

Not to be cited without prior permission of the author(s)

New Zealand Fisheries Assessment Research Document 99/18

A summary of biology and commercial landings and a stock assessment of paddle crabs, *Ovalipes catharus* (White, 1843) (Crustacea, Portunidae), in New Zealand

Darren W. Stevens

**NIWA
PO Box 14-901
Kilbirnie
Wellington**

May 1999

Ministry of Fisheries, Wellington

This series documents the scientific basis for stock assessments and fisheries management advice in New Zealand. It addresses the issues of the day in the current legislative context and in the time frames required. The documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

A summary of biology and commercial landings and a stock assessment of paddle crabs, *Ovalipes catharus* (White 1843) (Crustacea, Portunidae), in New Zealand

Darren W. Stevens

New Zealand Fisheries Assessment Research Document 99/18. 26 p.

1. EXECUTIVE SUMMARY

The paddle crab, *Ovalipes catharus* (White, 1843), is a common, versatile, and opportunistic predator found off sandy beaches, and in harbours and estuaries throughout New Zealand and east and south Australia. It is a large and fast growing species, reaching a maximum size of 150 mm carapace width (CW) after 4 or 5 years. Sex ratios are highly variable between and within populations. The species shows strong diel rhythms and seasonal patterns of movement.

Biological and fishery data of *O. catharus* is reviewed. Information on growth, reproduction, diet, movement, behaviour, natural mortality, size-frequency distributions, and size-weight relationships is provided. The commercial and non-commercial fisheries are described.

The market is mainly for large crabs (males over 80 mm CW). The fishery is probably lightly exploited. It seems unlikely that separate stocks of *O. catharus* occur in New Zealand waters.

2. INTRODUCTION

Swimming crabs (Family Portunidae) typically have a thin, smooth, carapace, long, flattened legs and paddle-shaped dactyls on their last pair of walking legs. Their thinner shell makes them lighter than many other crabs but more vulnerable to physical attack. It is thought that swimming may have evolved as a means of predator escape, but it also facilitates wide ranging foraging (McLay & Osborne 1985).

There are seven species of swimming crab in New Zealand waters, although only *Ovalipes catharus* has commercial potential (Osborne 1987a). *Portunis pelagicus* is known only from a single specimen captured in the Hauraki Gulf, *Scylla serrata* has a limited distribution in northern New Zealand, *Ovalipes mollerii* is found in small numbers in northern New Zealand (Osborne 1987a) and the Chatham Islands (N. Bagley, NIWA, pers. comm.), and *Macropipus corrugatus*, *Nectocarcinus antarcticus*, and *N. bennetti* occur commonly off the South Island (Osborne 1987a). Only *O. catharus* is known to be taken recreationally in New Zealand waters. Both *S. serrata* and *P. pelagicus* support commercial fishing (Armstrong 1985) and aquaculture industries in Southeast Asia and India, but are known in New Zealand as only occasional visitors (Wear 1980).

This document reviews the biological and fisheries data on *O. catharus* in New Zealand waters. Information is provided on stock structure, reproduction, age and growth, feeding, and behaviour. The commercial and non-commercial fisheries are described.

2.2 Literature review

There is an extensive literature on *O. catharus*. The key references are: life history and population biology - Kung (1973), Armstrong (1985), Osborne (1987a); feeding biology - Davidson (1987), Wear & Haddon (1987); impact on shellfish - Wear (1984); reproduction - Haddon & Wear (1993), Haddon (1994); relative growth - Davidson & Marsden (1987); and marketing - Cameron (1984). There have also been a number of postgraduate studies: Clark (1978), Richards (1992), and Davidson (1994).

Most studies deal with aspects of reproduction (Kung 1973, Wear 1982, Armstrong 1985, 1986, 1988, Osborne 1987a, Haddon 1994), growth (Wear 1982, Armstrong 1985, 1986, Osborne 1987a, Davidson 1987), diet (Armstrong 1986, Davidson 1987, Wear & Haddon 1987, Wear 1988b), feeding biology and behaviour (Wear 1984, Davidson 1986, Haddon & Wear 1987), population dynamics (Kung 1973, Clark 1978, Armstrong 1985, Osborne 1987a), seasonal movements (Osborne 1987a, 1987b), predation on bivalves (Haddon *et al.* 1987, Haddon 1988, Wear 1982, 1984, 1988b), and the potential of the fishery (Clark 1978, Armstrong 1986, Stead 1983, 1984, Anonymous 1984a, 1984b, Cameron 1984, Wear 1982, 1984, 1988a).

There have been other studies on systematics (Stevenson & Rees 1968), burying behaviour (McLay & Osborne 1985), respiratory and vascular physiology (Taylor 1990, Richards 1992, Davidson 1994, Davidson & Taylor 1995), avoidance of post-coital cannibalism (Haddon 1995), aquaculture prospects (Wear 1980), and larval development (Kung 1973, Wear & Fielder 1985), that are less applicable to stock assessment.

3. REVIEW OF THE FISHERY

3.1 Commercial fishery

Commercial interest in paddle crabs was first realised in New Zealand in 1977–78 when Napier fishers caught good numbers of large crabs just outside the surf zone of Westshore Beach in baited lift and set-pots (Anonymous 1983). Small landings were also taken off Paremata, Motueka, and Akaroa in 1977 (Figure 1), and elsewhere the following year (Anonymous 1983). Since then the fishery has expanded rapidly, although annual catches have varied, mainly due to marketing problems (Wear 1988a). Currently, about 450 t of paddle crabs are landed annually in New Zealand waters (*see* Section 3.1.1). Crabs are marketed live, as whole cooked crabs, or as crab meat (Wear 1988a).

Attempts were made to establish a soft-shelled crab industry in New Zealand in the late 1980s (Anonymous 1986). However, the potential is constrained by current commercial regulations that prohibit the targeting of paddle crabs by trawling or dredging (*see* Section 3.1.4).

Commercial fishing methods include set-pots, lift-pots, set-nets, dredges, and, on occasions trawling (Stead 1984, Wear 1988a). Bycatch can be a problem with set-nets (Wear 1988a) and it is labour intensive to remove the crabs. Crabs can not legally be targeted by trawling, and long trawl shots often damage the catch (Wear 1988a). Static methods, such as lift-pots and set-pots, minimise damage and provide the best quality crabs (Stead 1984). Potting is the most effective means of catching crabs (Stead 1984, Wear 1988a). Currently, unless specifically authorised permits are held, only hand-gathering and potting (not rock lobster pots) are legal methods for commercially targeting paddle crabs (*see* Section 3.1.3). Catch rates vary considerably with method, season, and area (Wear 1988a).

