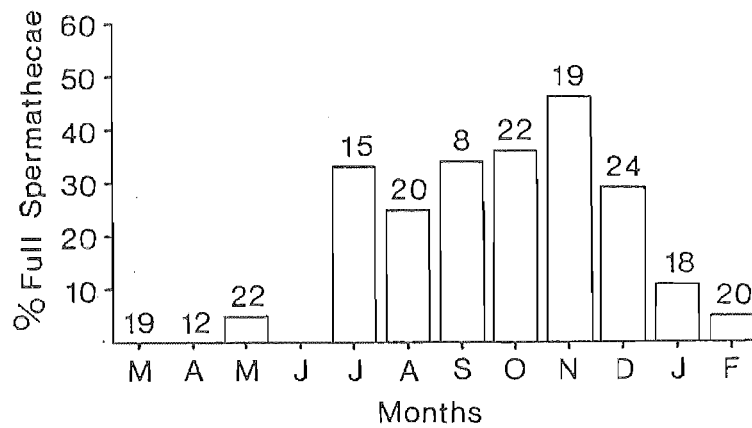


Fig. 4. *Ovalipes catharus*. Percentage of mature females with full spermathecae from Little Akaloa (March to December 1985) and Brighton (December to February 1986). Sample sizes given above each column.

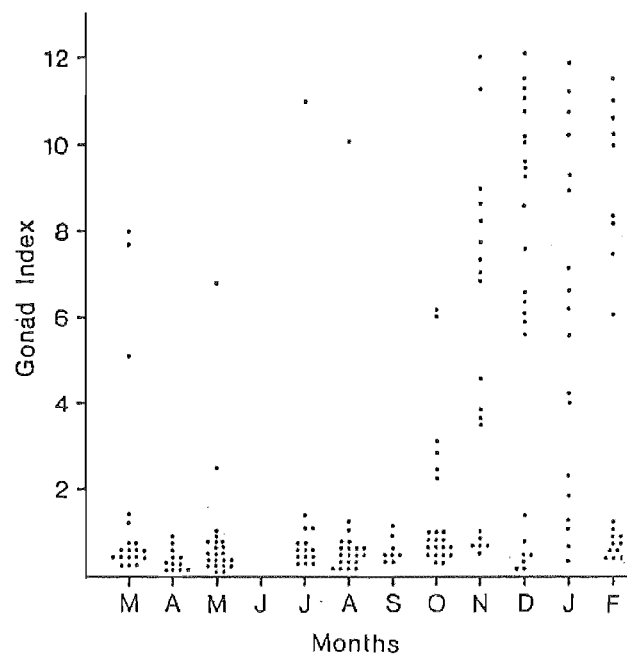


Fig. 5. *Ovalipes catharus*. Gonad indices for individual females caught from Little Akaloa (March to December 1985) and Brighton (December to February 1986).

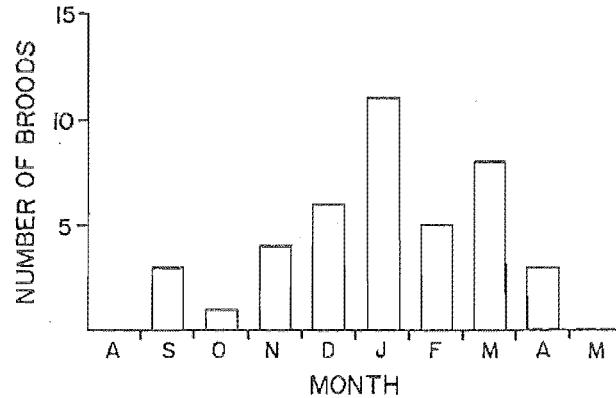


Fig. 6. *Ovalipes catharus*. Number of egg broods produced in the laboratory each month by a total of 26 females.

and 5). Under laboratory conditions, *O. catharus* produced broods between September 1984 and April 1985 (Fig. 6) although the majority of broods (74%) were found from November to March.

The sequence and timing of reproductive events in Pegasus Bay are summarized in Fig. 7. Mating is only possible when adult females are soft-shelled and this was most common at Little Akaloa from May to November. However, in the laboratory some females moulted much sooner after egg hatching (February to April). Gonad maturation occurs after

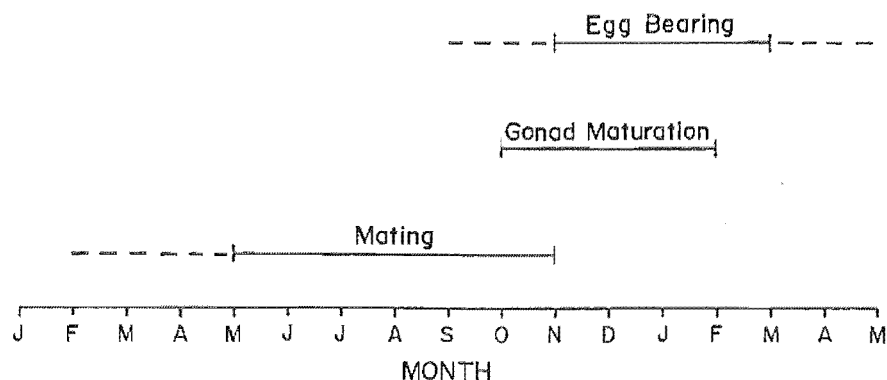


Fig. 7. *Ovalipes catharus*. Summary of seasonal reproductive events for females from Pegasus Bay. Solid lines are based on field data; dashed lines on laboratory observations.

mating and is followed closely by spawning and fertilization. In the laboratory, the interval between mating and spawning ranged from 38 to 299 days ($n=9$, $\bar{x}=136$ days). Considerable overlap occurred between the periods of gonad maturation and egg-bearing and implies that spawning was not synchronized and that females may spawn more than once in a season. The egg-bearing season for the population as a whole was at least five months long, but for individual crabs it may vary considerably depending upon the date that moulting and mating occurs.

Annual Fecundity

The relationship between brood size and CW was described best by a power curve ($r=0.65$, Fig. 8). No significant differences ($P>0.05$; ANCOVA) were found in the number of eggs per brood between early development eggs (stage 1 and 2, Table 2) and late development eggs

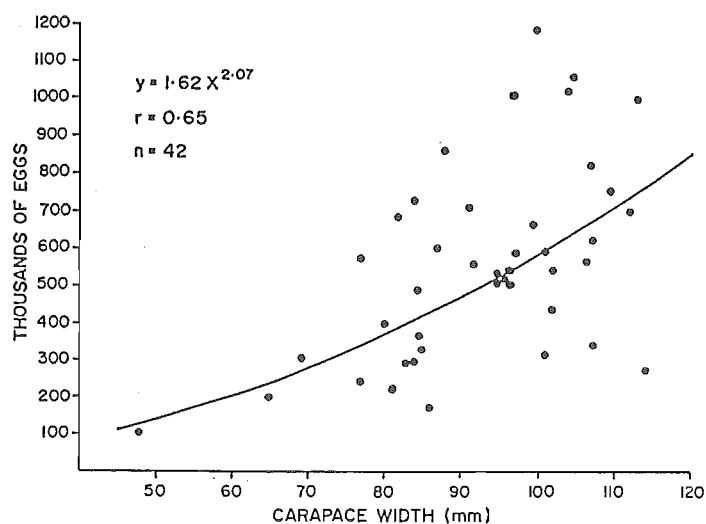


Fig. 8. *Ovalipes catharus*. Relationship between total number of eggs carried externally and carapace width of ovigerous crabs from Brighton and Little Akaloa.

(stage 3 and 4), or between crabs collected during 1984-85 (n=7) and 1985-86 seasons (n=35); thus the data for all ovigerous crabs have been combined in Fig. 8.

Mean development time for eggs (spawning to hatching) and mean interval between broods are given in Table 3 and show that it is possible for females to spawn at 50-day intervals. As at least five months of the year are available for egg production (Fig. 7), each female potentially has time to produce 3 broods annually depending on how long the supply of stored sperm lasts. Fig. 9 shows the number of broods produced by 17 females that were kept in the laboratory throughout one entire reproductive season. Larger females tended to spawn more often than smaller ones. Thus, on average 2.2 broods were produced per season by females >80 mm CW (n=12, s=0.9) compared with 1.2 broods for females <80 mm CW (n=5, s=0.4).

Table 3. Ovalipes catharus. Incubation period and interval between broods of ovigerous females kept in the laboratory.

	Incubation period	Interval between broods
Sample size	25	14
Mean (days)	30.9	18.0
Range	20-52	11-30

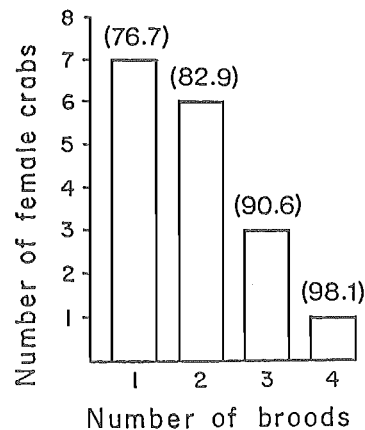


Fig. 9. *Ovalipes catharus*. Number of broods of eggs produced in the laboratory by individual crabs ($n=17$) during one reproductive season (September 1984 to April 1985). Mating and moulting did not occur between broods, all eggs were fertilized from a single insemination. Mean CW of females with stated spawning frequency given in brackets.

DISCUSSION

Sexual Maturity

Sexual maturity in female *O. catharus* was estimated on the basis of three characteristic changes in the morphology and anatomy of the crabs; (1) stage of gonad maturation, (2) physical evidence of copulation and (3) abdomen shape. If sexual maturity is defined as the stage at which females can produce eggs, then the presence of mature gonads is the appropriate criterion to use. The size at which 50% of females had mature gonads (71.5 mm CW) was larger than the size at which 50% of females showed signs of copulation (65.5 mm CW). All crabs >80 mm CW had both mature gonads and signs of copulation, whereas only 56% of the mated crabs <80 mm CW had mature ovaries. This accounts for the

difference in the two estimates of mean size at maturity and can be explained by the fact that females store sperm after mating and therefore gonad maturation can take place after copulation. However, this must occur within the same intermoult period because the stored sperm is not retained through a moult (see Chapter 7). If all the females which mate, attain mature gonads and spawn within the same intermoult period (which seems likely although it was not the case in *Cancer pagurus*; Edwards, 1978), then physical evidence of copulation is a better indicator of sexual maturity than gonad maturation.

The relative growth of secondary sexual characteristics commonly is used to estimate sexual maturity in Brachyura (Hartnoll, 1982). In female *O. catharus*, a change in abdomen shape accompanies sexual maturity as it does in many other Brachyura. Broadening of the abdomen increases space available for fixation of eggs to the pleopods and provides an incubation chamber. The size range over which changes in abdomen shape take place (50-70 mm CW) corresponds closely to the size range within which it is known that sexual maturity is attained. However, for the size range within which mature and immature crabs overlap, abdomen shape alone is not a reliable indicator of maturity.

A previous estimate of sexual maturity in *O. catharus* based on growth phases (Chapter 1) showed that the adult phase of growth began in the size range 50-60 mm CW. This is in reasonable agreement with results of the present study and supports the claim that the last two growth phases identified in the earlier study were characteristic of subadult and adult growth. Thus, it seems that Davidson and Marsden's (1987) estimate of size at maturity for *O. catharus* in Pegasus Bay was probably in fact the size at which the subadult growth phase started (Chapter 1). This illustrates the danger of using relative growth of secondary sexual characteristics to estimate maturity, without some

supporting evidence of gonad maturation.

Given that sexual maturity is first attained by crabs of a wide range of sizes (47-74 mm CW), the question that arises is what determines when this transition will occur, if not size itself? Data obtained in a previous study (Chapter 2) indicated that all maturing crabs could have been approximately the same age because crabs settling out of the plankton in January grew faster than those settling in March and would, therefore, be a larger size at the same age. However, I can think of no logical reason why age alone should determine the transition to sexual maturity except if the time interval required for the accumulation of resources necessary for gonad development was constant for all individuals. This seems unlikely when individuals experience different environmental conditions and have different growth rates depending on the date of settlement.

Alternatively, it is possible that all maturing crabs could have been in the same instar and that the range of sizes at maturity simply reflects the extent of size variation within the instar. Certainly, a more plausible explanation could be offered for crab development being closely linked with the moulting sequence given that moulting itself probably relies on the accumulation of energy resources. However, the size range over which maturity was attained seems to be slightly wider than that found for crabs in the 9th instar (Chapter 2) and it is more likely that these crabs belonged to instars 8, 9 and possibly also 10.

Most female *O. catharus* attain maturity in the same year as settling into the benthic population. Therefore, I suggest that the most likely factors governing the transition to sexual maturity in individual *O. catharus* are initially, a minimum required size (approximately 47 mm CW) or instar (instar 8) and beyond that, an interaction between date of settlement, growth rate and the onset of the population's breeding season. Early recruits reach the minimum size required for maturity before the

onset of the breeding season and, therefore, may postpone the pubertal moult until a larger size is attained. In contrast, late recruits only reach the minimum size requirement after the beginning of the breeding season, therefore being smaller and younger at the time of the pubertal moult.

Annual Fecundity

Adult *O. catharus* ranging in size from 48-115 mm CW carried between 1.0×10^5 and 1.2×10^6 eggs in a single brood. This estimate is very similar to those for three other portunid crabs of similar size (*Ovalipes ocellatus*, *Ovalipes punctatus* and *Portunus pelagicus*, see Fig. 10), although *Callinectes sapidus* carried greater numbers of eggs per brood (Fig. 10). The larger complement of eggs carried by *C. sapidus*, may in part be accounted for by a difference in egg size (Hines, 1982). Mean egg volume of *C. sapidus* (0.008 mm^3) is much smaller than that of *O. catharus* (0.022 mm^3). However, the dry weight of a brood of eggs produced by *C. sapidus* ranges from about 15-17% of dry body weight (Hines, 1982) compared to 10-12% of body weight for *O. catharus* and *O. ocellatus* (Hines, 1982). The relatively greater biomass of the brood of *C. sapidus* is probably related to the fact that the other two species continue to moult and grow after maturity, whereas *C. sapidus* females reach maturity during their terminal moult and therefore, do not need to partition resources between growth and reproduction.

Within the Portunidae it is not uncommon for females to produce two or more broods annually. Therefore, an estimate of annual fecundity of *O. catharus* requires additional knowledge of the average number of broods produced per season. Unfortunately, there do not appear to be any morphological traits which can be used to determine how many broods a female has produced. Some authors have estimated the

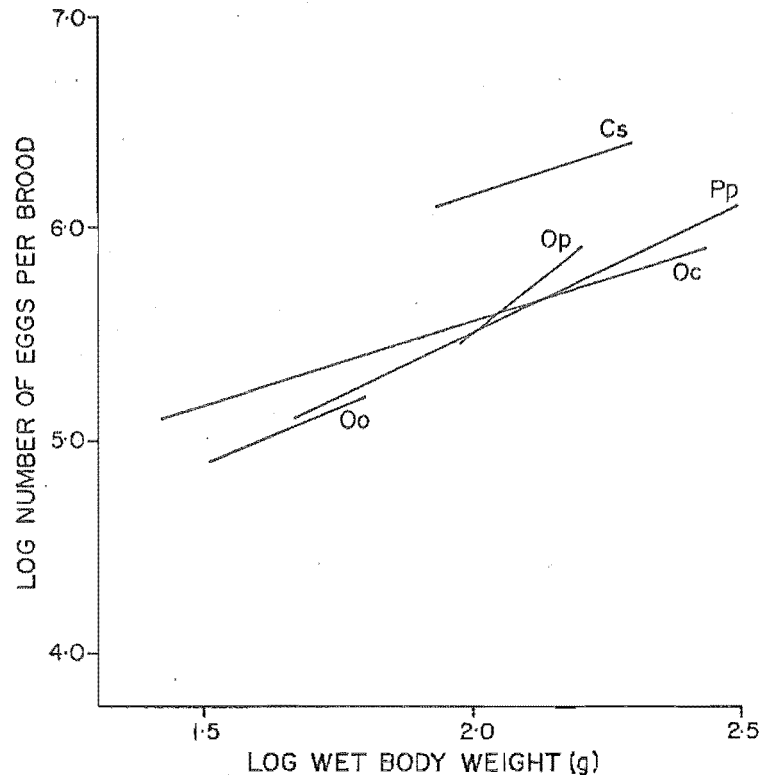


Fig. 10. *Ovalipes catharus*. Log number of eggs per brood versus log body weight for five species of portunid crabs. Regressions for individual species are indicated by initials corresponding to the following species and literature sources: *Callinectes sapidus* (Cs) (Hines, 1982; Olmi and Bishop, 1983), *Ovalipes catharus* (Oc), *Ovalipes ocellatus* (Oo) (Hines, 1982), *Ovalipes punctatus* (Op) (Kamei, 1976; Sasaki and Kawasaki, 1980), *Portunus pelagicus* (Pp) (Potter et al., 1983).

frequency of brood production based on studies of incubation times and numbers of broods produced by captive crabs (Ong, 1966; Ryan, 1967a; Morgan et al., 1983). Others have based their estimates on seasonal patterns of ovarian development, egg development, or extent of ovarian regeneration in ovigerous females from natural populations (Fielding and Haley, 1976; Rahaman, 1966; Pillay and Ono, 1978). However, female *O. catharus* do not show multiple peaks in gonad activity throughout the year. Furthermore, I was unable to detect any seasonal pattern in egg development and there was no evidence of gonad ripening in ovigerous

crabs (all ovigerous crabs had stage 3 gonads). The only suggestion that multiple spawning might occur in the field was provided by the length of the egg-bearing season of the population as a whole (5 months) and the observation that spawning of individual females was asynchronous during that period.