3.1.1 Annual landings

Landings have increased markedly from 775 kg in 1977 to 306 t in 1985 and 449 t in 1997–98 (CEL_R^{estimated}, Table 1). Annual catches have varied (Figure 2), mainly due to marketing problems, and estimates are likely to be conservative (Wear 1988a).

Estimates of annual landings of paddle crabs for the calendar years 1977 to 1986 and for the commercial fishing years 1986–87 to 1997–98 are given in Table 1. The best estimates for the calendar years 1977 to 1986 are from the Fisheries Statistics Unit (FSU) data summarised by Stead (1984) and Wear (1988a). More comprehensive data were unavailable from this period to the transitional year from FSU to the Quota Management System (QMS) in 1988–89. The best estimates for the fishing years

1989–90 to 1997–98 are the greater of the sum of the Catch Landing Return (CLR) plus the landed total on the Catch, Effort, and Landing Return ($CELR_{landed}$), or the Licensed Fish Receiver Return (LFRR) data. Usually the sum of the CLR and $CELR_{landed}$ was used, although the values were usually similar.

Recent communication with Ministry of Fisheries staff has highlighted a minor problem with catch/effort data from inshore fishing vessels ($CELR_{estimated}$). Sometimes PAD was designated as a target species on the CELR form and the weight given in the total (kg) column but no data were provided in the species code/weight column. This oversight means that these data are not entered into the $CELR_{estimated}$ totals for the fishing year. These data have been added to the $CELR_{estimated}$ totals in Table 1.

The $CELR_{estimated}$ and $CELR_{landed}$ values produced by smaller (generally inshore) vessels should agree with each other closely, as should the sum of the CLR (larger, generally deeper water vessels) and $CELR_{landed}$ and the LFRR data. For paddle crabs there is very little difference between these values (*see* Table 1) implying minimal (recorded) discards, and accurate reporting of catches. However, many paddle crabs are known to be discarded from inshore trawl operations targeting species such as flatfish (Wear 1988a), so it is likely they are not always recorded. This may have resulted in substantial under-reporting of catches. There is no legal requirement to record discards of paddle crabs as they are a non-quota species.

There is no clear seasonal trend to paddle crab landings (Figure 3), although in some years more crabs are caught during the autumn (February to May) and spring (September to December). Given the abundance of paddle crabs around much of our coast-line it is likely that catches are related to the availability of fishers and/or market demands.

The estimated primary value (i.e., port price) of New Zealand's paddle crab fishery was about \$431 000 in 1996–97 and \$472 000 in 1997–98. These estimates are calculated from the best estimates of landings from Table 1 and a 1995 port price of \$1050 per t (NZFIB 1996).

3.1.2 Fishing areas

The major ports of landing for paddle crabs in the early 1980s were Tauranga, Napier, Motueka, Mercury Bay, and Nelson (Stead 1984, Wear 1988a).

The estimated landings ($CELR_{landing} + CLR$) by Quota Management Area (QMA) for the fishing years 1989–90 to 1997–98 are presented in Table 2. They show the main fishing areas for paddle crabs to be the east coast of New Zealand (QMAs 1, 2, and 3), the Challenger area (QMA 7), and the Central west area (QMA 8). For the 1989–90 and 1990–91 fishing years the highest reported landings were in QMA 7 followed by QMAs 2, 3, and 1. Since the 1991–92 fishing year the Auckland east Quota Management Area (QMA 1) has reported the highest landings. This probably reflects the high population and subsequently larger market of the Auckland area rather than a greater crab biomass. In the 1997–98 fishing year there was a substantial increase in landings in the Central East Quota Management Area (QMA2).

The Chatham Islands (QMA 4), and the Sub-Antarctic Islands (QMA 6) have reported relatively low catches for most years. This is not surprising given the small size of the islands and their associated sandy coastlines, their relative isolation from local markets, and the prohibition on fishing within 12 n. miles of the Auckland Islands (Sullivan & Lang 1995). The reported landing of 55 t and 25 t of paddle crab from the Sub-Antarctic area in the 1995–96 and 1996–97 fishing years seems unusual, and needs verification. Most of these landings were taken from the Auckland Island Shelf in around 200 m depth. QMAs 3, 4, and 5 have individual competitive quotas of 100, 50, and 100 t respectively (*see* Section

3.1.3), although no area has ever come close to catching its quota. QMA 9 (Auckland west) has a low catch history, the reason for which is unknown. Commercial fishing is prohibited in the Kermadec Islands Quota Management Area (QMA 10) (*see* Section 3.1.3).

3.1.3 Regulations

Paddle crabs are a non-quota species and are subject to a few regulations governing commercial fishing. These regulations vary by QMA. The following information is taken from "Brooker's Fisheries Law" by Sullivan & Lang (1995).

Legalising the taking and possession of paddle crabs

For QMAs 1–5, 6–9

Paddle crabs (and numerous other species) "may be taken subject to competitive or individual quotas, method restrictions, etc." (Regulations 11 AB, 14 AA, 15 CB, 20 D)

Ovigerous females

For QMAs 2, 7, 8

"No commercial fisherman shall take ... any paddle crab that is carrying any external eggs or from which any of the external eggs have been removed by artificial means, ... or be in possession of such paddle crab ..." (Regulations 14D, 14F)

For QMAs 3–6

As above, but includes paddle crabs "from which the egg-bearing appendages have been removed ..." (Regulations 11J, 15H)

Fishing methods

For QMAs 2, 7, 8

"No commercial fisherman shall use any method other than hand-gathering or the use of a pot (not being a rock lobster pot) to fish for any paddle crab, octopus, or hagfish ..." This does not apply to commercial fishermen targeting rocklobster and paddle crabs caught as bycatch. (Regulation 14E)

For QMAs 1, 3, 4–6, 9

As above "unless that method is specifically authorised in a commercial fishing permit held by that commercial fisherman." In QMAs 1 and 9 there is a restriction on fishers with set net permits to a minimum net mesh size of 200 mm. (Regulations 5B, 11K, 15I)

Competitive quotas

For QMAs 3–5

Quota Management Areas 3, 4, and 5 are unique in the New Zealand paddle crab fishery in that they have annual competitive quotas of 100, 50, and 100 t respectively. Once a quota is deemed caught, the Director-General gives notice of the fact, and the fishery is closed for the remainder of that fishing year. (Regulations 11I, 15G)

Minimum legal size

For QMAs 3–6.

"No commercial fisherman shall take ... any paddle crab ... that has a carapace width of less than 75 mm at its widest point." (Regulations 11J, 15H)

Set net mesh restrictions

For QMAs 1, 9. *See Fishing methods.* (Regulation 5B)

Fishing prohibited

For QMA 10

“No commercial fisherman shall at any time take any fish, aquatic life, or seaweed from the waters of quota management area 10, or be in possession of any fish, aquatic life, or seaweed from those waters.” (Regulation 18A)

3.1.4 Management

The minimum legal size limit of 75 mm CW in QMAs 3, 4, 5, and 6 (Sullivan & Lang 1995) ensures that females have spawned at least once and males have mated (Armstrong 1986). The female broodstock are further protected by a market-driven demand for large crabs (generally over 100 mm CW: females rarely grow to this size) (Wear 1988a). Prohibiting the take of ovigerous female crabs (females carrying external eggs) may help prevent ‘egg overfishing’. Differences in growth and sex ratios between areas and diel and seasonal movements may need to be considered if paddle crabs are made a QMS species.

Paddle crabs are active mainly at night (Clark 1978), and commercial catches are likely to be greatest then. Pots are more selective, with minimal bycatch, and cause less damage than dredging, trawling, or set-netting (this is particularly important for ovigerous females). Restrictions on mesh size and/or escape gaps would allow undersized crabs to escape (Armstrong 1988).

A soft-shelled crab fishery directed towards the lucrative American and Asian markets would require amendments to the current commercial regulations to allow crabs to be targeted by trawling and/or dredging (M. Tait, NIWA, pers comm.). Soft-shelled crabs do not generally feed, and are, therefore, difficult to catch in pots. At present, they can legally be taken only by trawls or dredges, as a bycatch of other fisheries, for example, flatfish.

3.2 Non-commercial fisheries

3.2.1 Customary fisheries

There is no quantitative information on the current level of customary take. Historically, there seems to have been no specific targeting of paddle crabs, although they are likely to have been taken during shellfish collecting on sandy coasts.

3.2.2 Recreational fishery

Preliminary data from the 1996 national marine recreational fishing survey indicate that paddle crabs are seldom caught (Dave Fisher, NIWA, pers. comm.). Paddle crabs are taken as a bycatch of beach and estuarine seining and in set-nets throughout much of their geographical range.

3.2.3 Regulations

There are no specific recreational regulations for paddle crabs. Regulations which govern netting practices apply, in particular a maximum size of 60 m for set nets and that it is illegal to bait nets (Ministry of Fisheries 1995).

4 RESEARCH

4.1 Distribution and abundance

The paddle crab is found off sandy beaches, and in harbours and estuaries throughout mainland New Zealand, the Chatham Islands, and east and south Australia (Wear & Haddon 1987, Osborne 1987a). The distribution of *O. catharus* is probably limited by the availability of substrates suitable for burying. They are abundant from the intertidal zone to about 10 m depth (Paul 1986, Armstrong 1985, Wear 1988a), but they do occur in much deeper water, and have been caught several kilometres offshore in trawls and set nets (Stead 1983, 1984). The locations of research tows which caught paddle crabs is shown in Figure 4. There is a paucity of data, although this is not surprising given that paddle crabs are found in shallow water where trawlers rarely operate. It is likely that records of paddle crabs caught south of Stewart Island by research tows were either for *Nectocarcinus antarcticus* or *N. bennetti* (N. Bagley, NIWA, pers comm.).

Paddle crabs are likely to congregate in areas where preferred prey species are abundant (up to 10 m depth for most shellfish prey) (Armstrong 1985). Their distribution may also be influenced by competition with other crab species (see Section 4.8.1), and larval recruitment patterns (Armstrong 1985).

The paddle crab appears to have increased significantly in numbers since the 1970s, possibly as a result of a decline in predatory coastal fishes, such as snapper, *Pagrus auratus*, rig, *Mustelus lenticulatus*, and elephantfish, *Callorhynchus milii* (Stead 1983, 1984, Paul 1986, Wear 1982, 1984, 1988a); discards from fishing vessels (Wear 1982, Stead 1984); and/or "favourable hydrological conditions ... for larval survival and juvenile recruitment" (Wear 1982). Concern has been expressed as to the impact of an increased number of paddle crabs on commercially and historically important finfish (Stead 1983, 1984) and shellfish stocks (Wear 1982, 1984, Armstrong, 1986) in coastal waters.

4.2 Stock structure

It is not known whether biologically distinct stocks occur, although this seems unlikely given that the species is found throughout New Zealand waters, and, from tagging experiments, appears to be highly migratory (Wear 1982, Stead 1983). Paddle crabs tagged at Plimmerton beach, near Wellington, were recaptured 40 km away 1 month later (Wear 1982). Sand dominates 57% of New Zealand's 13 000 km of coastline, and all of this is potentially suitable habitat for paddle crabs (Wear 1988a). There is probably also widespread larval dispersal as larvae spend 2 months offshore in deeper water (to at least 700 m) before settling out as megalopae (Wear 1982). Genetically distinct populations may occur in isolated areas such as the Chatham Islands and Australia.

4.3 Reproduction

4.3.1 Early life history

As with other species of portunids, female paddle crabs can mate only after moulting. Male crabs protect and carry pre-moult females (pre-copulatory embrace, Kung 1973, Wear & Fielder 1985) for 3–4 days (up to 17 days) to ensure copulation (Kung 1973). Mating generally occurs during winter and spring (May to November) in sheltered inshore waters (Osborne 1987a), although Kung (1973) observed mating behaviour throughout the year in Paremata Harbour, near Wellington. Copulation generally lasts 12 to 36 hours but can last up to 4 days (Haddon 1994). Monthly examination of vasa deferentia from mature male crabs showed that they always contained mature sperm (Armstrong 1988).