The number of broods produced by female *O. catharus* in captivity is unlikely to be a very reliable indicator of natural spawning frequency. However, it does indicate that the quantity of sperm stored by a female after mating is sufficient to fertilize two or more broods of eggs and that gonad ripening can take place within a short interval after hatching of eggs. If the gonads of captive ovigerous females were at developmental stage 3 like the gonads of all ovigerous females collected in the field, development to stage 4 (vitellogenesis) must have taken place within 2-3 weeks (the interval between broods). This result is in agreement with that of Ryan (1967a) who found that oocyte growth up to the stage of vitellogenesis took 2 weeks in female *Portunus sanguinolentus* and that vitellogenesis took a further 1-2 weeks.

The laboratory-based estimate of mean incubation period (30.9 days at about 13-17°C) agrees well with that for other portunids at similar temperatures (Wear, 1974). Therefore, information from the natural population on length of the egg-bearing season combined with laboratory estimates of potential number of broods produced, incubation period, and interval between broods suggests that *O. catharus* generally will spawn two or more times annually. Hines (1982) found an approximately isometric relationship between annual brood weight and body weight in 20 species of Brachyura with annual egg production being about 21.5% of body weight. This also suggests that *O. catharus* would produce 2 broods annually as a single brood weighs about 10-12% of body weight.

Previous workers have found that brood size was greater in crabs

carrying their first brood than in those carrying subsequent broods within an intermoult period (Ong, 1966; Fielding and Haley, 1976; Morgan et al., 1983). This relationship was not investigated in *O. catharus* but if true then it could help explain some of the considerable variation in brood size among crabs of a given size. I observed an approximately 4 fold range in numbers of eggs per brood for any given crab size, and other factors resulting in this could be the variable success of individuals in accumulating energy for a brood (Hines, 1982) and mating with males which produce different sized spermatophores (Haynes, 1968). Alternatively, the smaller size of any broods produced after the first brood in a season could be a consequence of reduced time available for energy accumulation (Morgan et al., 1983) or perhaps reduced viability, or quantity of stored sperm (Paul and Adams, 1984).

As mentioned earlier, *O. catharus* breeding for the first time may do so later in the reproductive season than larger females because of a need to grow early in the reproductive season. Earlier spawning of larger adult females has been observed also in subtidal stone crabs, *Menippe mercenaria* (Cheung, 1969), intertidal grapsids, *Sesarma cinereum* and *S. reticulatum* (Seiple, 1979), the xanthid, *Panopeus herbstii* (Lipcius, 1985) and the fiddler crab *Uca lactea perplexa*, which also displayed size dependent brooding (larger females producing more broods annually than smaller ones) (Nakasone and Okadome, 1981). Lipcius (1985) in his review of size dependent reproduction and moulting in long-lived decapods, noted that larger female palinurid and nephropid lobsters also demonstrated earlier spawning and that the larger females of *Panulirus* produced more annual broods than smaller females. The production of fewer broods by smaller females can be explained by both time constraints due to the shorter season (Lipcius, 1985) and resource constraints resulting from the energetic costs of growth (Hartnoll, 1985).

In summary, *O. catharus* females were found to reach maturity in the first reproductive season after hatching with the size at pubertal moult depending upon individual growth rate and timing of settlement. These 0+ year crabs would moult to maturity early in the reproductive season and produce probably only one brood. Larger 1+ and 2+ year crabs would breed earlier in the reproductive season and produce two or more broods annually. A female surviving to maximum size would probably experience 4 reproductive seasons (see Chapter 2) and produce 7-8 broods in a lifetime.

CHAPTER 4

CHAPTER 4

Seasonal distribution and movements of the paddle crab Ovalipes catharus in Pegasus Bay, New Zealand.

INTRODUCTION

The paddle crab, *Ovalipes catharus* (White, 1843), has been recorded from Northland to Stewart Island and at Chatham Island. It occurs off surf beaches and in estuaries and harbours, mainly on sandy bottoms (Stead, 1983). Armstrong (1986) and Stead (1983) both found that the abundance of *O. catharus* varied seasonally with catches being highest off surf beaches in summer. In contrast, reports from fishermen and my own observations indicate that *O. catharus* is most abundant in winter in sheltered harbours and bays. In a laboratory study (Chapter 1), I found that 74% of adult crabs moulted between June and November, and a field study has shown that females mate immediately after moulting in winter and spawn predominantly between November and March (Chapter 3). The results of tagging experiments led Wear (1982) and Stead (1983) to suggest that *O. catharus* is a highly migratory species and if so the high abundance of crabs in bays and harbours during winter and off surf beaches in summer may be the result of migrations which occur in relation to breeding and moulting cycles.

Habitat partitioning between adult and juvenile portunid crabs has been reported in other studies (Darnell, 1959; Klein Breteler, 1976; Hill et al., 1982; Potter et al., 1983) and adults are known to move between

different habitats in relation to moult stage (Hines et al., 1987) and breeding cycle (Cargo, 1958; Hill, 1975; Norse and Fox-Norse, 1977; Paul, 1982; Potter et al., 1983). The present study was conducted at two locations in Pegasus Bay, Little Akaloa which is a shallow, sheltered bay on Banks Peninsula and Brighton which has an expansive, exposed shoreline. The aim of the study was to investigate distribution patterns of *O. catharus* in relation to size, moulting and breeding cycles, and possible seasonal migrations.

METHODS

The population of *O. catharus* at Little Akaloa (Fig. 1) was sampled on 22 occasions between January 1984 and December 1985. Crabs were caught using lift pots 80 x 80cm with a bottom of galvanised steel mesh (24 mm) and sides of nylon netting (mesh size 10 mm). The pots were baited with filleted fish frames, usually red cod or tarakihi, and set for 30 minutes at a time. After 2 or 3 sets, the pots were rebaited. The number of pots used and the number of sets per day varied from month to month but catch per unit effort was calculated for each month as the total number of crabs caught divided by the product of the number of pots and the number of 30 minute sets.

The pots were effective at catching crabs larger than 30 mm carapace width (CW); smaller crabs were caught by towing a 2 m beam trawl (mesh size 10 mm). On most occasions, two or three 15-minute trawls were done but either outboard motor failure or bad weather prevented the use of the trawl on five occasions: January, July, August and November 1984 and November 1985. During three trips, only the trawl was used (March

and April 1984, September 1985) and as a result smaller samples were obtained. When only one sampler was used the size range of crabs was not necessarily complete (see Figs. 2 and 3).

Crabs were caught in lift pots at Little Akaloa for a mark recapture experiment. Crabs that were active and had no more than two missing limbs were tagged as described in Chapter 2 and released. Most recaptures were made during regular sampling trips or tagging trips and all recaptured crabs were measured and released again. Eight tagged crabs were returned from Little Akaloa by amateur fishermen in response to a poster advertising the experiment.

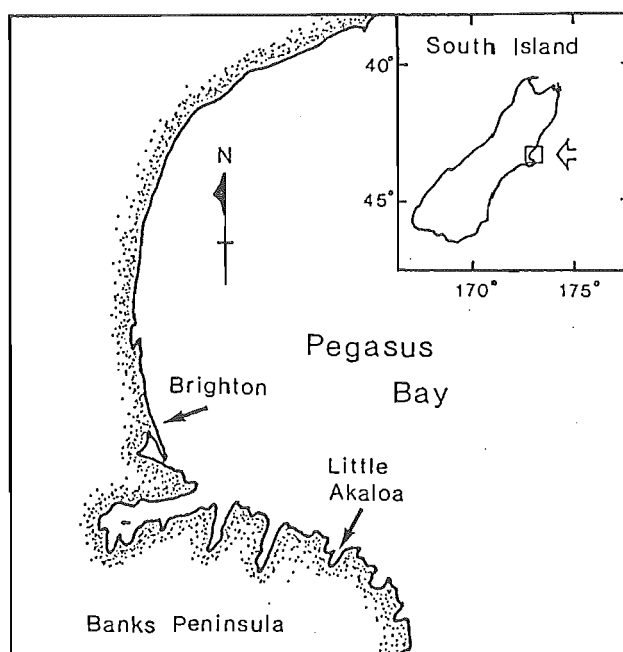


Fig. 1. Map of Pegasus Bay showing sampling sites at Little Akaloa and Brighton.

The population of *O. catharus* at Brighton was sampled in the area shown in Fig. 1. Crabs were caught on nine occasions, between June 1984 and May 1985 using an otter trawl with a cod end of mesh size 25 mm. Two or three 20-30 minute trawls were made each time and catch per unit effort was calculated as the total number of crabs caught, divided by the number of trawls.

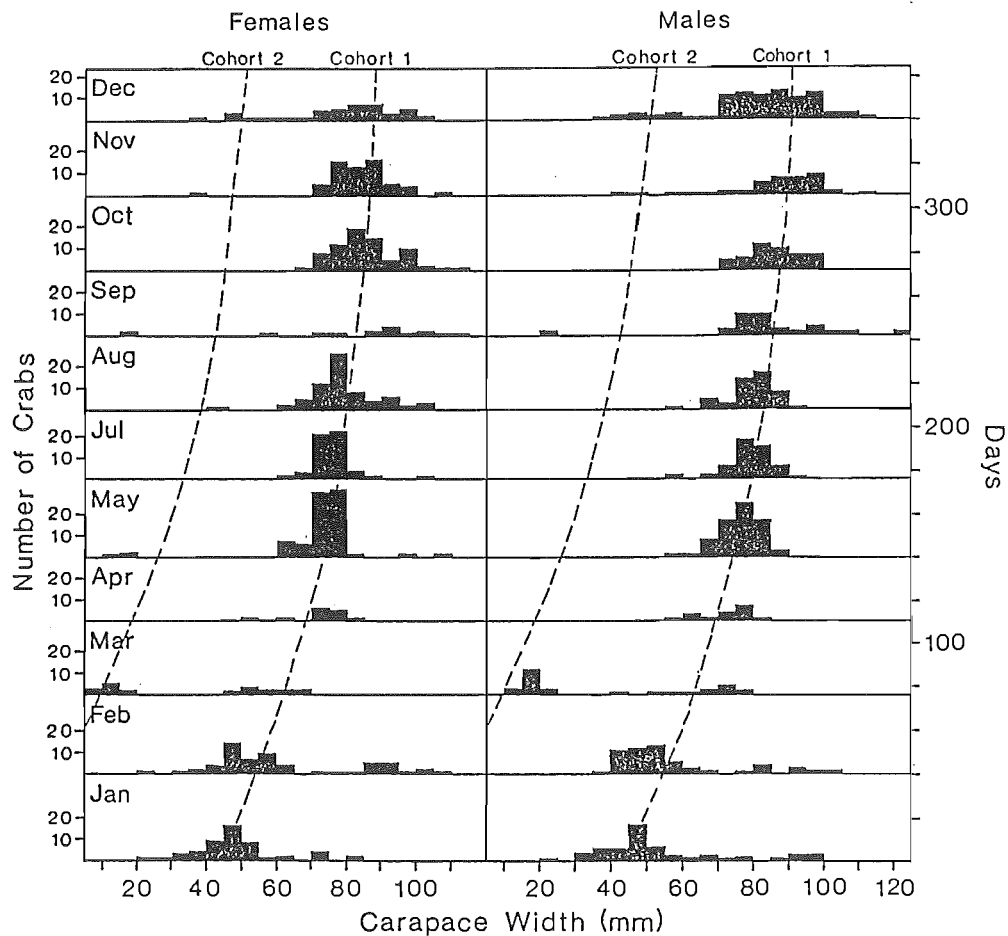


Fig. 2. *Ovalipes catharus*. Monthly size-frequency distributions of crabs caught at Little Akaloa in 1984. Dashed lines indicate probable progression in size of separate cohorts.

RESULTS

Little Akaloa Population

Size-frequency distributions of male and female *O. catharus* from Little Akaloa 1984 are shown in Fig. 2. Throughout the year the population consisted of two main cohorts. Individuals of cohort 1 had carapace widths of 35-60 mm in January and had grown to 75-90 mm CW by December. Individuals of cohort 2 entered the benthic population

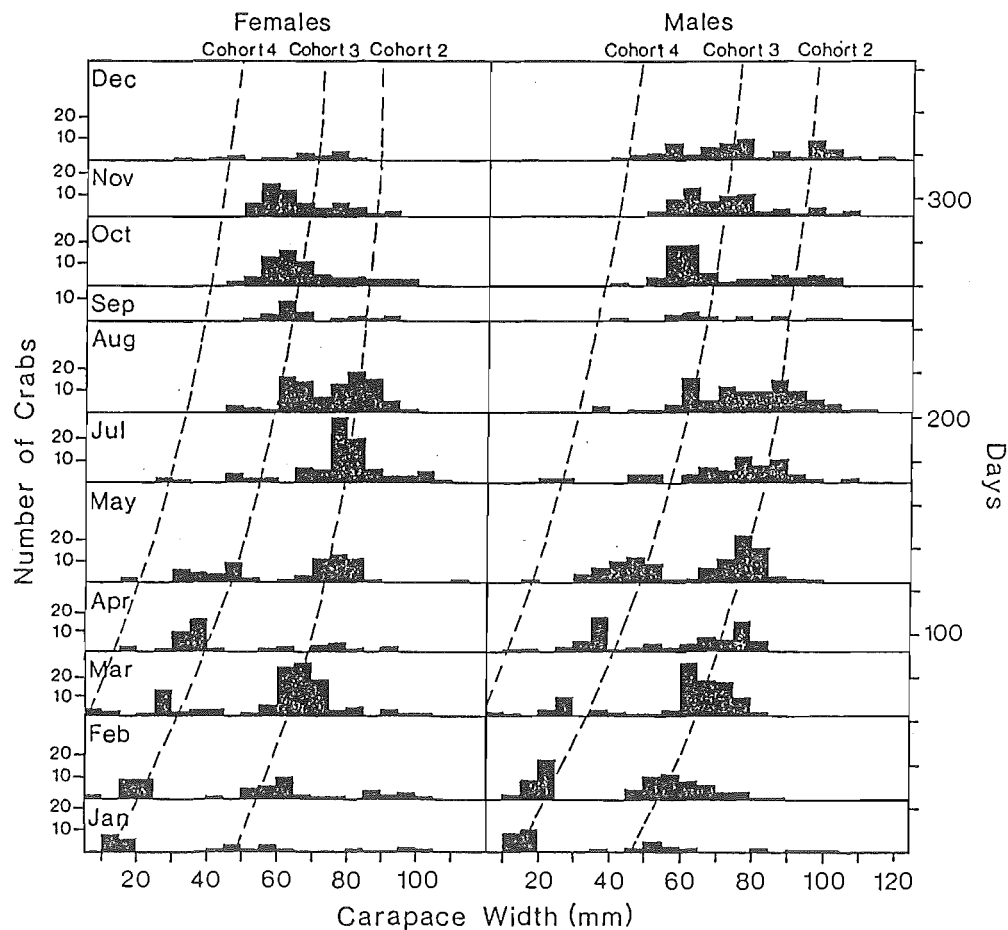


Fig. 3. *Ovalipes catharus*. Monthly size-frequency distributions of crabs caught at Little Akaloa in 1985. Dashed lines indicate probable progression in size of separate cohorts.

predominantly in March. However, they were not caught again in appreciable numbers until December, by which time they had grown to 40-60 mm CW. Fig. 3 shows the size frequency distributions of male and female crabs from the same population in 1985. Few individuals belonging to cohort 1 were present after December and it is probable that large numbers of this cohort had migrated out of the bay. Cohort 2 (the March '84 recruits) increased in numbers and its members grew larger in the first half of 1985; after August this cohort too declined in abundance. As in the previous year, March 1985 saw recruitment to the population of small individuals (cohort 4) that were not seen again in appreciable numbers until December. The main difference in population structure between the two years was the appearance of a large recruitment group in January 1985 (cohort 3) the equivalent of which was not observed the previous year. Cohort 3 was present throughout the year and its members had grown to 65-85 mm CW by December.

To summarise, the population of crabs at Little Akaloa consisted of four recognizable cohorts in 1984-85. Cohort 1 probably entered the population in about March 1983 and most of its members appeared to have migrated out of the population by January 1985. Cohort 2, the March '84 recruits, appeared to be segregated from the adult population during juvenile life but was present in the sampling area from December 1984 to August 1985 after which its numbers declined. Members of cohort 3, the January '85 recruits, provided no indication of habitat segregation during their juvenile life but instead were present in the sampling area from the time of settlement through to attainment of adult size. However, their numbers also declined at the end of the year. Cohort 4, the March '85 recruits, showed the same pattern as its counterpart from the year before in being absent from the sampling area during most of juvenile life.