After copulation the male crab generally guards the female until she is no longer sexually receptive (post-copulatory embrace, Haddon 1995), thereby protecting the female when she is soft-shelled and vulnerable. Pre- and post-copulatory embraces have been reported for a number of portunid crabs and appear to be universal in the family (e.g., Dunham 1978, Berrill & Arsenault 1982). It is likely that these behavioural responses are initiated by sex pheromones (Dunham 1978).

Sperm are stored by females in paired spermatheca (seminal receptacles), where they remain viable for several months (Wear & Fielder 1985, Osborne 1987a). When the ovaries mature, the eggs are fertilised as they pass down the oviducts (Wear & Fielder 1985), and released through paired female genital openings (vulvae) on the ventral surface (Kung 1973). The abdominal pleopods are beaten backwards, forwards, and outwards to pick up the eggs on specialised setae attached to the pleopods (Kung 1973). Females are thought to migrate to deeper water to spawn, and it is likely that all ripe ova are discharged (Osborne 1987a). Spawning takes place while the female is buried and lasts for at least 12 hours (Kung 1973). The timing of spawning appears to vary with location, but generally occurs over the warmer months (September to March) (Kung 1973, Armstrong 1985, Osborne 1987a, 1987b). Haddon & Wear (1993) observed three distinct spawning peaks in ovigerous females from Plimmerton beach, near Wellington; August, late November to early December, and early January to early April.

Two spawning mechanisms have been observed in *O. catharus*: non-synchronous (Osborne 1987b) and group-synchronous (Armstrong 1988). In Wellington (Kung 1973, Wear 1982, Haddon & Wear 1993), Tasman Bay (Osborne 1987a), and Canterbury (Osborne 1987a), spawning does not appear to be synchronised (non-synchronous spawning) and females may spawn several times during the season, depending on the availability of stored sperm: sperm cannot be retained through a moult (Osborne 1987a, Haddon & Wear 1993).

In Blueskin Bay, Otago, Armstrong (1988) found that paddle crabs were group-synchronous, with one clutch of eggs developing to maturity over winter, and spawned between September and February. His evidence was based on oocyte size-frequency analysis from which “it appeared that one clutch of oocytes was developed and spawned completely.” There was “no evidence of multiple spawning using sperm from a single copulation ...” This apparent discrepancy may reflect a difference in water temperature between the more northern study sites and Otago (Haddon & Wear 1993). Armstrong felt that Kung’s (1973) study supported “an alternative spawning mechanism in the Wellington population whereby a clutch of oocytes is matured, held in arrested development and then released in batches over the spawning season.”

After spawning the eggs are incubated until they hatch (Osborne 1987a). In laboratory studies, incubation periods varied with the ambient water temperature (Kung 1973). Eggs spawned in mid summer hatched on average 15 days earlier (mean = 35 days) than those spawned in spring (mean = 50.2 days) (Kung 1973).

O. catharus has a typical portunid larval life of eight zoea stages and a (crab-like) megalopa (Wear & Fielder 1985), which lasts for about 2 months in total (Wear 1982). The larvae are thought to live offshore in deeper water, migrating inshore in the megalopa stage to settle (Wear & Fielder 1985) from January to May (Osborne 1987a).

4.3.2 Size at sexual maturity

Criteria which have been used to designate sexual maturity in paddle crabs include the presence of eggs in females, external secondary sexual characteristics (Kung 1973, Clark 1978), evidence of physical signs of copulation (Osborne 1987a), changes in relative growth – including secondary sexual characteristics (Kung 1973, Clark 1978, Davidson & Marsden 1987, Osborne 1987a, Armstrong 1988), and maturity of the gonads (Osborne 1987a, Armstrong 1988).

As female paddle crabs mature the abdomen broadens to increase space available for egg attachment and provide an incubation chamber. Sexual maturity in males is more difficult to detect externally. Kung (1973) found the colour on the inner surface of the immovable (fixed) claw finger to be a reasonable indicator of sexual maturity. In immature crabs the finger is mainly white with a small red spot. As the crab matures the finger develops a distinctive red patch in sub-adults which extends to cover half or more of the finger in mature crabs.

Paddle crabs from Wellington, Tasman Bay, and Canterbury mature at a smaller size than those from Otago (Armstrong 1988). This is likely to be related to differences in water temperature with latitude (Osborne 1987a, Armstrong 1988). Similar inverse relationships with water temperature and size at sexual maturity have been shown for a number of decapods, including the rock lobster *Jasus edwardsii* (Annala *et al.* 1980).

In Paremata Harbour, Kung (1973) found that female crabs mature at 45 mm CW, and males mature at 50 mm CW (Armstrong 1988). This estimate was based on the relative shape of the abdomen in females (width to length ratio), and the coloration of the claws in males (Armstrong 1988).

In the Wellington area, Wear (1982) found that females mature at 58 mm CW and males at 67 mm CW, although it is not known what characters were used to designate sexual maturity.

In Tasman Bay, Osborne (1987a) found that 50% of females reach maturity at 50.1 mm CW. This is considerably smaller than for crabs in Pegasus Bay (65.5 mm CW) and probably a function of increased growth rates (*see* Section 4.4) enabling early recruits to reach maturity and produce a brood of eggs within the same breeding season as settlement.

In Canterbury, Davidson & Marsden (1987) found that male crabs reach the pubertal moult at 40 mm CW and females at 35–40 mm CW but the usefulness of this criterion as an indicator of sexual maturity is refuted by Osborne (1987a).

In Pegasus Bay, Canterbury, Osborne (1987a) found that most females reach maturity in the first reproductive season after hatching with late recruits maturing at a smaller size and earlier age. According to Osborne (1987a), the size at which 50% of females showed signs of copulation was 65.5 mm CW, while at 71.5 mm CW 50% of females had mature gonads: 97% of females over 70 mm CW had mated, while 74% of females under 70 mm CW had not mated.

In Blueskin Bay, Otago, Armstrong (1988) found that the size at which 50% of females were mature (ovaries visible to the naked eye) was 55–59.9 mm CW, while 100% were mature over 65 mm CW. At 60–64.9 mm CW, 50% of males were mature (contained sperm in their vasa deferentia), while 100% were mature over 75 mm CW. Based on the ratio of female abdomen width to carapace width, a mean size at maturity for females crabs of 55 mm CW was extrapolated from regression lines.

4.3.3 Brood fecundity

A number of estimates of brood fecundity (the number of eggs per brood) have been made (Table 3). They range from 82 000 to 2 100 000 eggs per brood.

Although the sample sizes are small, fecundity is highly variable, and there may be annual differences. It appears that females from the cooler waters of Otago (Armstrong 1985) may have larger broods than those from the warmer waters of Canterbury (Osborne 1987a) and Wellington (Kung 1973, Haddon 1994). However, paddle crabs from Otago produce only one brood of eggs per season (*see* Section 4.3.1) while those further north commonly produce two and on occasions three broods per season. Variation in brood fecundity can occur from disease, egg predation (*see* Section 4.8), natural

developmental failures (Perkins 1971 in Haddon 1994), and variation in energy reserves for reproduction (Osborne 1987a).

4.3.4 Number of broods per year

There is no morphological way of determining the number of broods a female has had during a given season, so estimates of annual fecundity are little more than speculative. Larger females generally produce more broods per season than smaller ones, although there is considerable variation.

Laboratory experiments conducted by Haddon & Wear (1993) provided the following estimates for 30 captive females from 34 to 103 mm CW in Wellington waters.

Female size class	Broods per season
< 65	1.2
66–80	2.0
81–90	2.44
91–100	3.0
> 100	3.33*

*All crabs > 100 mm CW died before extruding their last batch of eggs. This figure includes this batch.

Similar experiments by Osborne (1987a) provided the following estimates for 17 captive females from Canterbury waters.

females < 80 mm CW	1.2 broods per season
females > 80 mm CW	2.2 broods per season

It is thought that newly recruited (0+) crabs would moult to maturity late in the breeding season and produce only one brood. Larger crabs (1+ and 2+) would breed earlier in the season and produce at least two broods annually. Osborne estimated a mean captive incubation period of 30.9 days at a mean interval between broods of 18 days. Based on these data, it is possible for a female paddle crab to spawn at 50 day intervals and produce three broods over the course of a 5 month reproductive season, depending on the availability of stored sperm. This is in close agreement with the findings of Kung (1973) who found a mean interval between broods of 62 days and up to three broods per year.

4.3.5 Annual fecundity

Annual fecundity is determined by the number of eggs per brood (brood fecundity) and the number of broods per year (Osborne 1987a). Generally both these parameters are size dependant (Osborne 1987a) and highly variable.

Osborne (1987a) found that crabs from Tasman Bay had a longer breeding season than those at Pegasus Bay, Canterbury, and probably produced more broods of eggs per season since season and temperature affect metabolism and egg development. This may help explain the single synchronous spawning per year observed in the southerly population in Blueskin Bay, Otago, by Armstrong (1988), and the presence of three distinct egg-bearing peaks in Plimmerton Beach near Wellington by Haddon & Wear (1993) (*see* Section 4.3.1).

Osborne (1987a) used a modified Caddy egg per recruit model to “determine the number of eggs produced by 1000 individual recruits entering a fishery.” The model was used for the Pegasus Bay and Tasman Bay populations (Table 4). While there are inherent problems with calculating annual fecundity (*see* Section 4.3.4) it is a useful comparison.

The reproductive potential for each instar was calculated as follows:

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

where E_m is the total number of eggs produced in instar m , S_m is the proportion of sexually mature females in instar m , D_m is the extrusion factor (essentially the number of broods per season) for instar m , Q_m is the mean number of late stage eggs per female (brood size) in instar m , N_m is the number of females in instar m .

The total egg production (E_t) for all instars was calculated as follows:

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

where \max = the instar of the largest sized female crab.

The results of this egg production comparison are presented in Table 4. The mean size at maturity is smaller in Tasman Bay than Pegasus Bay, and this is reflected in the larger proportion of sexually mature females in instars 8 and 9 in Tasman Bay than in Pegasus Bay. The relationship between carapace width and brood fecundity was not significant ($P > 0.05$ ANOVA), but the numbers of broods per year is thought to be greater in Tasman Bay (*see* Section 4.3.4). This is because the Tasman Bay crabs have a longer reproductive season than those in Pegasus Bay (8 against 5 months). As a result, "the overall reproductive potential of the Tasman Bay population may be as much as three times that of the Pegasus Bay population" (*see* Table 4). "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."

4.4 Age and growth

Crustacean ageing is difficult as all calcified structures are lost at each moult. Female crabs moult during winter before mating, and males are thought to moult slightly later after the females have left for their spawning grounds (Osborne 1987a, 1987b). Crustacean growth is based on two components: the moult increment or the change in size at each moult, and intermoult duration (moult frequency) or the time period between successive moults (Osborne 1987a). As premoult size increases the moult increment and intermoult duration increase, although the relationship is not linear. Factors which can influence crustacean growth rates between and within populations include temperature, food quality and quantity, salinity, and parasitism (Hartnoll 1982).

O. catharus is a relatively large and fast growing species. In Canterbury waters, *O. catharus* reaches a maximum size of 130 mm CW (males only) after 13 postlarval moults and 3 to 4 years after settlement (Osborne 1987a). Other studies have reported larger maximum sizes for male crabs: 140+ mm CW (Wear 1982) and 150 mm CW (Stead 1983, Armstrong 1985, Paul 1986).

Osborne (1987a) found three distinct growth phases in paddle crabs from Canterbury waters, based on premoult size, moult increment, and intermoult duration:

- Juveniles (less than 30 mm CW) grow very rapidly and moult many times.
- Sub-adults (less than 55 mm CW) grow more slowly than juveniles. The growth phase lasts for two intermoult periods and is thought to correspond to the development of gonads.

- Adults (greater than 55 mm CW) grow more slowly due to gonad maturation, and in females, the development of secondary sexual characteristics (i.e. the abdomen becomes broader).

As females mature (instar 8 onwards, Osborne 1987a, Haddon 1989) there is a significant reduction in growth rate, thought to be due to the greater energy costs of egg bearing than sperm production (Osborne 1987a). Because of this, females crabs attain a smaller maximum size (115 mm CW, Osborne 1987a) than males (150+ mm CW, Armstrong 1985).