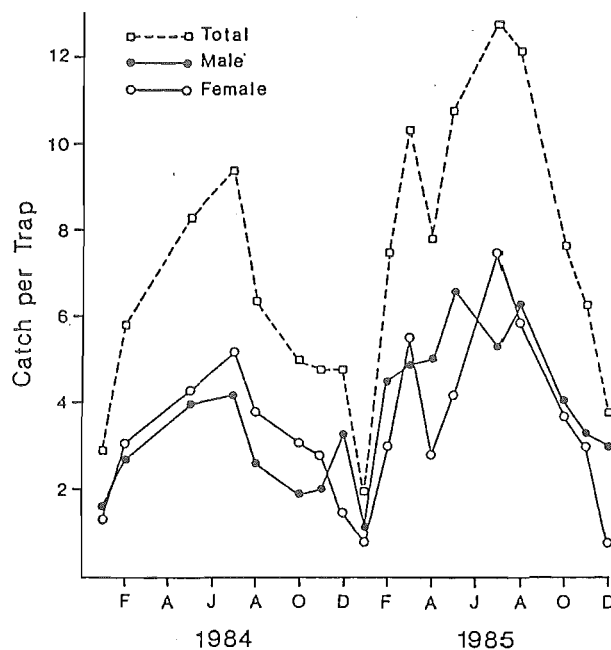


Fig. 4. *Ovalipes catharus*. Catch per unit effort at Little Akaloa 1984-85.

The pattern of increasing abundance in the first half of the year and declining abundance in the second half of the year is shown clearly in Fig. 4. Abundance (numbers of crabs per trap) was maximal in winter and minimal in summer, and was higher in 1985 when recruitment was greater than 1984.

Further evidence of crab migrations was obtained from a mark recapture experiment. Between January 1984 and January 1985 a total of 2657 crabs were tagged and released at Little Akaloa (Table 1). At intervals between February 1984 and December 1985, 343 tagged crabs were recaptured. Most of the crabs that were recaptured had been tagged and released before October 1984 (97%). The low percentage of recaptures of crabs that were tagged and released between October and December 1984 supports the contention that they migrated out of the population shortly after their release. The few crabs that were tagged in

Table 1. *Ovalipes catharus*. Numbers of tagged crabs released between January 1984 and January 1985 at Little Akaloa, and number subsequently caught.

Months	No. of releases	No. subsequently caught	% subsequently caught
Jan	128	12	9.4
Feb	37	4	10.8
May	92	7	7.6
Jun	544	97	17.8
Jul	1050	138	13.1
Aug	96	14	14.6
Sep	449	62	13.8
Oct	84	1	1.2
Nov	86	4	4.7
Dec	83	2	2.4
Jan	8	2	25.0
Total	2657	343	

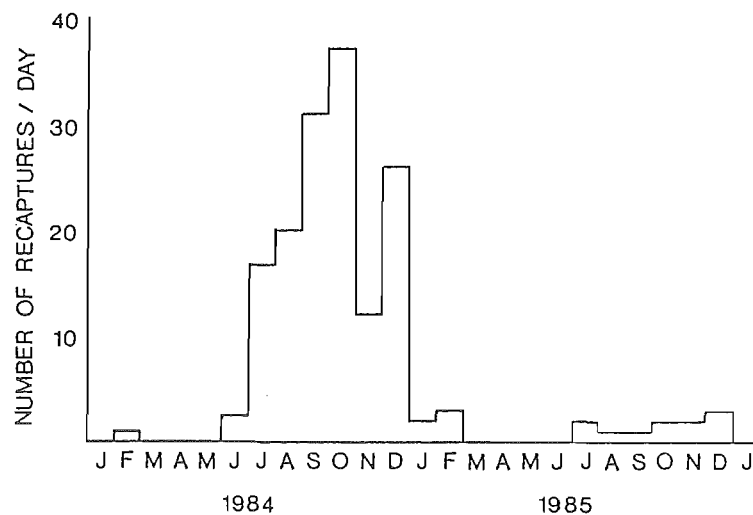


Fig. 5. *Ovalipes catharus*. Number of tagged crabs recaptured per day at Little Akaloa 1984-85.

January 1985 may not have joined the general outward migration as 25% of them were recaptured one month later.

Most crabs were recaptured from July to December 1984 and a few were taken during the equivalent period in 1985 (Fig. 5). This suggests that at least some crabs that had migrated away from Little Akaloa returned the following winter. Of the 11 tagged crabs which returned to the population in 1985, all were males and only two had moulted since being released.

Brighton Population

The relative abundance of male and female crabs at Brighton from June 1984 to April 1985 is shown in Fig. 6. Abundance of male crabs was maximal in summer and minimal in winter whereas numbers of females increased only slightly in spring and early summer and declined

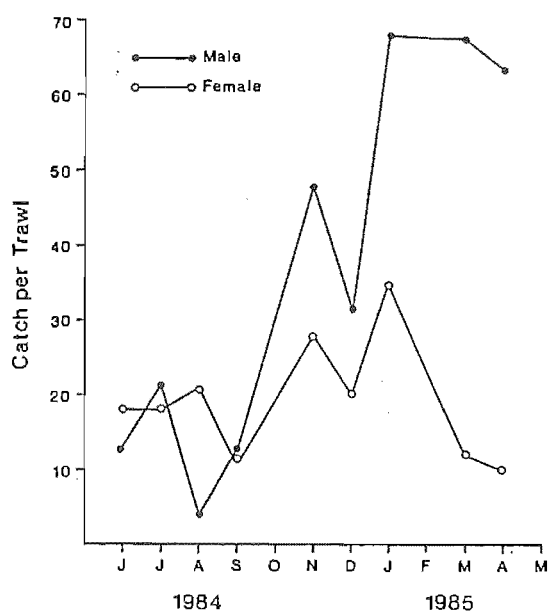


Fig. 6. *Ovalipes catharus*. Catch per unit effort at Brighton from June 1984 to April 1985.

again in mid summer. Although the sampling program was not long enough to demonstrate a cyclic pattern of seasonal abundance, reports from local fishermen that crab catches tend to be high in summer and low in winter indicate that such a pattern does exist. The increase in abundance of males at Brighton coincided closely with the decline in abundance of males at Little Akaloa. This suggests that male crabs migrate from sheltered, confined bays on to expansive, high wave energy beaches in spring.

On the other hand, the summer decline in female abundance at Little Akaloa corresponded with only a small and temporary increase in abundance at Brighton. The relatively low abundance of female crabs in both areas during the summer months corresponds with the period of egg-bearing in Pegasus Bay. The few ovigerous females collected during the two sampling programs, especially at Brighton (Table 2) suggests that females may aggregate in shallow areas outside of those sampled or perhaps in deeper waters. On one occasion (January 1986), 20 out of 28 (71%) female crabs caught close to shore Brighton in a fisherman's set net

Table 2. *Ovalipes catharus*. Numbers and percentage of adult females (> 65 mm CW) and ovigerous females in 7 samples from Little Akaloa (LA) and Brighton (Br).

Samples	No. of females (% of total adults)	No. of ovigerous females (% of total females)
LA Jan '84	6 (32%)	1 (17%)
LA Feb '84	17 (55%)	1 (6%)
LA Nov '84	59 (60%)	2 (3%)
Br Nov '84	14 (19%)	3 (21%)
LA Dec '84	34 (31%)	3 (9%)
LA Jan '85	4 (44%)	1 (25%)
Br Jan '85	24 (24%)	2 (8%)

were carrying eggs, but the fisherman considered this unusual and took only 9 more ovigerous females during the rest of the summer. His observations suggest that wherever ovigerous females aggregate, it is not far from the rest of the population and occasionally they may intermingle.

DISCUSSION

Distribution of Juveniles

At times of high adult abundance at Little Akaloa, juvenile crabs appeared to occupy habitats other than those of the adults. In March of both years, evidence of recruitment of newly settled crabs into the population was obtained but small crabs were caught in trawls only occasionally during winter and spring. By December, when adult abundance had declined, members of the March recruitment cohort had increased in abundance in the areas trawled. Wear and Haddon (1987) reported a high level of cannibalism in *O. catharus*, and noted that it accounted for as much as one third of the diet at some localities. In the laboratory, the risk of cannibalism increased as the size differential between individuals increased (pers obs) although all crabs were vulnerable at ecdysis. Gotshall (1978) suggested that the presence of large numbers of adult *Cancer magister* may restrict survival of an incoming year class because of foraging on juveniles by adults. Such a situation could occur in *O. catharus*, and juveniles may seek refuge from cannibalism by occupying a different habitat.

Segregation of habitat between adults and juveniles has been found in the portunids, *Callinectes sapidus* (Darnell, 1959) and *Portunus pelagicus*

(Potter et al., 1983) whose juveniles occur in shallower waters than adults. In *Carcinus maenas* (Klein Breteler, 1976), *Scylla serrata* (Hill et al., 1982) and the cancrid crab *Cancer irroratus* (Krouse, 1976), juveniles reside in intertidal areas seeking shelter in small creeks, pools, under stones and in seagrass or mangrove beds whereas adults occur in subtidal areas.

The cohort of newly settled *O. catharus* which appeared in the Little Akaloa population in January 1985 did not seek shelter elsewhere but remained in the sampled area throughout the year. This may have been because settlement occurred during a period of low adult abundance when the threat of cannibalism was low.

Distribution and Movements of Adults

Throughout autumn and winter at Little Akaloa, crab abundance was very high. So high in fact that it is hard to imagine the food supply being great enough to support the population. In a dietary study of *O. catharus* Davidson (1987) found that during winter feeding activity at Little Akaloa was generally lower than in other seasons but still relatively high. However, a large proportion of the diet of adult crabs was algae (42%) and decapods (37%) which are less preferred foods than bivalves (9%), fish (1%) and small soft-bodied crustaceans (4%). In contrast, adult crabs at Brighton and nearby Taylors Mistake throughout the year were feeding predominantly on bivalves (17% and 64%), fish (24% and 15%) and crustaceans (predominantly mysids) (53% and 15%) respectively, and only small amounts of Decapoda and algae.

There must be a reason for *O. catharus* aggregating at Little Akaloa during winter under suboptimal foraging conditions, and one possibility is that it is associated with moulting and mating of adults which takes place

at that time of year (Chapter 3). Moulting under crowded conditions does not appear to provide any obvious advantage to males which are very vulnerable to cannibalism during ecdysis, but females mate immediately after moulting and are protected by their mates. Therefore, males and females aggregating during the female moulting season could ensure an adequate supply of large mates for females. Sloan (1985) found that king crabs (*Lithodes aequispina*) were distributed at different depths according to sex, but that males and females aggregated at a particular depth during the mating season. Hines et al. (1987) found that pre-moult female *Callinectes sapidus* did not occur in the areas where pre-moult males aggregated but instead moulted in areas where intermoult males were abundant. They also found that males aggregated in sheltered, low salinity creeks to moult and the reasons they suggest for this may be applicable to the *O. catharus* situation at Little Akaloa.

Firstly, aggregating in sheltered areas for moulting may minimize mortality due to predation and cannibalism during the vulnerable period surrounding ecdysis. Although intermoult crabs readily attack soft crabs, late pre-moult and early post-moult crabs cease feeding (pers obs) and therefore, would not be a threat to each other. Furthermore, it is likely that as in the creek where *C. sapidus* were found moulting, the shallow water at the head of Little Akaloa Bay is relatively free of fish large enough to feed on large, soft crabs.

Secondly, Hines et al. (1987) found that although not actively feeding, early, postmoult *C. sapidus* frequently consume their exuviae in the laboratory, presumably to provide minerals required for recalcification of the exoskeleton. If crabs are frequently separated from their exuviae before feeding in the field, moulting aggregations would make it easy to find another exuviae nearby.

It is generally accepted that brachyuran males need to be hard-shelled

in order to mate (Lipcius, 1985), and several authors have reported male crabs moulting before females and therefore being hard-shelled in time for mating (Penn, 1977; Conan, 1985; Lipcius, 1985). Adult male *O. catharus* kept in the laboratory moulted slightly later than females (pers obs) and at Little Akaloa Bay, females leave the population in spring slightly earlier than males which suggests that males may wait until after mating and emigration of females before moulting themselves.

The gradual decline in abundance of *O. catharus* at Little Akaloa after July indicates that after moulting, crabs leave the bay possibly in search of better foraging areas. If crabs move from Little Akaloa to Brighton in spring, they would be joining a population that is foraging more actively according to the scale of foregut fulness used by Davidson (1987). The increase in abundance of male crabs at Brighton in spring therefore would seem to result from the movement of crabs from sheltered bays and estuaries like Little Akaloa.

The whereabouts of adult female *O. catharus* during the warmer months (including the egg-bearing season) is, as yet, unknown. After mating, they leave shallow, protected areas like Little Akaloa Bay but unlike males they do not reappear at Brighton. There are three possible explanations for the absence of ovigerous females from either sampling area. It is possible that ovigerous females may become inactive and cease feeding in which case they would not be caught by trawls or baited traps. The tendency for ovigerous females to behave this way has been reported in the fiddler crab, *Uca pugilator* (Colby and Fonseca, 1984) and the cancrid, *Cancer pagurus* (Howard, 1982). However, such behaviour has not been reported previously in portunid crabs for which sparse abundance of ovigerous females within a population is usually attributed to spawning migrations (Cargo, 1958; Hill, 1975; Norse and Fox-Norse, 1977; Sasaki and Kawasaki, 1980; Paul, 1982; Potter et al., 1983). In the

laboratory, ovigerous *O. catharus* exhibited no reduction in activity or feeding (pers obs) and Davidson (1987) found that most of the ovigerous females he examined had been feeding recently.

Alternatively, females may aggregate in shallow areas away from the main population and more extensive sampling is needed to identify these areas. Examples of such behaviour have been provided by Park (1969) who reported a dense aggregation of ovigerous females of the portunid *Cronius tumidulus* in an area separate from the rest of the population in Biscayne Bay, Florida, and Norse and Fox-Norse (1977) who found ovigerous females of the pelagic portunid *Euphylax dovii* aggregating in shallow waters well away from the oceanic habitat of the rest of the population. Females of several other portunid crabs inhabiting brackish waters make spawning migrations into higher salinity waters (Cargo, 1958; Hill, 1975; Paul, 1982; DeVries et al., 1983; Potter et al., 1983) which are associated with the higher salinity requirements of eggs and larvae (Costlow and Bookhout, 1959; Sandoz and Rogers, 1944; Hill, 1974).

Finally, it is possible that females migrate offshore into deeper, stiller water to incubate their eggs in the manner of *Cancer pagurus* (Howard, 1982), *Ovalipes punctatus* (Sasaki and Kawasaki, 1980), *Portunus pelagicus* (Smith, 1982), and the king crab *Lithodes aequispina* (Sloan, 1985). The adaptive significance of such offshore migrations might be related to enhancing larval retention in certain areas e.g. fiords (Sloan, 1985) or enhancing larval survival in the food rich, planktonic environment of offshore waters (Smith, 1982). Except for the final megalopal stage, the larvae of *O. catharus* are rarely found in inshore waters and it is presumed that they live offshore in deeper water (Wear and Fielder, 1985). I consider this to be the most likely explanation of the distribution of ovigerous *O. catharus*, but because a few ovigerous females were caught within Pegasus Bay it is possible that females are not moving

far away to spawn and under certain conditions may reunite with the rest of the population.

More extensive sampling of deep and shallow areas, and a detailed study of the distribution of early larval stages may help to answer the question of female movements and spawning behaviour.

CHAPTER 5

CHAPTER 5

Latitudinal variation in life history traits of Ovalipes catharus (Decapoda, Portunidae). 1. The effects of temperature on growth.

INTRODUCTION

Studies involving the effects of temperature on crustacean growth are of two basic types. One type relates to populations which are geographically separate and hence under different temperature regimes (Fusaro, 1978; Berrill, 1982). Growth differences in such populations may be due to genetic factors as well as to temperature effects. The other type of study involves the temperature response of a single population, either in the wild in different seasons (Travis, 1954; Astthorsson and Ralph, 1984) or under laboratory conditions (for a review see Hartnoll, 1982). Under these circumstances it can be assumed that the response is purely a physiological one (Hartnoll, 1982).

The growth rate of juvenile *Ovalipes catharus* varies depending upon the time of settlement of megalopae (Chapter 2) and this suggests that growth may be temperature dependent. In the present study, size-frequency analysis (see Chapter 2) is used to estimate growth rate of crabs in Tasman Bay, and the estimate obtained is compared with that for a more southern population living in colder waters. To test the hypothesis that differences in growth rate between the two populations could be attributed to temperature effects directly, a study of crab growth was conducted in the laboratory under temperature regimes similar to those at the two locations and with all other conditions kept constant.