Most paddle crabs studied by Osborne (1987a) in Canterbury waters showed no consistent intermoult period. Individual crabs seemed to grow by a series of random moult increments, punctuated at times by compensatory moults. Compensatory growth is a negative feedback mechanism, “whereby specimens which are too large for that instar experience a smaller than normal moult increment, and vice versa” (Hartnoll & Dalley 1981). This results in individuals of a specified number of instars being all reasonably close to the same size (Hartnoll & Dalley 1981). In apparent contrast, Wear (1982) found that growth is fairly constant in *O. catharus* from Wellington waters, and that with each moult CW increases by about 22 % (compare this figure with Tasman Bay (Table 5) and Pegasus Bay (Table 6)).

In the Wellington area, Haddon (1989) found that male and female crabs of about 100 mm CW were at least 3 years old, while larger crabs could be 4 or 5 years old.

A rise in temperature increases the frequency of moults in crustaceans (Hartnoll 1982). In general, paddle crabs from warmer, more northern, waters have a shorter intermoult duration and a larger moult increment than crabs from cooler, more southern waters. For example, crabs from Tasman Bay moult on average 10 times in their first year, and live for 3–4 years. Crabs from the cooler waters of Pegasus Bay moult nine times in their first year and live for 4–5 years (Osborne 1987a).

Seasonal growth differences within populations are also important. Osborne (1987a) found that newly recruited crabs were present in Pegasus Bay from January to May of each year. In the laboratory early (January) recruits grew very rapidly reaching instars 7 or 8 by May, while later recruits grew slowly over the winter, and did not reach instar 7 or 8 until May the following year.

4.5 Sex ratios

There is considerable variation in sex ratios between and within populations, possibly due to a sampling bias towards larger crabs (mainly males) in some studies, resource partitioning, differential mortality, and seasonal movements (*see* Section 4.9.3).

Kung (1973) found the number of females was always less than the number of males in a study in Paremata Harbour. Peaks in female numbers occurred when the females were associated with the males for mating. This apparent male bias could be due to differential mortality, or a movement offshore of mature females to spawn and incubate their eggs (Kung 1973).

Clark (1978) found marked differences in sex ratios between his study sites at Plimmerton and Paremata. At Paremata the sex ratio was reasonably stable, with females dominating 5 of the 10 samples. In contrast, at Plimmerton there was considerable variation, often with a complete reversal of the sample composition. Clark found that in both populations high numbers of females corresponded to low numbers of males, and that activity may be influenced by neap and spring tides.

Wear & Haddon (1987) found that in 6 out of 11 sites sampled in central and northern New Zealand, females dominated the catch. Haddon (1995) suggested that this skewed sex ratio may have been due to females receiving protection from their partners while they were soft-shelled.

Osborne (1987a) found that males generally dominated the catch at Brighton Beach, Pegasus Bay. Males were most abundant over the summer and least abundant during the winter. These changes in abundance were closely paralleled by changes in the population of male crabs in nearby Little Akaloa Bay on the north side of Banks Peninsula, suggesting a migration "from sheltered confined bays on to expansive, high wave energy beaches in spring" (*see* Section 4.9.4). Female crabs were less abundant during the summer in both areas, and this seemed to correspond with the period of egg-bearing in Pegasus Bay.

Armstrong (1985) found no "significant difference between the numbers of each sex in Blueskin Bay", Otago, except in March and April when females dominated the sample, and October when males dominated the catch. The greater number of females in March and April is thought to correspond to the return of females from deeper water after spawning, but the reason for the greater number of males in October is unknown. Males dominated the catch at neighbouring Victory Beach throughout most of the year. Armstrong felt this may be due to "differential mortality or behavioural changes such as reduced feeding or movement."

4.6 Size-frequency distributions

Brachyuran size is generally given as carapace width, CW, as total length is not appropriate because the abdomen is tucked underneath the ventral surface of the body. Extensive size-frequency distributions of paddle crabs are available for Wellington (Kung 1973, Clark 1978), Canterbury (Davidson 1987, Osborne 1987a), and Otago (Armstrong 1985). These distributions are highly variable and influenced by a number of parameters including, area, season, time of day, tide, sampling method, and depth. Generally, paddle crabs grow faster, mature earlier, and produce more broods with increasing temperature and decreasing latitude (*see* Section 4.3.2).

Size variation within instars is relatively small and does not vary significantly from year to year (Osborne 1987a) (refer to compensatory growth in Section 4.4). From extensive size-frequency data, Osborne was able to distinguish clear modes in separate male and female distributions representing instars 2 to 10 from Pegasus Bay (*see* Table 5). This is not common in large decapod crustaceans where usually only the first few juvenile instars are separable (Osborne 1987a). Instars 11 to 13 were more difficult to detect, but they were discernible and calculated based on data from captive growth studies (*see* Table 5).

Similar cohorts were separable for Tasman Bay crabs (Table 6), although "the progression of instar modes ... was not as clear cut in Tasman Bay as it was in Pegasus Bay." This appears to be mainly due to the longer recruitment period (and breeding season) in Tasman Bay (Osborne 1987a). Given that females from the Wellington area are ovigerous for most of the year, with three distinct spawning peaks (*see* Section 4.3.1), it seems unlikely that clear modes would be separable from size-frequency data.

4.7 Size-weight relationships

Davidson & Marsden (1987) studied relative growth of the paddle crab in Canterbury waters and described the relationship between carapace width and wet weight (not defined but assumed to be the weight of a live crab with any excess water blotted off). Regression lines were "significantly different" for male and female crabs.

log wet weight for male crabs = $-3.46 + 2.89 \log CW$ ($n = 44, r = 0.99$)

log wet weight for female crabs = $-3.32 + 2.79 \log CW$ ($n = 25, r = 0.99$)

4.8 Feeding

Paddle crabs are versatile, generalist, and opportunistic predators (Wear & Haddon 1987, Wear 1988b). Prey includes shellfish, crabs, shrimps, amphipods, isopods, polychaetes, several fish species (Wear & Haddon 1987), cumaceans (Davidson 1987), and, on occasions, algae and decapods (Davidson 1987). Diet is generally, however, dominated by either molluscs or crustaceans.

A high proportion of the molluscs eaten are tuatua, *Paphies subtriangulata*, pipi, *P. australis*, and toheroa, *P. ventricosa*, while the burrowing ghost shrimp *Callinassa filholi*, isopods, and amphipods are important crustacean prey items (Wear & Haddon 1987). During the winter, when paddle crabs move into sheltered inshore waters to moult and mate, food may become scarce and less desirable food items, such as algae and decapods, may become important components of the diet (Davidson 1987). Small crabs feeding in the intertidal zone often have algae in their stomachs (Kung 1973). Paddle crabs may target algae as it is a valuable source of carotenoids which are essential for proper embryonic development (Dersan Kour & Subramoniam 1992), growth (Petit *et al.* 1997), and pigmentation (Castilo & Negre-Sadargues 1995) in Crustacea. Crustaceans can not synthesize carotenoids and must obtain them from their diet (Dersan Kour & Subramoniam 1992).

Cannibalism is common, particularly on small crabs and during the winter moulting season when many crabs are soft shelled and vulnerable to attack. In some areas, cannibalised congeners account for as much as one-third or more of the diet (Kung 1973, Wear & Haddon 1987). Predation of eggs on ovigerous females may also occur. Haddon (1994) observed that in laboratory conditions, small paddle crabs (under 40 mm CW) would circle an ovigerous female and cut off parts of the egg mass with their claws and eat them.

Although diet varies considerably between areas, there appear to be no dietary differences between male and female crabs (Wear & Haddon 1987, Wear 1988b). Low water temperatures “greatly suppress locomotor and feeding activity” (Kung 1973). In the laboratory, pre-moult (and recently moulted) crabs actively avoided potential food (Haddon 1995).

Davidson (1987) found diel changes in diet in Pegasus Bay. Predation on crustaceans was highest during daylight hours (51.3% of diet), while predation on bivalves was highest at night (52.5% of diet). Seasonal changes also occurred, although this was thought to be due to the availability of food rather than selective feeding.

In Pegasus Bay, Davidson (1987) found that large crabs “do not forage as actively as small crabs.” There was a decrease in the percentage of foreguts containing food with increasing crab size. Of small crabs (30–70 mm CW), 60–70% contained food in their foreguts while only 20–30% of large crabs (greater than 100 mm CW) had foreguts that contained food. Large crabs consumed mainly larger prey, such as decapods and teleosts, while small crabs consumed much smaller, soft-bodied crustaceans such as amphipods, mysids, isopods, and cumaceans. This is probably due to a loss of cheliped dexterity with increasing crab size (Osborne 1987a).

4.8.1 Interspecific competition

The three species which apparently commonly occur with *O. catharus* in some areas are the cancer crab, *Cancer novaezealandiae*, the spider crab, *Notomithrax peronii*, and the related red swimming crab, *Nectocarcinus antarcticus*. Clark (1978) felt “the presence of these other crab species (*C. novaezealandiae* and *Notomithrax peronii*) in the pots significantly reduced the catch of *Ovalipes catharus*” in Paremata Harbour, Wellington. Armstrong (1985) suggested that *C. novaezealandiae* and *N. antarcticus* both common in the waters of Blueskin Bay, Otago, may influence the depth distribution of *O. catharus*.

4.8.2 Impact on shellfish

Interest has focused on the impact of an apparent increase in paddle crab numbers on commercial species, in particular shellfish (Armstrong 1986). Feeding studies (Wear & Haddon 1987, Haddon 1988, Wear 1988b) have shown that although paddle crabs eat large toheroa and other shellfish, they mainly eat bivalve shellfish spat (Haddon 1988). Shellfish spat are abundant, and easily processed with a minimum of energy expenditure. In contrast larger shellfish are more difficult to retrieve and process and energy expenditure is greater.

Four strategies are employed by paddle crabs to process shellfish, depending on prey size.

1. Shellfish spat are scooped or shoveled into the mouth (along with a great deal of sand) with the chelipeds (Wear & Haddon 1987).
2. Slightly larger shellfish (toheroas 20–50 mm, tuatua, cockles and pipis up to 30 mm, and *Macamona* up to 60 mm) are crushed between the claws of all but the smallest crabs (Wear 1984).
3. Larger shellfish are manipulated with the claws until the opening edges are at "right angles to the lateral crushing action of the mandibles, thereby allowing chips to be made in the shell margin." The claws are then inserted into the gap between the valves. For the larger tuatua and toheroa the shellfish were repeatedly hammered on the sand to force the valves open, the robust crushing claw enabling the more slender, sharper cutting claw to cut the adductor muscle and gain entry (Wear 1984).
4. The largest toheroa (over 120 mm) were opened only by very large crabs. The siphon tube was cut off while the toheroa was still buried forcing the shellfish to surface after about 24 hours. After a small amount of marginal chipping, the shellfish was easily consumed (Wear 1984).

Experiments by Wear (1984) and the Materials Technology Group of the former DSIR showed that "the required crushing force was directly related to shell thickness and was independent of species. A force of 20 kg was able to crush-fracture most shellfish and chip the shell edge of all shellfish, except large *Dosinia*. Thus species with thinner shells (e.g., *Macamona* and toheroa) are likely to be more vulnerable to predation.

Paddle crabs may influence shellfish recruitment in some areas by preying heavily on spat and small individuals (Wear & Haddon 1987), although Haddon (1988) found an abundance of small shellfish (20–40 mm) in his study area, indicating that paddle crabs were "not having too great a destructive influence" on shellfish stocks.

4.9 Movement and behaviour

4.9.1 Diel rhythms

Paddle crabs are most active in dusk or early evening, when light intensity is reduced (Clark 1978, Stead 1983, Armstrong 1986). Most crabs remain buried beyond the intertidal zone during the day (Clark 1978, Stead 1983). As light levels decrease towards dusk they move inshore to feed in the shallow intertidal zone, possibly for much of the night (Clark 1978). As light intensity increases towards dawn, they gradually return to deeper water. This significant diel rhythm has important implications for the commercial fishery. Catch rates from crab potting are likely to be greatest in the late evening and at night when crabs move inshore.

4.9.2 Tidal rhythms

Both Kung (1973) and Clark (1978) noted that although catches are high at dusk, they decrease significantly at high tide, before slowly increasing over several hours, then decreasing before dawn. Neap and spring tides did not appear to affect the catch rate (Kung 1973).