The "day-degree" approach was used to study the relationship between crab growth and temperature by equating growth to the accumulation of daily mean temperatures above a certain threshold. This approach has been used previously to predict development rates and time to maturity in plants (Wang, 1960), insects (Ross and Merritt, 1978; Cudney and Wallace, 1980) and freshwater crustaceans (McLay, 1977) but appears to have been applied to marine Decapoda only once (Campbell, 1983). In Campbell's study, moulting frequency of lobsters (*Homarus americanus*) was found to be dependent upon the annual accumulation of day-degrees (Campbell, 1983), and the successful use of the technique in the present study suggests that it is an approach worthy of more widespread consideration.

METHODS

O. catharus was collected from Motueka Beach, Tasman Bay (Fig. 1) on nine occasions between January 1985 and May 1986. On seven of the nine sampling days an area close to shore (water depth 2-3 m) was sampled by towing a 2 m beam trawl and setting baited lift pots from a 4 m boat fitted with a 10 hp outboard motor. In June and August sea conditions were too rough to use a small boat so lift-pots were set and lifted from a commercial fishing boat in slightly deeper water (6-10 m). In addition, all crabs caught in two overnight set pots lifted by the fisherman were measured. As the mesh on the fisherman's pots was large, only crabs greater than 80 mm CW were caught. Three other collections (December, January and May) were supplemented by two pots of crabs taken from the same fishing boat (see Figs. 7 & 8). All crabs caught were sexed and maximum carapace width was measured with calipers to the nearest 0.1 mm. A polymodal analysis was performed on the

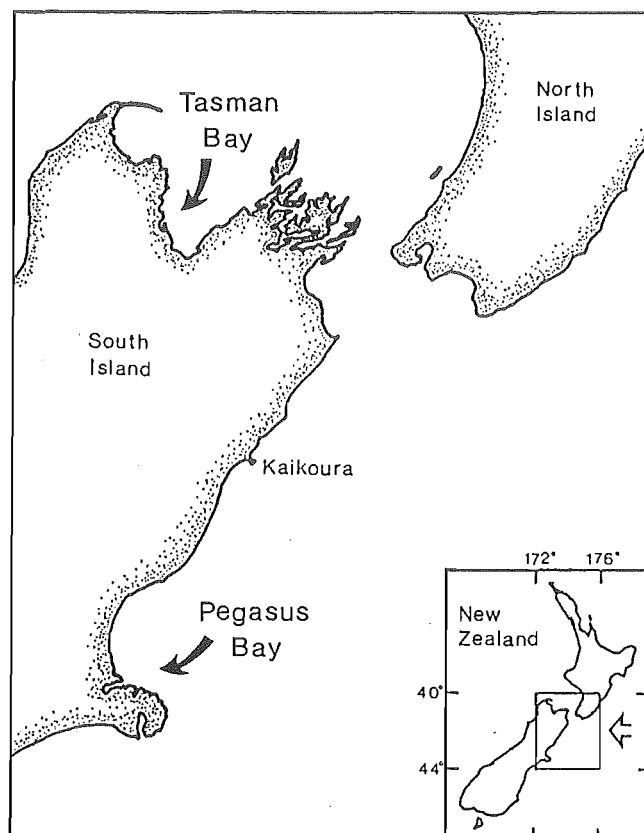


Fig. 1. Map of central New Zealand showing sampling sites at Pegasus Bay and Tasman Bay.

size-frequency distributions of male and female crabs caught in Tasman Bay using the program described by MacDonald and Pitcher (1979). For more detailed information on the use of this program see Chapter 2.

In order to compare growth rates under two different temperature regimes, records of monthly sea surface temperatures were obtained from the NZ Meteorological Service satellite pictures for Tasman Bay and for Pegasus Bay where growth rates of *O. catharus* had been measured (Chapter 2). The average difference in sea surface temperature between the two sites was about 3°C throughout the year (Fig. 2).

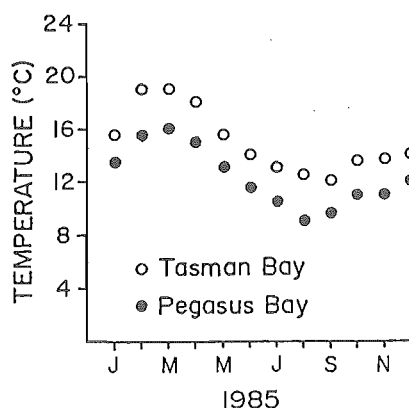


Fig. 2. Sea surface temperatures obtained by satellite for the first week in each month for Pegasus Bay and Tasman Bay.

From February to March 1985, an experiment was run at the Edward Percival Field Station, Kaikoura (Fig. 1) to monitor the growth of juvenile crabs under different temperature regimes. Ambient temperature of water coming into the laboratory was not appreciably different from that in Pegasus Bay (see Ottaway, 1976). Tempunits were used to raise the temperature in two 160 litre, flow-through wooden aquaria. In one of these the volume of inflowing water was regulated so that temperature was maintained 3°C above ambient. In the second aquarium, the same technique was used in an attempt to raise the ambient temperature by 6°C. However, the flow of water was too slow to prevent the inlet water pipes from silting up and a stable temperature was not achieved. Consequently, data on crab growth obtained in this aquarium were not used.

Seventeen crabs were maintained in the experimental aquarium (ambient + 3°C) and 36 were kept in two control aquaria (ambient temperature) under conditions described in Chapter 1. Crabs ranged from 8.4 to 52.3 mm CW. During the 60-day experiment, diurnal water temperature in the control aquaria ranged from 15.5 to 17°C whereas in

the experimental aquarium it ranged from 19 to 20°C. The relationships of percentage moult increment (Y) and intermoult duration (Y) to pre-moult size (X) for the experimental and control temperatures were approximated by the linear function: $\log_{10} Y = a + bX$, and compared by analysis of covariance using the statistical package BMDP1R on the Burroughs computer at the University of Canterbury.

RESULTS

The Effect of Temperature on Growth in the Laboratory

During the 60-day experiment, 69 moult records were obtained from 36 crabs kept at ambient sea temperature and 57 records were obtained from the 17 crabs kept at 3°C above ambient. No significant difference

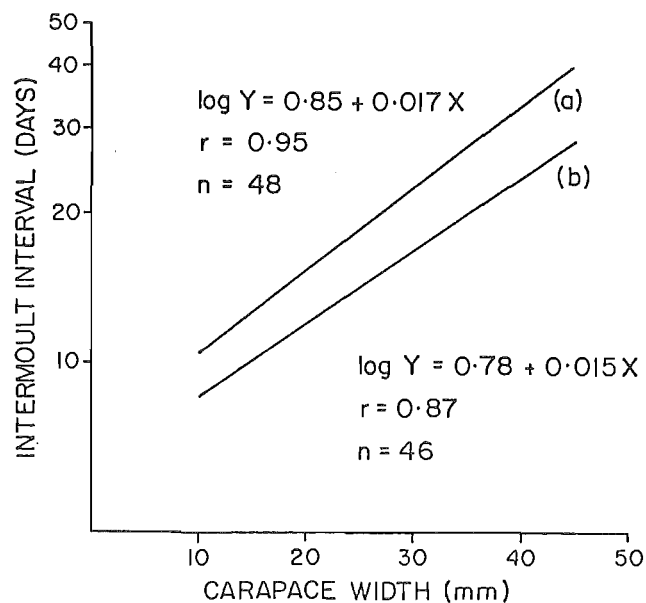


Fig. 3. *Ovalipes catharus*. Regressions of log intermoult interval on carapace width for crabs kept in the laboratory at (a) ambient temperature and (b) 3°C above ambient.

was found between the regressions of log percentage increment on pre-moult size for the two groups of crabs ($P=0.295$, ANCOVA). However, crabs kept at the higher temperature had significantly shorter intermoult durations than those kept at ambient temperature ($P<0.001$, ANCOVA; Fig. 3). The regressions of log intermoult duration and log percentage increment on size, were used to construct growth curves for the two temperature groups (Fig. 4). In the time it took crabs to grow to instar 7 at ambient temperature, they grew to instar 8 at the higher temperature.

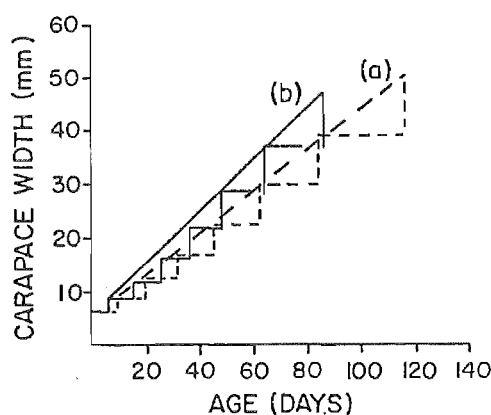


Fig. 4. *Ovalipes catharus*. A generalized scheme of growth in the laboratory at (a) ambient temperature and (b) 3°C above ambient.

The differences in growth rates observed in these experiments are assumed to be attributable to temperature affects alone as all other variables were kept constant. If so, growth of experimental and control crabs, expressed in terms of "physiological time" (accumulation of degree-days above a certain threshold temperature) should be the same. In order to calculate day-degrees, a minimum temperature threshold of 5°C was assigned. Selection of this figure was based on studies of growth of homarid lobsters which are cold temperate species existing naturally in water temperatures of approximately 2°C to 25°C (Aiken, 1980). Crabs kept in water of ambient temperature grew from instar 2 to instar 7 (an average increase of 29.8 mm CW) in an average of 74.7 days

(0.40 mm/day). Average water temperature over this period was 16.25°C, total degree days above 5°C was 840, and mean growth rate therefore was 0.035 mm/degree-day. In contrast, crabs kept at 3°C above ambient temperature grew on average 28.2 mm CW (instar 2 to instar 7) in 56.7 days (0.50 mm/day) at an average temperature of 19.5°C (822 degree-days; 0.034 mm/degree-day). Mean growth rate of crabs kept at the higher temperature therefore was about the same as that of control crabs when considered in terms of degree-days.

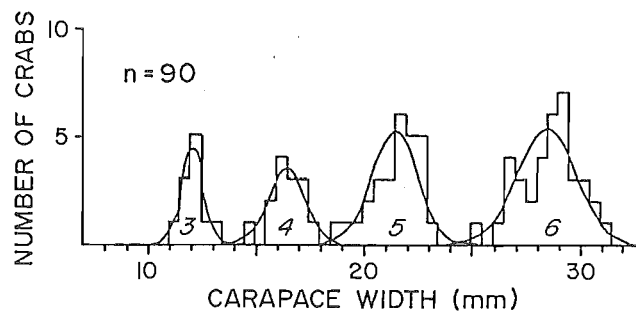


Fig. 5. *Ovalipes catharus*. Size frequency and fitted instar distributions of juveniles caught in Tasman Bay, 1985-86.

Field Study of Growth

MacDonald and Pitcher's (1979) technique for estimating instar parameters from size-frequency data identified four instars between 11 and 32 mm CW in the Tasman Bay population (Fig. 5). Laboratory observations of megalopae and early postlarval instars indicate that the first of these was probably postlarval instar 3. The same technique enabled seven further instars to be identified from the size frequency data available for male and female *O. catharus* greater than 30 mm CW

(Fig. 6). Table 1 gives the parameters of the normal distributions shown in Figs. 5 and 6 and also the size increments and percentage increments between instar means. As was found in Chapters 1 and 2, moult increments increased up to instar 11 in males and instar 9 in females and then decreased, whereas percentage increment declined as size increased. After instar 9, growth increment of female crabs declined markedly so that they reached a smaller maximum size than males.

To estimate the frequency of moulting of *O. catharus* in Tasman Bay, changes in instar frequency with time were recorded. Newly settled crabs entered the population during December and January 1986 and grew rapidly to instars 9-10 by May (Figs. 7 and 8). Those recruited about May 1985 had grown to instar 9 by January, instar 10 by March and instar 11 by July 1986. Moulting to subsequent instars was presumed to occur about once a year.

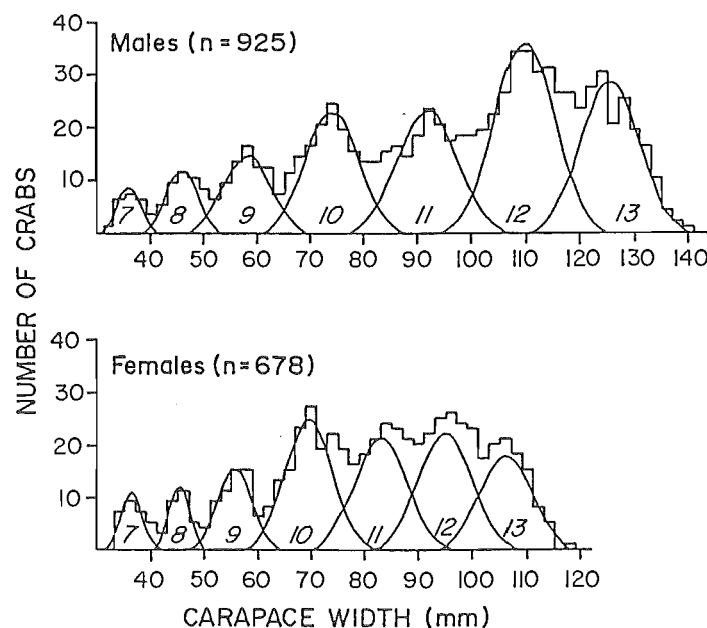


Fig. 6. *Ovalipes catharus*. Size frequency and fitted instar distributions of male and female crabs from Tasman Bay, 1985-86.

Table 1. *Ovalipes catharus*. Instar parameters, size increment between instars and increment as percentage of premoult size for crabs from Tasman Bay. Size and increment measurements in mm CW. Tests of significance were performed on differences between fitted and observed distributions (see Fig. 6). (*) means value was constrained (see Chapter 2).

	3	4	5	6	7	Instar 8	9	10	11	12	13
Juveniles \bar{x}	12.1	16.5	21.5	28.5							
S.D.	0.51	0.85	1.06	1.38							
increment	4.4	5.0	7.0	-							
% increment	36.4	30.3	32.6	-							
Goodness of fit	$\chi^2 = 19.769$, df = 29 P >0.10										
Males \bar{x}					35.9	45.8	58.2	74.1	91.8	109.6	125.4
S.D.					2.21	3.13	4.69	*5.0	*5.5	*5.5	5.53
increment				7.4	9.9	12.4	15.9	17.7	17.8	15.8	-
% increment				26.0	27.6	27.1	27.3	23.9	19.4	14.4	-
Goodness of fit	$\chi^2 = 13.022$, df = 38, P >0.10										
Females \bar{x}					36.6	45.2	55.5	69.7	83.0	94.9	106.1
S.D.					2.35	1.19	3.39	*4.5	*5.0	*5.0	*5.0
increment				8.1	8.6	10.3	14.2	13.3	11.9	11.2	-
% increment				28.4	23.5	22.8	25.6	19.1	14.3	11.8	-
Goodness of fit	$\chi^2 = 8.801$, df = 27, P >0.10										

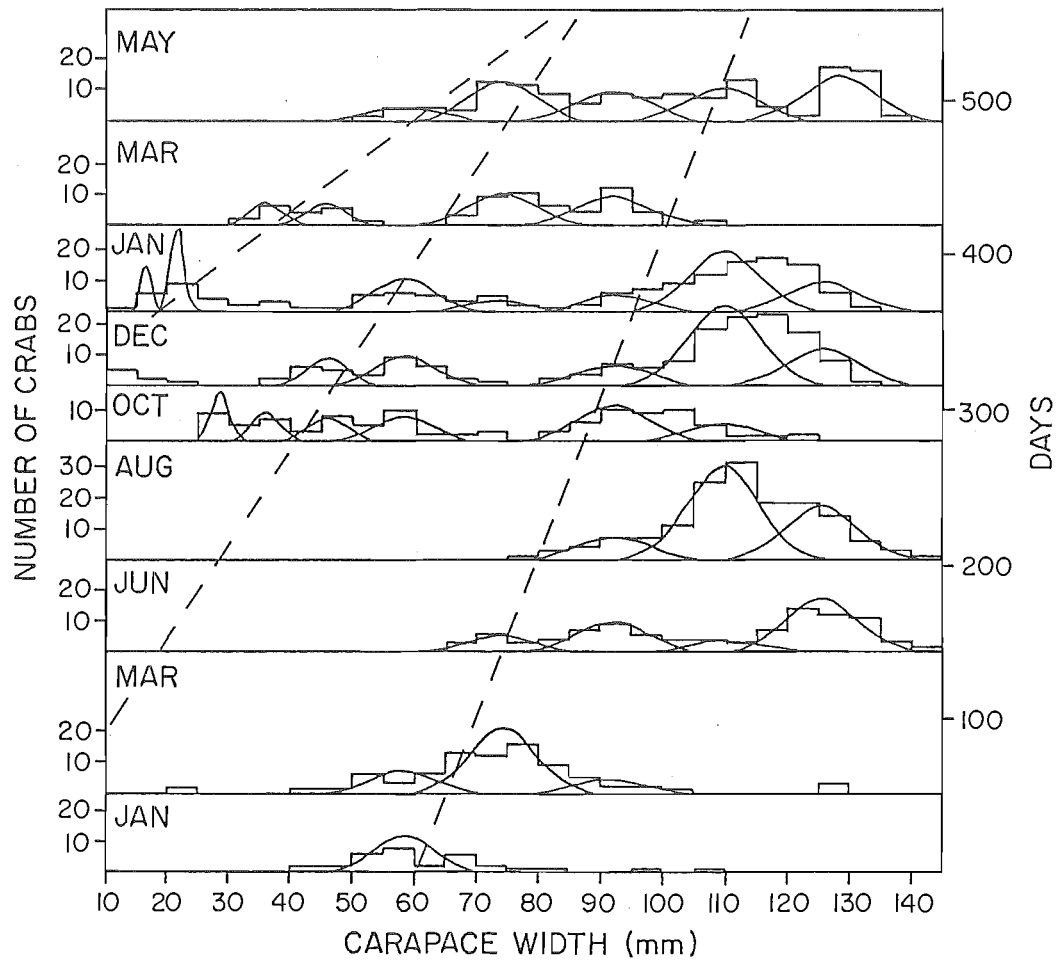


Fig. 7. *Ovalipes catharus*. Bimonthly size-frequency distributions and fitted instar distributions of male crabs from Tasman Bay, January 1985 to May 1986. Parameters of instar distributions are given in Table 1. (---) indicate approximate growth of individual cohorts.

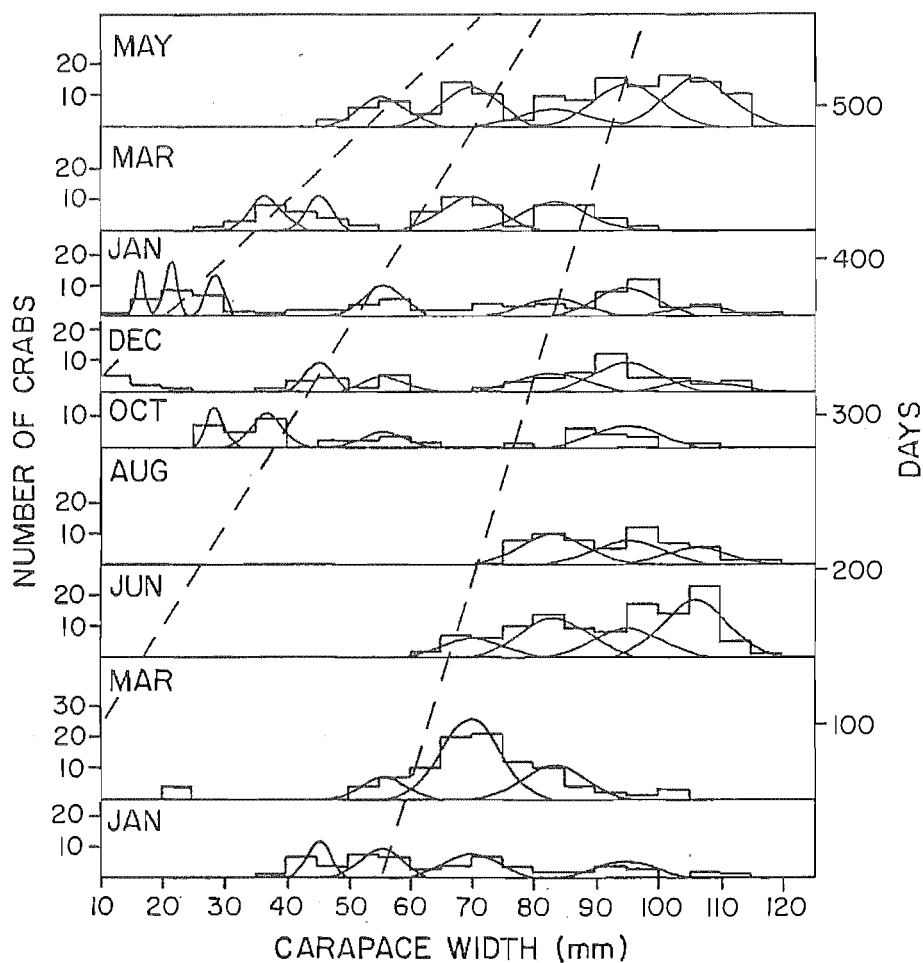


Fig. 8. *Ovalipes catharus*. Bimonthly size-frequency distributions and fitted instar distributions of female crabs from Tasman Bay, January 1985 to May 1986. Parameters of instar distributions are given in Table 1. (---) indicate approximate growth of individual cohorts.

A generalized growth curve for the Tasman Bay population was constructed (Fig. 9) by combining instar size data (Table 1) with approximate moult frequency data (Figs. 7 and 8). This indicated that in Tasman Bay, *O. catharus* grew to instar 11 in the first year and with annual moulting would have reached maximum size (instar 13) after 3 years. In contrast, crabs grew to instar 10 in year one in Pegasus Bay (see Chapter 2). Fig. 10 shows that development to instars 9 and 10 in each population requires an equivalent number of day-degrees, and indicates that differences in growth rates are the result of differences in temperature regimes.

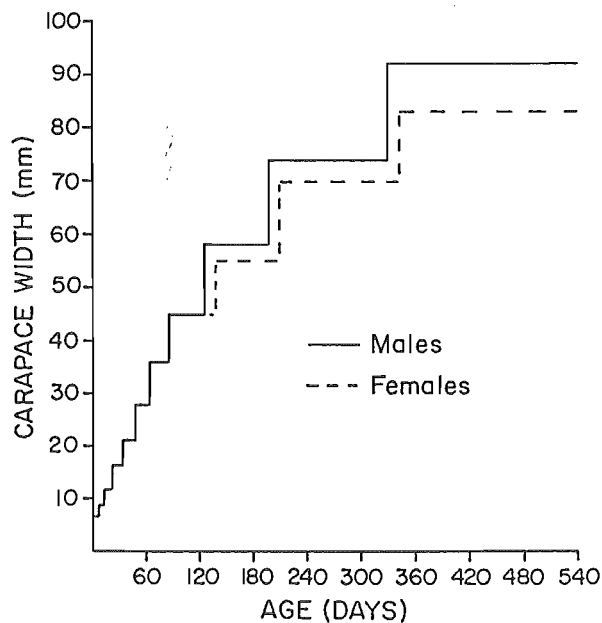


Fig. 9. *Ovalipes catharus*. A generalized scheme of growth for the first 11 instars of male and female crabs in Tasman Bay.

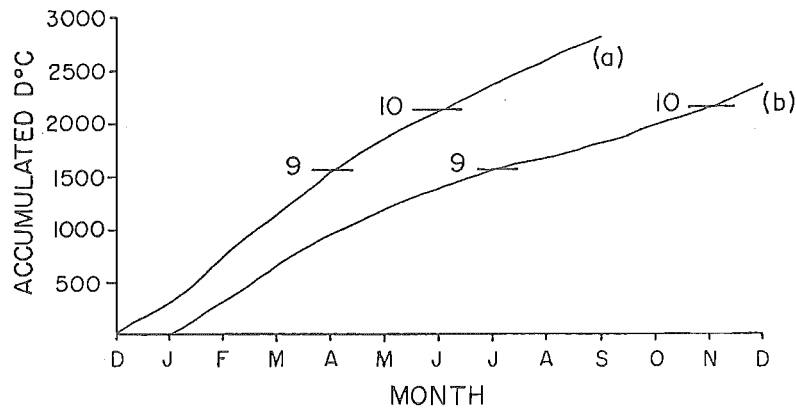


Fig. 10. *Ovalipes catharus*. Accumulation of day-degrees in sea temperature above 5°C for (a) Tasman Bay and (b) Pegasus Bay. Times to reach instars 9 and 10 are shown for each location.

DISCUSSION

Field Estimates of Growth Rate

The occurrence of several distinct modes in a size-frequency distribution of *O. catharus* from Pegasus Bay is reported in Chapter 2, and the assumption that these modes represented instars was supported by the laboratory study on growth presented in Chapter 1. The present study confirmed these earlier findings that size variation within instars of a population of *O. catharus* is low, enabling instars to be distinguished by size frequency analysis. Estimation of cohort growth rate by following the progression of instar modes through time was not as clear cut in Tasman Bay as it was in Pegasus Bay. This was mainly because fewer samples were taken over a shorter period and because recruitment occurred for a longer time in Tasman Bay (see Chapter 6). Consequently, separate cohorts were not as easily distinguished as they were at Pegasus Bay. Nevertheless, the predicted growth rate of 0+ crabs was similar to

that of crabs kept in the laboratory at a temperature regime close to that of Tasman Bay.

Effect of Temperature on Moults Increment

Hartnoll (1982) stated that although the effects of temperature on moults increment of crustaceans are variable, the majority of examples in the literature indicate a reduction in the increment with an increase in temperature. In the laboratory, moults increments of *O. catharus* were not significantly affected by increasing temperature by 3°C although after two months, crabs at the experimental temperature (ambient + 3°C) were smaller at a particular instar than those at ambient temperature.

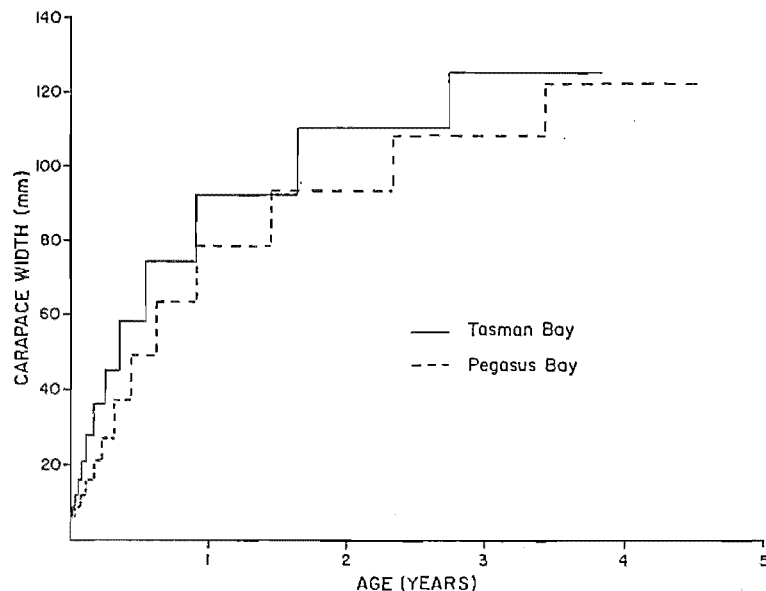


Fig. 11. *Ovalipes catharus*. Comparison of average growth curves from Tasman Bay and Pegasus Bay.

Field estimates of growth rates for the populations at Pegasus and Tasman Bays indicated that in the first year, average moult increments were slightly smaller in Tasman Bay (Fig. 11). If members of both populations undergo the same number of moults to reach maximum size, and this seems to be the case, then maximum size attained in Pegasus Bay would be expected to be greater than in Tasman Bay. However, after the first year, moult increments of Pegasus Bay crabs became smaller than those of Tasman Bay individuals, presumably in response to environmental factors other than temperature (see Chapter 6). As a result, the maximum size attained by members of the two populations was very similar (Fig. 11).

Effect of Temperature on Moult Frequency

Temperature is the most important environmental factor affecting the moult frequency of crustaceans, and universally a rise in temperature increases moult frequency (Hartnoll, 1982). In the laboratory, *O. catharus* moulted on average six times in the first 100 postlarval days when kept at ambient temperature (Chapter 1). In contrast, an extrapolation of laboratory results indicated that crabs kept at 3°C above ambient would moult seven times in the same period. A similar pattern was apparent in the field. Thus, Pegasus Bay crabs moulted on average, nine times and Tasman Bay crabs 10 times in their first year. Thereafter, moulting occurred once a year at both locations and resulted in a maximum life span of 4-5 years in Pegasus Bay and 3-4 years for the faster growing population in Tasman Bay.

The effect of temperature on moult frequency can be seen not only between geographically separate populations but also within a population in different seasons. In Chapter 2 it was pointed out that crabs entering

the Pegasus Bay population in January moulted eight times in the first six months, whereas crabs settling in March experienced cooler water temperatures during their juvenile growth phase and moulted only six times in the first six months. Other factors which could contribute to observed differences in growth rates between populations of *O. catharus* and between seasons within a single population include food quality and quantity, salinity, and parasitism (Hartnoll, 1982). Although each of these factors warrants further investigation in the field and in the laboratory, results of the present study indicate that differences in temperature alone may be adequate to explain differences in growth between Pegasus Bay and Tasman Bay crabs.

In the laboratory, growth of juvenile *O. catharus* was related directly to the accumulated day-degrees experienced by individuals. Similarly, field studies at Pegasus and Tasman Bays showed that development to instar 10 required an equivalent number of day-degrees. This relationship between growth and heat input holds only for the first year of postlarval life because after that moulting becomes a seasonal event and temperature is no longer the most important factor determining intermoult duration.

CHAPTER 6

CHAPTER 6

Latitudinal variation in life history traits of Ovalipes catharus (Decapoda, Portunidae). II. Female size at maturity and fecundity.

INTRODUCTION

Size at onset of sexual maturity and fecundity are important parameters used for determining reproductive potential of crustacean populations, and are particularly important components of assessment models for exploited species. Several authors have reported variations in these and other life history traits for geographically separate populations (Fusaro, 1978; Somerton, 1981; Campbell and Eagles, 1983; Campbell and Robinson, 1983; Jones and Simons, 1983; Wenner et al., 1985). An understanding of intraspecific life history variation can have implications for management of an exploited species in different parts of its distributional range and contribute to an understanding of the reproductive adaptations of a species to its environment.

In Chapter 5 it was shown that *Ovalipes catharus* grew faster in Tasman Bay than in the more southern Pegasus Bay and that the difference in growth rate was attributable mainly to differences in environmental temperature. Different growth rates can lead to differences in the age and size at maturity and generation time (Wenner et al., 1974). Furthermore, higher temperatures may lengthen the breeding season and therefore the rate of egg production by crabs in Tasman Bay might be expected to be greater than in Pegasus Bay.

In the present study, differences in critical life history traits between

the two populations were examined and assessed in terms of total population fecundity by using an egg per recruit model (Campbell and Robinson, 1983). As well as estimates of fecundity and size at maturity, an egg per recruit model requires estimates of total mortality which can be obtained from an analysis of size-frequency distributions (Annala, 1979; 1980). Total mortality of female *O. catharus* is attributed solely to natural mortality in the model as females are rarely subjected to fishing mortality because of their small size.

METHODS

Reproductive Biology

From January 1985 to May 1986, 368 non-ovigerous female *O. catharus* >30 mm carapace width (CW) were collected from Tasman Bay during bimonthly sampling trips using set pots, lift pots and a beam trawl as described in chapter 5. Ovigerous females were caught occasionally during these sampling trips, but most were collected by a local fisherman. Ovigerous crabs were frozen on the day of capture and later were thawed and preserved in seawater-formalin for 24-48 hours before dissection. All other crabs were preserved without freezing. Using the same methods described in chapter 3, the vulva and spermatheca of each female were examined for evidence of copulation; whole ovaries were removed, dried and weighed and gonad indices were calculated. The numbers and stages of development of eggs of 58 ovigerous crabs were estimated (see Chapter 3).

Egg Per Recruit Model

An empirical egg per recruit model was developed for the American lobster by Caddy (1977, 1979) to determine the potential number of eggs produced by 1000 individual recruits entering a fishery. The Caddy model was modified slightly by Campbell and Robinson (1983) to take account of females extruding eggs more than once per intermoult period. The model incorporates assumptions similar to those in the usual dynamic pool models of Beverton and Holt (1957) and Ricker (1958). However, the empirical growth functions based on moult frequencies and increments are used to calculate moult instars instead of the usual von Bertalanffy function that expresses growth in terms of age in years (Campbell, 1985). In the model, total egg production was determined from the sum of eggs produced in each instar in the population. The reproductive potential per instar, m , was expressed as

$$E_m = S_m \cdot D_m \cdot Q_m \cdot N_m$$

where

E_m = total number of eggs produced in instar m ,

S_m = proportion of sexually mature females in instar m ,

D_m = proportion of females extruding eggs in instar m ,

Q_m = mean number of late stage eggs per female in instar m ,

N_m = number of females in instar m .

Values for E_m were accumulated for each instar, and the total egg production (E_t) for all instars calculated as

$$E_t = \sum_{m=1}^{\max} E_m$$

where \max is the instar of the largest sized crabs.

Input Parameters

Egg per recruit calculations were performed on populations of *O. catharus* from Pegasus Bay and Tasman Bay. Calculations began with 1000 individuals entering the first instar ($m=1$), which I defined as the first instar in which sexual maturity was attained. Mean instar sizes are given in Chapters 2 and 5 for Pegasus Bay and Tasman Bay females, respectively. The proportion of sexually mature (S_m) females in each instar was estimated from logistic functions describing the relationship between proportion of crabs mating and CW. The mean number of eggs carried by females in each instar (Q_m) was estimated from the relationship between brood size and CW in the two populations (data for Pegasus Bay from Chapter 3). The proportion of females extruding eggs (D_m) was assumed to be related to length of reproductive season and length of intermoult period. The average number of egg broods per year for Pegasus Bay females was estimated to be two (Chapter 3). Instars of approximately one year duration in Pegasus Bay were assigned an extrusion factor (D_m) of 2 whereas a factor of 3 was used for Tasman Bay crabs which have a longer reproductive season. Instars of less than one year duration were assigned an extrusion factor of one or two depending upon duration of instar and reproductive season.

Mortality Estimates

One thousand individuals were assigned to the first mature instar and survival to subsequent instars was estimated from data on population structure. Hartnoll (1978) stated that if constant, regular recruitment is assumed, the proportion of each instar in a steady state population will be represented by the product of its survival and duration as follows:

$$P_m = N_m \cdot I_m / \sum_{m=1}^{\max} N_m \cdot I_m$$

where

P_m = the proportion of instar m in the population,

N_m = the number of individuals in instar m ,

I_m = the duration of instar m in days.

For *O. catharus*, recruitment is seasonal and populations do not occur in a steady state from month to month (see Chapters 2 and 5). However, if size-frequency distributions are combined for regular intervals over a period of one year, a steady state distribution can be approximated. This was done for both Pegasus Bay (Chapter 2) and Tasman Bay (Chapter 5) crabs and the proportions of each instar in the two populations (P_m) were calculated using a polymodal analysis (MacDonald and Pitcher, 1979). The duration of each instar (I_m) can be estimated from studies of growth of *O. catharus* from Pegasus Bay and Tasman Bay (Chapters 2 and 5). Therefore, survival from one instar to the next was calculated as follows:

$$N_{m+1} = N_m \cdot (P_{m+1}/I_{m+1}) / (P_m/I_m)$$

RESULTS

Female Reproductive Biology in Tasman Bay

The size-frequency distribution of mated and unmated female *O. catharus* from Tasman Bay is shown in Fig. 1. Mating had occurred in 91% of females >50 mm CW whereas 79% of females <50 mm CW had not mated. The smallest female to show physical signs of copulation was 40.8 mm CW and the largest female showing no evidence of copulation was 62.2 mm CW. The relationship between proportion of mature crabs and CW was described best by a logistic curve. The size at which 50%

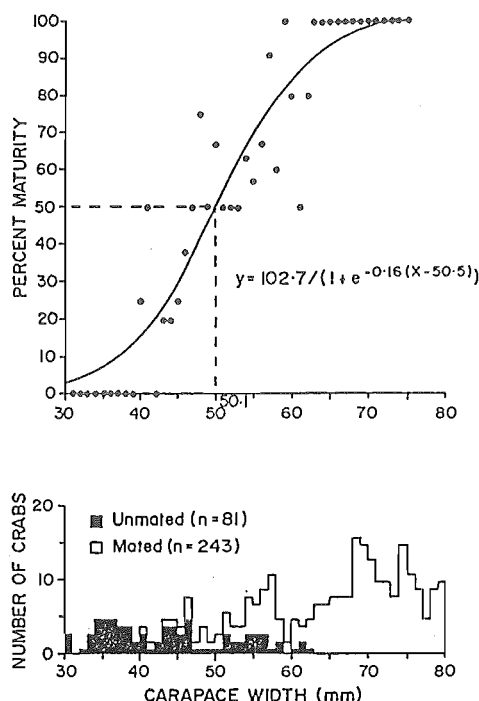


Fig. 1 *Ovalipes catharus*. Size distribution of mated and unmated females from Tasman Bay 1985-86 and the percentage mature in each 1 mm size class.

of Tasman Bay females were mature was estimated to be 50.1 mm CW.

A proportion of *O. catharus* females had ripe ovaries (Stage 4) throughout the year in Tasman Bay (Fig. 2). However, most females with large ovaries were found between August and March and the few ovigerous crabs collected were also caught between these months. Evidence used to indicate the length of the reproductive season of *O. catharus* in Pegasus Bay (from November to March) included a period when females were scarce and presumed to be incubating eggs elsewhere (see Chapter 4). Fig. 3 shows that the proportion of females in the adult population (crabs >60 mm CW) in Tasman Bay, declined after June and increased again in March. Therefore, the reproductive season in Tasman Bay is estimated to be about 8 months long (from August to March).

The relationship between brood size and CW of Tasman Bay females

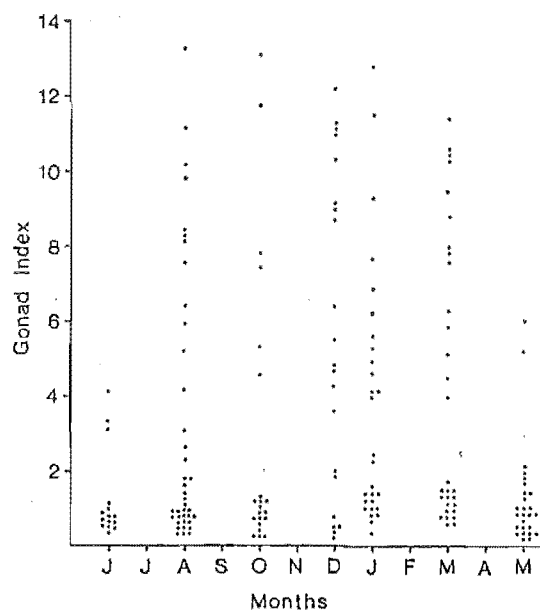


Fig. 2 *Ovalipes catharus*. Gonad indices for individual females caught in Tasman Bay, June 1985 - May 1986.

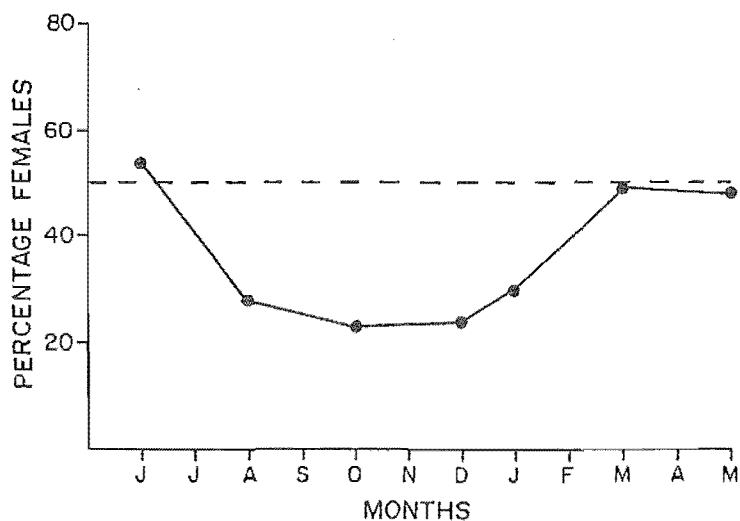


Fig. 3 *Ovalipes catharus*. Sex ratio of crabs from Tasman Bay, June 1985 - May 1986.

was described best by a power curve (Fig. 4). No significant differences ($P > 0.05$; ANCOVA) in this relationship were observed between early and late developing eggs or between crabs collected during the 1984-85 ($n=16$) and 1985-86 seasons ($n=42$). The smallest ovigerous crab seen was 45.9 mm CW but most were larger than 65 mm CW. No ovigerous crabs between 48 and 67 mm CW were collected, probably because most collections were made by fishermen who only take large crabs.

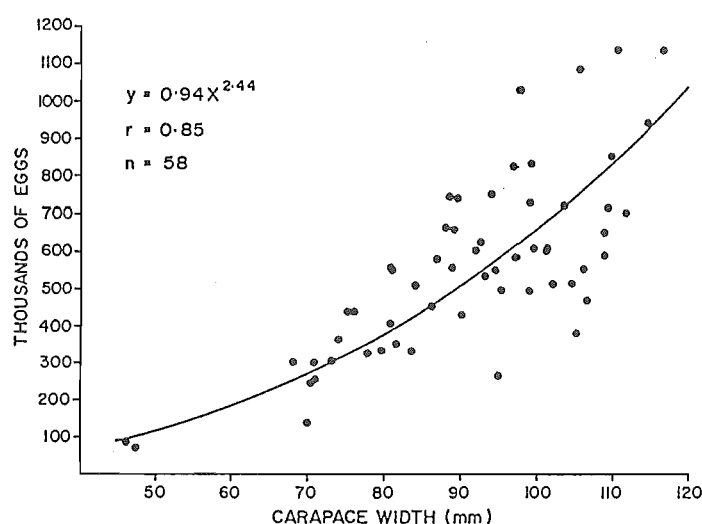


Fig. 4 *Ovalipes catharus*. Relationship between total number of eggs carried externally and carapace width of ovigerous crabs from Tasman Bay.

Natural Mortality of Females

The instar in which sexual maturity was first attained in both populations was instar 8. Therefore, mortality and fecundity schedules were computed for instar 8 onwards. The estimates of natural mortality of *O. catharus* given in Table 1 are based on the assumption that there was no bias in the sampling method over the size range of crabs involved (40-120 mm CW). In Pegasus Bay, samples were taken using an otter

Table 1. *Ovalipes catharus*. Estimates of mortality between instars in Pegasus Bay and Tasman Bay, based on the proportion of each instar in the natural populations (P_m) and the duration of each instar in days (I_m) (see text for equation). N_m is the number of individuals in instar m . Numbers in brackets are values of mortality and N_m that were assigned in cases where the calculated values were aberrant.

Instar	Pegasus Bay				Tasman Bay			
	P_m^a	I_m^a	N_m	Mort (%)	P_m^b	I_m^b	N_m	Mort (%)
8	0.17	60	1000	15.3	0.05	40	1000	-25.7 (15)
9	0.24	100	847.1	31.2	0.11	70	1257 (850)	-4.5 (30)
10	0.33	200	582.4	78.1	0.23	140	888.6 (595)	39.1
11	0.13	360	127.5	30.7	0.21	210	362.2	38.9
12	0.09	360	88.3	55.6	0.22	360	221.3	18.2
13	0.04	360	39.2	100	0.18	360	181.1	100

^a Data from Chapter 2

^b Data from Chapter 5

trawl which should have been equally efficient at catching crabs of all sizes within this range. However, in Tasman Bay, samples were taken using baited pots which tend to catch a disproportionate number of crabs >60 mm CW. Therefore, instars 8 and 9 were almost certainly under-represented in the Tasman Bay samples and resulted in the negative estimates of mortality for instars 9 and 10 shown in Table 1. The mortality values used for these two instars in the egg per recruit model were set at the same level as those for the Pegasus Bay population. Fig. 5 shows the expected size-frequency distributions of female crabs in two steady state populations with mortality schedules as in Table 1, and the actual size distributions of crabs taken from Pegasus Bay and Tasman Bay. Mortality of crabs >80 mm CW clearly was much higher in Pegasus Bay than Tasman Bay and could be expected to result in a considerable difference in the reproductive potentials of the two populations.

Eggs Per Recruit

The input parameters for the egg per recruit model are given in Table 2. The minimum instar in which sexual maturity was reached in both populations was instar 8 although 100% maturity was not reached until instar 11. The Tasman Bay population had a higher proportion of mature crabs in instars 8 and 9, reflecting the smaller mean size at maturity in this population (50.1 mm CW cf 65.5 mm CW in Pegasus Bay; see Chapter 3). The relationship between number of eggs per brood and crab size was not significantly different in the two populations ($P > 0.05$; ANCOVA) but the number of broods produced per year was believed to be greater in Tasman Bay. This was because Tasman Bay crabs bred for 8 months whereas Pegasus Bay crabs were limited to the warmer season and only had a reproductive season of five months.

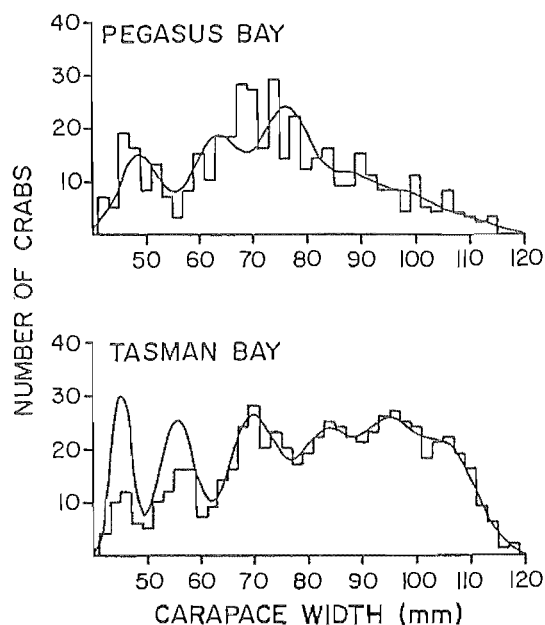


Fig. 5 *Ovalipes catharus*. Observed and expected size-frequency distributions of female crabs from Pegasus Bay and Tasman Bay based on the mortality schedules given in Table 1. Means and standard deviations of instar sizes are from Chapters 2 and 5.

As a result of a smaller mean size at maturity, a longer reproductive season and greater survival to a large size, the overall reproductive potential of the Tasman Bay population may be as much as three times that of the Pegasus Bay population (Table 2). Estimates of the relative contributions made by the various size classes to total egg numbers in the two populations is shown in Fig. 6. In Tasman Bay, the greatest contributor to total egg numbers was instar 13 (>100 mm CW) whereas in Pegasus Bay, crabs in instar 10 (68-75 mm CW) had the highest contribution. The current minimum size limit of 100 mm CW for the crab fishery puts 20% of total egg production at risk in Tasman Bay compared to only 10% in Pegasus Bay.

Table 2. *Ovalipes catharus*. Input parameters used in the egg per recruit model (see Methods), egg production for each instar (E_m) and total egg production of the population (E_t) for Pegasus Bay and Tasman Bay. Data on mean instar sizes taken from Chapters 2 and 5.

	Instar (m)	Mean Size	Sm	Dm	Qm	Nm	E_m
Pegasus Bay	8	48.8	0.03	1	131537	1000	3,946,110
	9	63.1	0.38	1	224200	847.1	72,169,532
	10	76.3	0.93	1	332517	582.4	180,101,848
	11	88.8	1.00	2	455546	127.5	116,164,230
	12	99.1	1.00	2	572043	88.3	101,022,794
	13	109.4	1.00	2	702322	39.2	55,062,045
							$E_t = 5.28 \times 10^8$
Tasman Bay	8	45.2	0.30	1	95710	1000	28,713,000
	9	55.5	0.71	1	157941	850	95,317,394
	10	69.7	0.98	2	275364	595	321,129,497
	11	83.0	1.00	2	421667	362.2	305,455,575
	12	94.9	1.00	3	584721	221.3	388,196,272
	13	106.1	1.00	3	767652	181.1	417,065,332
							$E_t = 1.56 \times 10^9$

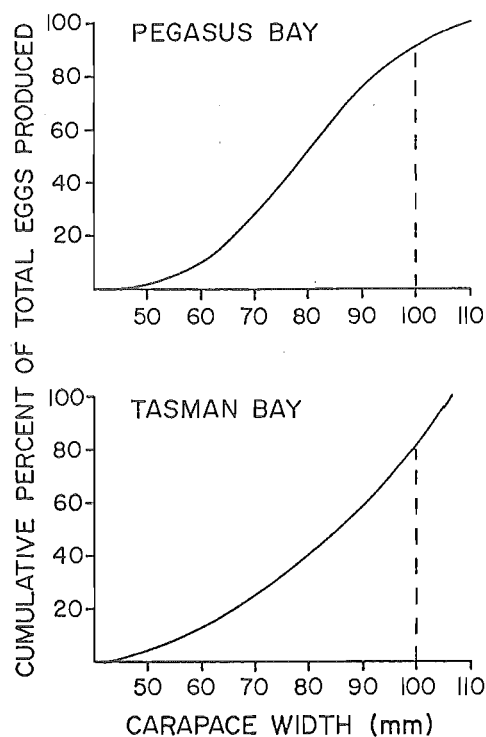


Fig. 6 *Ovalipes catharus*. Relative egg production of crabs of different carapace width from Pegasus Bay and Tasman Bay. Dashed lines represent the current minimum takeable size limit of 100 mm CW.

DISCUSSION

Size at Onset of Maturity

Many authors have reported a relationship between latitude (or water temperature) and size at onset of maturity (SOM) for decapod crustaceans such that as water temperature increases, SOM decreases (spiny lobsters: Sutcliffe, 1952; Annala et al., 1980; homarid lobsters: Templeman, 1936; brachyuran crabs: Berrill, 1982; Campbell and Eagles, 1983; Jones and Simons, 1983). However, information from Berry (1971) and Heydorn (1969) for *Panulirus homarus* and from Somerton (1981) for *Chionoecetes bairdi* indicate just the opposite trend, with smaller SOM occurring in

colder water. The way in which water temperature may influence size or age at maturity, and whether it is a causal relationship is not clear.

Templeman (1936) suggested that the size at which female *Homarus americanus* become sexually mature is the result of differential growth of the ovary and the remainder of the body. High summer temperatures are favourable for growth in length, but even more favourable for ovarian development. Therefore, lobsters mature at a smaller size and at an earlier age in areas with high summer temperatures than in areas with low summer temperatures. Annala et al. (1980) suggested that SOM is probably determined by an interaction between temperature and one or more other factors such as growth rate, age, metabolic rate, population density and food availability. Selection pressure from fishing (Charnov, 1981) and predation pressure, as in planktonic cladocerans (Lynch, 1980), may also result in SOM variation between populations.

In Chapter 3 it was suggested that SOM for *O. catharus* in Pegasus Bay depended upon the interaction of settlement period, growth rate and breeding season. Early recruits in Pegasus Bay had 10 months in which to grow to maturity before the beginning of the next breeding season whereas late recruits had only 6 months and therefore, would mature at an earlier age and smaller size. The minimum instar in which sexual maturity was attained in Tasman Bay (instar 8) was the same as that for Pegasus Bay. However, the mean SOM was lower in Tasman Bay (50.1 mm CW) than in Pegasus Bay (65.5 mm CW). The reason for this is likely to be the earlier and longer breeding season and settlement period and the faster growth rate (Chapter 5) of crabs in Tasman Bay. Thus, early recruits to the Tasman Bay population (settling in October) could reach the minimum size at maturity and produce a brood of eggs by January, i.e. within the same breeding season as settlement occurred. Later recruits would have 4-7 months before the next breeding season in

which to grow to maturity. To summarise, the higher water temperature of Tasman Bay appears to influence size and age at maturity by increasing growth rate and lengthening the breeding and settlement periods of *O. catharus*.

Annual Fecundity

Generally, the breeding seasons of crabs are longer at lower than higher latitudes (Sastry, 1983). Typical examples which exemplify this condition are the breeding seasons of *Hemigrapsus nudus* and *Pugetta producta* in Puget Sound and Monterey Bay (Knudsen, 1964; Boolootian et al., 1959), *Petrolisthes elongatus* in New Zealand (Greenwood, 1965; Jones, 1977) and *O. catharus* in Pegasus Bay and Tasman Bay (present study). Nevertheless, the relative importance of different environmental factors in the synchronization of breeding activities are poorly understood and temperature, day-length and food availability may all influence the length of the breeding season of *O. catharus*.

Although no definitive information is available on the frequency and duration of oogenic cycles in either population of *O. catharus* (see Chapter 3) it is likely that oocyte growth is at least as fast in Tasman Bay as in Pegasus Bay. In fact, elevated temperatures have been reported to bring about a reduction in oogenic cycle duration by increasing oocyte growth rate (Fusaro, 1980; Sastry, 1983), and if this applies to *O. catharus* then the longer breeding season in Tasman Bay might allow a greater frequency of oogenic cycles, i.e. more broods of eggs per year.

The effect of latitude on numbers of eggs per brood in marine crustacea is variable, and numbers of eggs carried by a female may increase with latitude (Jones and Simons, 1983), decrease with increasing latitude (Reaka, 1979), or be independent of latitude (Efford, 1969). In

the present study, I found no significant difference in the average number of eggs per brood for similar-sized females from Pegasus and Tasman Bays although brood sizes of the former were more variable.

Possible reasons for the greater variation in egg numbers in Pegasus Bay are given in Chapter 3 and include the variable success of individuals in accumulating energy for a brood (Hines, 1982), and mating with males which produce different sized spermatophores (Haynes, 1968). Alternatively, it has been suggested that differences in brood size may depend on whether the brood of eggs was the first one in a season or a subsequent brood. The latter could be smaller as a result of reduced time available for energy accumulation (Morgan et al., 1983) or perhaps because of reduced viability, or quantity of stored sperm (Paul and Adams, 1984). The quantity and life expectancy of stored sperm in spermathecae would probably be relatively constant within a species and therefore would not explain intraspecific differences in brood size. That variation in brood size is greater in Pegasus Bay despite the fact that Tasman Bay crabs probably produce more broods annually, suggests that energy reserves for reproduction are more limiting in Pegasus Bay than they are in Tasman Bay.

A point of interest here is the observation by Davidson (1987) that in Pegasus Bay large *O. catharus* do not forage as actively as small crabs. The percentage of crabs with foreguts containing food declined with size from 60-70% for small crabs (30-70 mm CW) to 20-30% for large crabs (>100 mm CW). Large crabs in Pegasus Bay consumed predominantly larger prey such as decapods and teleosts, whereas small crabs consumed smaller, soft bodied crustaceans including amphipods, mysids, cumaceans and isopods. The reduction of small crustaceans in the diet of crabs of increasing size is most likely attributable to a decrease in cheliped dexterity. The reduced foraging activity of large crabs may be due to a

shortage of suitable food types (e.g. bivalves) to replace the small crustaceans characteristic of the diet of smaller crabs. In Pegasus Bay, bivalves have relatively low importance as prey items (25%) (Davidson, 1987), whereas the diet of *O. catharus* in Tasman Bay (all size classes combined) was dominated by bivalves (56%) (Wear and Haddon, 1987) and reflected the high abundance of these prey items in the area (pers obs). Similarly, bivalves were an important component of the diet of large crabs taken from nearby Golden Bay and made up 65% of items ingested (Wear and Haddon, 1987). These observations support the suggestion that large crabs in Pegasus Bay are more limited in the energy reserves available for reproduction than are crabs in Tasman Bay.

Natural Mortality

The method used to estimate natural mortality of female *O. catharus* in Pegasus and Tasman Bays assumed that the populations were in a steady state and therefore, that their size frequency distributions were a function of size-specific mortality and growth rates. Average individual growth rate estimates for the two populations (Chapters 2 and 5) enabled natural mortality to be calculated, and indicated that it was higher in Pegasus Bay with a peak between instars 10 and 11. Warmer water increased survival of *Callinectes sapidus* (Winget et al., 1976) and may have enhanced survival of *O. catharus* in Tasman Bay. Alternatively, possible food limitation in Pegasus Bay (discussed above) may have inhibited moulting and survival.

If energy resources available for growth of large crabs in Pegasus Bay are limited, one would expect size increments as well as moulting frequency and survival to decline (Chittleborough, 1975). Although average size increments during ecdysis of 0+ crabs in Pegasus Bay were

larger than those of similar-sized crabs in Tasman Bay (attributed to differences in temperature, see Chapter 5), those for older Pegasus Bay crabs were smaller.

Comparison of Reproductive Potentials

A summary of differences in life history traits between *O. catharus* from Tasman Bay and Pegasus Bay is given in Table 3. Crabs in Tasman Bay had greater survival to large size, faster growth rates, and an earlier and longer breeding season. These characteristics resulted in the attainment of maturity at a smaller size and younger age and probably also greater frequency of brood production than in Pegasus Bay. Similarly, a population of *Carcinus maenas* on the central coast of Maine had later settlement of megalopae, slower growth, delayed maturity, delayed spawning, a longer generation time, and a longer life span than populations in warmer waters in southern Britain and Holland (Berrill, 1982).

Table 3. *Ovalipes catharus*. Comparison of major life history traits of populations from Pegasus Bay and Tasman Bay.

	Pegasus Bay	Tasman Bay
Breeding Season	Nov - Mar	Aug - Mar
Larvae Settlement Period	Jan - May	Oct - May
Mean Size at First Mating	65 mm CW	51 mm CW
Mean Age at First Mating	9 months	4 months
No. of Eggs per Brood	$1 \times 10^5 - 1 \times 10^6$	$1 \times 10^5 - 1 \times 10^6$
Annual No. of Broods	1 - 2	1 - 3
Survival to Large Size	low	high
Highest Contribution to Fecundity	Instar 10	Instar 13
Minimum Generation Time	9 months	5 months

The egg per recruit model used to assess the combined effects of the different life history traits upon reproductive potential in the two populations indicated that the life-time fecundity of a cohort (in terms of eggs per instar 8 recruit), was approximately three times greater in Tasman Bay than Pegasus Bay. The potential for growth of the population in Tasman Bay was increased further by the shorter generation time; the minimum interval between one generation and the next in Tasman Bay being about 5 months compared with about 9 months in Pegasus Bay. It should be noted at this juncture however, that comparisons of potential for reproduction and growth of populations is not particularly informative without information on stock-recruitment relationships since increases in egg production do not necessarily translate into higher recruitment at some later date (Campbell, 1985). As yet such information is unavailable for *O. catharus* in New Zealand.

Egg per recruit models have been used in the past to assess the reproductive potential of lobster populations (*Homarus americanus*) and to predict biological implications of management policies, particularly minimum size limits for the fishery (Campbell and Robinson, 1983; Campbell, 1985). At present, there is only a very small paddle crab fishery in New Zealand and there has been no need to apply management restrictions because catch size and minimum takeable crab size are market-forced. However, the present study serves to illustrate that significant differences in life history traits may exist between populations throughout their distributional range and therefore, stresses the importance of individual population studies. An egg per recruit model has the potential to be a useful management tool should the fishery expand.

CHAPTER 7
GENERAL DISCUSSION

GENERAL DISCUSSION

Information on several aspects of the life history of *O. catharus* have been presented in the previous chapters and discussed with reference to the relevant literature published on the specific topics. The purpose of this section is to bring together the information on growth, reproduction and movements, and to present a general overview of *O. catharus* ecology and life history. Although most of my findings and observations have been presented earlier, this section includes some new observations that are relevant to the general treatise but that did not fit easily into the preceding chapters.

Life History in Pegasus Bay

A generalized scheme of the post-larval life history of *O. catharus* in Pegasus Bay is shown in Fig. 1. Recruitment of newly settled crabs occurs mainly from January to May but timing and intensity of recruitment are probably highly variable from year to year. For example, at Little Akaloa, I observed one main pulse of recruitment in March 1984, but two pulses in 1985, a large one in January and a smaller one in March. As mentioned in Chapter 4, juveniles were rarely caught (particularly when adult abundance was high) so it is possible that the recruitment season was longer and settlement within the season more constant than indicated by my sampling program. However, the distinctness of cohorts at Little Akaloa is in agreement with observed narrow pulses of recruitment. Nevertheless, at Brighton cohorts were less distinct which may indicate that the pulses observed at Little Akaloa occurred when water currents or other factors were favourable for megalopae to enter the bay.

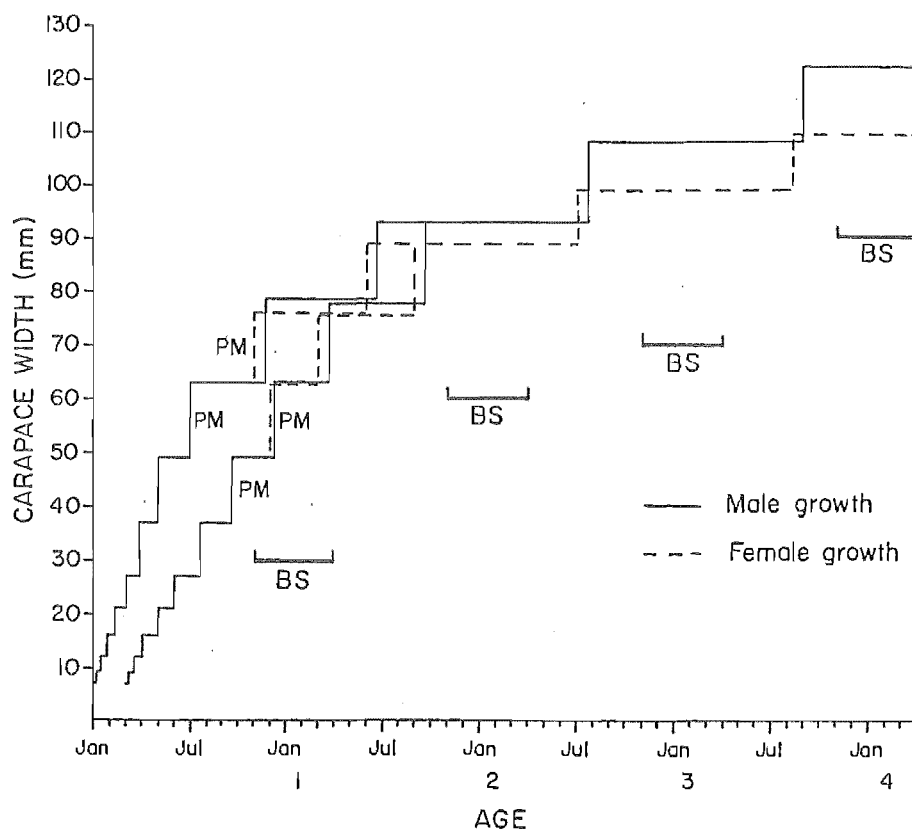


Fig. 1. *Ovalipes catharus*. A generalised scheme of the life history of crabs in Pegasus Bay. PM = pubertal moult, BS = breeding season.

Fluctuations in abundance and recruitment are characteristic of several commercially exploited crab populations and may be the result of fishing or the consequence of a vast array of interacting environmental and biotic factors intrinsic to the marine ecosystem (Jamieson, 1986). One reason put forward to explain the apparent "population explosion" of *O. catharus* in New Zealand is that favourable hydrological conditions in recent years may have improved larval survival and juvenile recruitment onto sandy shores (Wear, 1982). The marked fluctuations in abundance and recruitment observed at Little Akaloa in the two years of this study suggest that hydrological conditions (sea temperatures or current patterns) may well play an important part in the success of the species. As a

consequence, future problems for a developing fishery may include unpredictable recruitment and the resultant fluctuations in stock density.

The juvenile life history of *O. catharus* is characterised by very rapid growth, particularly in the first five or six instars (Chapter 1), and there was some evidence for the existence of habitat partitioning between adults and juveniles (Chapter 4). Large size at settlement (discussed below) and rapid juvenile growth enabled female *O. catharus* to attain sexual maturity within their first year of benthic life. As shown in Chapter 3, the earliest instar in which mating occurred in females was instar 8 but the range of sizes in which mating first occurred corresponded to instars 8-10. Different settlement times and growth rates of juvenile crabs (Chapters 1 and 2) resulted in the presence of a wide size range of 0+ females at the beginning of the breeding season (November) and maturity was probably attained at whichever instar an individual was in at that time (Fig. 1). Those females that mated in instars 8 or 9 probably produced at least one brood of eggs and moulted once or twice during the season so that most crabs were in instar 10 at the end of their first breeding season (March) (see Chapter 4). Mean size at maturity of male *O. catharus* was not studied but probably occurs at a similar or larger size than that of females. The reproductive activity of small adult males may be quite low as indicated by the observation that large males compete more successfully for mates (discussed below).

After the first breeding season, moulting is presumed to occur once a year during autumn or winter (Chapter 4). Evidence obtained from tagging studies and from crabs kept captive in the laboratory showed that large individuals have intermoult periods of at least one year duration. It is not uncommon to catch large crabs with carapaces that are worn around the edges and heavily encrusted with hydrozoans, features which suggest that in some crabs, moulting does not occur every year. Reasons

for this may be cold water temperature or perhaps low food availability (see Chapter 6) both of which might inhibit moulting of large crabs. The occurrence of only small numbers of crabs in the last two instars in Pegasus Bay where temperatures are cold and food may be limited is in accordance with such a suggestion.

Besides repairing damaged limbs, annual moulting has obvious advantages for reproductive success in both males, for which an increase in size would increase the likelihood of obtaining mates that are smaller in size, and for females which can only mate and replenish their supply of stored sperm when in the soft-shelled (post-moulting) condition. Observations on mating *O. catharus* in the laboratory showed that males mated only with females smaller than themselves (prior to moulting) and this is in agreement with observations made by Kung (1973) on this species. Furthermore, when groups of males competed for a single pre-moult female in the laboratory, I found that the largest male in the group was always the eventual mating partner.

The interval between mating and spawning in the laboratory was as long as 11 months for one female and 7-8 months for three others and indicates that sperm remain viable for at least this period of time. The maximum viable life span of sperm in the spermathecae is not known for *O. catharus* but was estimated to be 2 years in the majid *Chionoecetes bairdi* (Paul, 1984). It is also not known how many broods of eggs may be fertilized from one insemination, but in the laboratory female *O. catharus* were shown to produce up to four broods of fertilized eggs without re-mating. Therefore, it is possible that female *O. catharus* could produce several broods of eggs over two breeding seasons without requiring a second moult or mating. Despite this, there would still be an advantage for females to moult before each breeding season in order to increase in size and therefore, increase the size of their broods (see

Chapter 3).

It is important that mating occurs when females undergo their annual moult because sperm from the previous mating are believed to be lost at ecdysis. The spermathecal wall in brachyurans is integumental in origin (Bauer, 1986) and therefore is lost at ecdysis, presumably along with all unused sperm. However, Ryan (1967a) and Cheung (1968) observed that part of the chitinous lining of the spermathecae of *Portunus sanguinolentus* and *Menippe mercenaria* respectively, was broken off and not shed with the rest at moult. Therefore, sperm was retained through the moult and in females that were not allowed to re-mate, it was used to fertilize subsequent eggs. I have observed the complete spermathecal wall in cast exoskeletons of female *O. catharus* and assume that all sperm that were in the spermatheca would have been lost. I have not examined the spermathecae of newly moulted, unmated females to check that they were empty, but none of 12 females that were prevented from mating in the laboratory produced eggs in the next breeding season whereas 10 females that mated subsequently produced eggs. It seems highly unlikely therefore, that *O. catharus* females retain sperm through a moult and consequently, it is imperative that mates are available at the time of the annual female moult.

Information presented in Chapter 4 suggested that some *O. catharus* undertake annual migrations into shallow, protected bays and harbours where they spend the winter. These migrations may alleviate some of the predatory pressures associated with the vulnerable period surrounding ecdysis but also they may serve to bring males and females together in dense aggregations at the time of mating. Mating behaviour of *O. catharus* is similar to that described by Hartnoll (1969) for other Portunidae except that males were never seen to carry females after mating. A premating embrace lasting up to 10 days was observed before

the female moulted, and after moulting the pairs stayed in the copulatory position for up to 12 hours before separating. In the laboratory, male *O. catharus* demonstrated a stylized searching behaviour which included the production of acoustic signals that appeared to be elicited by chemical cues in the water in which a pre-moult female was present. Ryan (1966) found that water in which pre-moult females of *Portunus pelagicus* had been kept, elicited searching behaviour in males, whereas water in which intermoult females had been kept did not. Further study indicated that a pheromone was released in the urine of the female (Ryan, 1966).

There is certainly scope for future studies on the mating behaviour of *O. catharus* to identify firstly, the nature and origin of any chemical attractant and secondly, the information content of the male acoustic display. Males produce a rasping sound by rubbing the series of ridges on the ventral surface of both chelae across a sharp ridge on the distal portion of the merus of each first walking leg. The function of such stridulatory behaviour could be to attract females or to advertise the intentions of the male as sexual rather than aggressive.

After mating, females leave the shallow bays and harbours and presumably move to spawning areas although the whereabouts of these is still to be determined. Crab fishermen working in shallow, coastal areas catch a few ovigerous crabs but generally the proportion of females in the catch is very low. This led me to conclude that females aggregate in specific areas, possibly deeper waters, to incubate their eggs (see Chapter 4). Future studies on *O. catharus* should give priority to locating spawning areas so that more detailed information on the reproductive biology of the species can be obtained.

In the present study, indirect evidence was used to obtain approximate estimates of the breeding season and the number of broods of eggs produced per season (see Chapter 3). The main breeding season

in Pegasus Bay, 1984-85 was estimated to be November to March (Fig. 1) but changing environmental conditions from year to year probably affect its limits. In 1987 for example, a local fisherman reported that ovigerous females were present as early as August. Given that the breeding season in 1984-85 was approximately 5 months long, that egg incubation takes about one month, and that the interval between broods is at least two weeks (Chapter 3), it was estimated that most crabs 1+ and older would produce two or three broods per season. Newly matured 0+ crabs probably produce one or two broods in their first season depending on size at first mating and the number of moults occurring during the season. Therefore, female *O. catharus* which survive to maximum size could pass through four breeding seasons in a lifetime and produce up to 10 broods of eggs. With the breeding season occurring between November and March and the main recruitment season being between January and May, larval development time is estimated to be 1-2 months.

Like females, male crabs appear to moult during winter and spring but probably wait until after mating, when females start leaving the mating area (Chapter 4). After their annual moult, males move to feeding grounds where they spend the rest of the year. In Pegasus Bay at least, it is likely that a crab fishery would be viable only in summer and autumn when large males would be most abundant along stretches of sandy beach and other areas where suitable prey (e.g. bivalves) are available. During winter and spring when males are mating and moulting, high densities of crabs may occur in bays and harbours but heavy exploitation should be avoided at these times in order to protect the breeding potential of the population and to avoid taking soft-shelled crabs with low quality meat.

Larval Life History

A clue to the whereabouts of ovigerous females may be found by a study of the distribution of the larvae. The larval stages of *O. catharus* have not been fully described so they were reared at the Edward Percival Field Station, Kaikoura so identifications could be made. Larvae were kept at $16 \pm 1^{\circ}\text{C}$ and fed on freshly hatched nauplii of *Artemia*. Eight zoeal stages occurred before metamorphosis to the megalopa, the first of which appeared 55 days from hatching allowing an average intermoult duration of 7-8 days for each zoeal stage (Table 1). Mortality was highest in the first two zoeal stages and the megalopa and was probably related to food requirements of these stages. Freshly hatched *Artemia* were slightly too large for small zoeae to capture easily and although many fed successfully others apparently did not. The very high mortality of megalopae may also have been due to a dietary deficiency. Sulkin (1978) found that although rotifers were adequate food for early *Callinectes sapidus* larvae, development to megalopae was not possible when only a rotifer diet was used, therefore suggesting that megalopae have more complex dietary requirements.

The larval life of *O. catharus* is unusually long and the megalopae are exceptionally large compared to those of other Portunidae (Table 2). The only other portunids listed in Table 2 to have eight zoeal stages are *Callinectes sapidus* and *C. arcuatus* but most of the species studied to date, including *Ovalipes ocellatus* have no more than six zoeal stages. The very large size of the megalopae of *O. catharus* may be an adaptation to a cold temperate environment in which reproduction is seasonal and where rapid growth to sexual maturity in the first year of benthic life would be aided by large size at settlement. Unfortunately, all the other species in Table 2 are tropical or warm temperate species so

Table 1. *Ovalipes catharus*. Results of a larval rearing experiment conducted at the Edward Percival Field Station at a temperature of $16 \pm 1^\circ\text{C}$. Number of individuals in each larval stage, and the total number and percentage of larvae surviving in 5 day intervals following hatching. I-VII represent the 8 zoeal stages, M = megalopa.

Days after hatching	I	II	III	IV	V	VI	VII	VIII	M	Total number of larvae	% survival
0	280									280	-
5	255									255	91.1
10	32	208								240	85.7
15	3	112	111							226	80.7
20	1	25	192	4						222	79.3
25		1	23	179	10					213	76.1
30			1	29	172	10				212	75.7
35				6	103	101				210	75.0
40					16	143	50			209	74.6
45					2	22	164	18		206	73.6
50							44	133		177	63.2
55							2	163	3	168	60
60								111	28	139	49.6
65								18	49	67	23.9
70									23	30	10.7
75									19	19	6.8
80									10	10	3.6
85									0	0	0

Table 2. Comparison of selected characteristics of larval life history between species of Portunidae. Data all based on laboratory studies from the following sources (in the order that they appear on the table): Fielder et al. (1984), Kurata and Omi (1969), Greenwood and Fielder (1980), Yatsuzuka et al. (1984), Yatsuzuka and Katsushi (1980), Greenwood and Fielder (1979), Yatsuzuka and Katsushi (1982), Costlow and Bookhout (1959), Dittel and Epifanio (1984), Costlow and Bookhout (1966), present study. (*) = field based data.

	No. of zoeal stages	Time to megalopae	Time to 1st crab	Mean size of megalopae (CL)	Mean size of 1st crab (CW)	Rearing Temp.
<i>Charybdis feriata</i>	6	21	-	3.0 mm		26°C
<i>C. acuta</i>	6	24	30	2.3 mm	3 mm	26°C
<i>C. callianassa</i>	5	15	-	1.9 mm	1.4 mm	26°C
<i>C. japonica</i>	5-6	15	19	2.1 mm	1.9 mm	26°C
<i>Portunus pelagicus</i>	4	13	18	1.7 mm	2.5 mm	26°C
<i>P. rubromarginatus</i>	3	10	-	1.62 mm	-	25°C
<i>P. trituberculatus</i>	4-5	13	17	2.0 mm	3.0 mm	26°C
<i>Callinectes sapidus</i>	6-8	35-47	45-55	2.0 mm	2.5 mm	25°C
<i>C. arcuatus</i>	8	51	69	-	2.9 mm	24°C
<i>Ovalipes ocellatus</i>	5	13	18	1.4 mm	1.0 mm	25°C
	5	18	26	1.4 mm	1.0 mm	20°C
<i>O. catharus</i>	8	60	-	4.5(5.3 mm)*	(6.3 mm)*	16°C

it is impossible to compare development of *O. catharus* with that of other cold water species.

Wear and Fielder (1985) stated that *O. catharus* larvae "are rare in the inshore shallow-water and harbour plankton in spite of the abundance of adults of this species nearby." They did, however, find 16 late zoeae in an Agassiz trawl sample from a depth of 527-680 m at East Cape in January 1979, and as a consequence stated, "It must be assumed, therefore, that the larvae live offshore in deeper water, perhaps near the bottom in late zoeal stages, and migrate inshore in the megalopa stage when they may occur in surface plankton samples" (Wear and Fielder, 1985). I also found no *O. catharus* larvae in an intensive plankton sampling program off the Kaikoura peninsula in summer 1984-85. However, megalopae were caught at Kaikoura during December and January by attracting them to the surface at night with a strong light in an area where juvenile *O. catharus* occurred. That metamorphosis was imminent in these megalopae was determined by taking them back to the laboratory where they moulted to the first crab stage within 3 days. Clearly, a more detailed study is required of the distribution and ecology of *O. catharus* larvae but at present it seems as though they may occur in oceanic rather than coastal waters. Therefore, the movements of *O. catharus* females in relation to spawning may be associated with the feeding and dispersal requirements of the larvae.

Total larval development time based on laboratory rearing was estimated to be 70-80 days. However, larval growth rates can be strongly dependent on temperature and food availability (Sandoz and Rogers, 1944; Sulkin, 1975; Dawirs, 1979; Anger and Dawirs, 1981) and, therefore, larval growth in the field would be expected to differ somewhat from that observed in the laboratory and to vary between years and seasons (Anger, 1983). Nevertheless, my estimate of a 1-2 month planktonic phase, based

on breeding and recruitment seasons, seems a little short considering the number of stages involved, and it is possible that the breeding season in Pegasus Bay starts a little earlier than estimated.

Life History in Tasman Bay

My study of a population of *O. catharus* in Tasman Bay was not as intensive as that in Pegasus Bay and was designed mainly to obtain preliminary estimates of reproductive traits and growth rate for comparison with the Pegasus Bay population. The size distribution of crabs at any one time was more evenly spread than at Pegasus Bay and

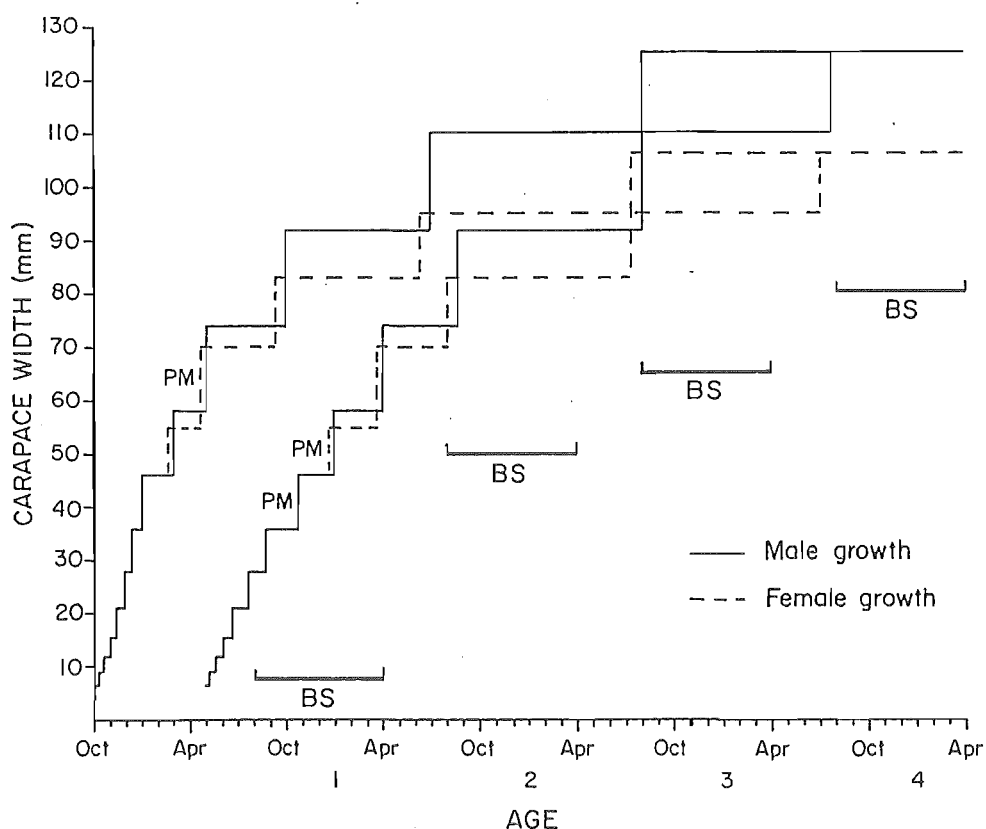


Fig. 2. *Ovalipes catharus*. A generalised scheme of the life history of crabs in Tasman Bay. PM = pubertal moult, BS = breeding season.

as a result cohorts were less distinct (see Chapter 5). However, I was able to obtain estimates of growth rates (Chapter 5), size at maturity, breeding season and fecundity (Chapter 6), and a preliminary scheme of the post-larval life history of *O. catharus* in Tasman Bay is shown in Fig. 2. Recruitment occurred over a longer period in Tasman Bay (approximately October to May) than Pegasus Bay and was the main reason for the greater size distribution of crabs each month. Like crabs in Pegasus Bay, those in Tasman Bay reached maturity within their first year of benthic life (either instars 8, 9 or 10). However, because of their faster growth rates and the earlier breeding season (beginning in August), a greater proportion of Tasman Bay crabs attain maturity in instars 8 and 9 (Fig. 2) than in Pegasus Bay (Fig. 1). Therefore, mean size at maturity was lower in Tasman Bay than Pegasus Bay. At the end of the first breeding season moulting became an annual winter event as in Pegasus Bay and females surviving to maximum size pass through 3 or 4 breeding seasons. The length of the breeding season (8 months) suggests that females may produce three broods annually, i.e. up to 11 or 12 broods in a lifetime.

Like Pegasus Bay crabs, those in Tasman Bay moulted 13 times after settlement of megalopae, before attaining maximum size. Even though the abundance of instar 13 crabs was quite in high Tasman Bay, none were caught that appeared to belong to a 14th instar. In Pegasus Bay the high mortality of large crabs (Chapter 2) and the relationship of decreasing percentage moult increment on premoult size (see Chapter 1) suggested that growth of *O. catharus* was indeterminate and therefore, maximum size was determined by mortality. However, the observation of large numbers of instar 13 crabs in Tasman Bay suggests that *O. catharus* may have determinate growth. Further investigation is required into the ability of instar 13 crabs to moult to a 14th instar and for the existence

of a mechanism which terminates moulting.

In summary, the overall life history patterns were similar in the two crab populations studied and differences in particular life history traits were mainly in response to environmental factors, primarily temperature.

CONCLUSION

Ovalipes catharus was studied in Pegasus Bay over a period of 24 months and at Tasman bay for 12 months with the main objectives being to estimate growth rates, female size at maturity and annual fecundity, and to investigate how environmental factors affect these traits. The main points arising from this study are:

1. Variation in individual moult increments resulted in increasing variation in size within successive juvenile instars. However, after sexual maturity, size variation within instars decreased which suggests there is a negative feedback mechanism operating whereby individuals which are large for a given instar undergo a smaller increment than individuals which are small for that instar. The nature of this mechanism requires further investigation.
2. The relatively low size variation within instars enabled instars to be recognized as modes in size frequency distributions. As a result, reliable estimates of growth rates of crabs in a natural population were obtained using size frequency analysis.
3. Sexual maturity was attained by females in their first year of benthic life as a consequence of their large size at settlement and rapid juvenile growth rates. The size at which maturity was attained depended on the settlement date and growth rate of individuals in relation to the onset of the population's breeding season.

4. Life history traits in two geographically separated populations (Pegasus Bay and Tasman Bay) differed primarily in response to environmental temperatures. Increased temperature prolonged the breeding season and enhanced growth rates of crabs in Tasman Bay. This in turn resulted in sexual maturity being attained sooner and at a smaller size than in Pegasus Bay. Higher temperature and greater food availability may also have been responsible for the enhanced survival of large crabs in Tasman Bay and were predicted to result in an increase in brood production rate.
5. Seasonal movements of crabs appeared to occur in relation to moulting and breeding cycles. Males and females were observed to aggregate in a shallow, sheltered bay (Little Akaloa) during winter and mate there at the time of the female moult. Males probably moulted when females had migrated away after mating. Males moved to foraging areas to spend the summer and autumn whereas females migrated to spawning grounds, the whereabouts of which are as yet unknown but are probably offshore in deeper water.

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