4.9.3 Spatial distribution

Juvenile crabs tend to occupy different habitats to the adults when adult crabs are abundant, probably to avoid predation (Osborne 1987a, 1987b). Often they settle out to nursery areas in sheltered harbours and estuaries (Wear 1982). During periods of low adult abundance, newly settled and juvenile crabs may occur in large numbers in the same areas as the adults (Osborne 1987a, 1987b).

4.9.4 Seasonal movement

Results from tagging suggest that *O. catharus* is highly migratory (Wear 1982, Stead 1983). Tagging and field studies by Osborne (1987b) in Little Akaloa Bay and Pegasus Bay, Canterbury, showed strong seasonal movements related to breeding and moulting cycles. Male and female crabs aggregate and mate in sheltered, inshore waters (harbours, bays, and estuaries) during winter at the time of the female moult (Osborne 1987a, 1987b). After mating it is thought the “females migrate offshore into deeper, stiller water to incubate their eggs” (Kung 1973, Osborne 1987a, 1987b), while males are thought to moult after most of the females have left and then move to open exposed shores in spring in search off more favourable foraging areas (Osborne 1987a, 1987b). This may at least partially explain the high level of seasonal and regional variability in sex ratios (*see* Section 4.7).

4.10 Natural mortality

Osborne (1987a) initially assumed a constant annual rate of 10% natural mortality based on the estimates for rock lobster (Annala 1979, Campbell 1985), but later estimated total mortality of female paddle crabs in Pegasus Bay, Canterbury and Tasman Bay (Table 7). She assumed that the total mortality of female crabs could be attributed to natural mortality as females are smaller and rarely subjected to fishing mortality.

Pegasus Bay crabs were caught using an otter trawl, and those from Tasman Bay were caught using baited pots. Baited pots catch a disproportionate number of large crabs and instars 8 and 9 were thought to be under-represented. This resulted in the negative mortality estimates for instars 9 and 10 in Table 7.

Osborne 1987a calculated survival from one instar to the next as:

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

where: N_m is the number of individuals in instar m , P_m is the proportion of instar m in the population, and I_m is the duration of instar m in days.

The correlation between the expected size-frequency distributions of female crabs from the mortality estimates and the actual size-frequency distributions was very close. The estimates indicate that natural mortality of crabs over 80 mm CW was much higher in Pegasus Bay than in Tasman Bay. This might result in a considerable difference in the reproductive potentials of the two populations (Osborne 1987a). The reasons for this difference are unknown, though the warmer water in Tasman Bay may enhance survival or food limitation in Pegasus Bay may have inhibited moulting and survival.

4.11 Predators

Paddle crabs are a major food item in the diets of at least 30 species of fish, many commercial, including snapper (*Pagrus auratus*), rig (*Mustelus lenticulatus*), and groper (*Polyprion oxygeneiosis*) (Stead 1984, McLay & Osborne 1985). Many crabs avoid predation by rapid burying or swimming with the aid of their paddle-shaped fifth pereopods. Aspects of the burying behaviour of the paddle crab were covered by McLay & Osborne (1985).

4.12 Other research

Kung (1973) examined the structure and function of the male and female reproductive systems in detail and looked at aspects of gonad, embryonic and larval development. Davidson (1987) investigated the structure and function of the foregut, foregut clearance rates, and predatory efficiency. Taylor (1990) examined the mechanics of the circulatory system, while Davidson & Taylor (1995) investigated the maintenance of respiratory water current in buried and unburied crabs. Haddon *et al.* (1997) looked at the depth and density of burial of toheroa (*Paphies ventricosa*) to minimise predation from crabs.

5. STOCK ASSESSMENT

5.1 Biomass estimates

No estimates of current or virgin biomass are available. The landings, CPUE, and area data are considered too unreliable or incomplete to allow modelling.

5.2 Yield estimates

For fisheries such as the paddle crab which have unreliable or incomplete CPUE data, for which the non-commercial catch is not known, for which the commercial fishery is market driven and probably under-exploited, and for which discards are high, MCY can not be estimated.

6. MANAGEMENT IMPLICATIONS

Paddle crabs occur throughout New Zealand waters wherever suitable habitat occurs, and appear to be highly migratory. The larvae occur offshore in deeper water and there is probably widespread mixing. It is likely that paddle crabs in New Zealand waters comprise one large stock (except perhaps the Chatham Islands), possibly with sub-populations. The differences in growth rate, size at first maturity, and fecundity (particularly the number of broods) appear to be largely environmentally regulated. At lower temperatures and higher latitudes, paddle crabs grow more slowly, mature at a larger size, have a shorter breeding season, and produce fewer broods per year.

Given that the fishery is market driven and probably lightly exploited, accurate estimates of MCY are not possible. The current commercial regulations, in particular, prohibiting the take of ovigerous females, restricting the taking of paddle crabs except by potting (not rock lobster pots) or hand gathering (unless special permits are held) offer considerable but unquantified protection to the fishery. The competitive quotas and the MLS set in some areas are inconsistent and do not in practice constrain the fisheries. Quotas are never met and the local market is for large crabs (generally well above the MLS), hence there may be significant variation in catch. The regulations would need to be amended for development of a soft-shelled fishery.

7. ACKNOWLEDGMENTS

This work was financially supported by the Ministry of Fisheries under project number PIQM01. I thank John Booth, Larry Paul, Neil Bagley, Terese Kendrick, Jeffrey Shields, and Chris O'Brien for providing assistance and constructive criticism and Maria Struzak for providing much needed data at often short notice.

8. REFERENCES

- Annala, J. H. 1979: Mortality estimates for the New Zealand rock lobster, *Jasus edwardsii*. *Fishery Bulletin* 77: 471–480.
- Annala, J. H., McKoy, J. L., Booth, J. D., & Pike, R. B. 1980: Size at the onset of sexual maturity in female *Jasus edwardsii* (Decapoda: Palinuridae) in New Zealand. *New Zealand Journal of Marine and Freshwater Research* 14: 217–227.
- Anonymous, 1983: Profit in paddle crabs. *FIB Bulletin*, May 1983: 13
- Anonymous, 1984a: Promising export potential for paddle crabs. *Catch* 84, 11: 8.
- Anonymous, 1984b: Looking at crab markets. *Catch* 84, 11: 17.
- Anonymous, 1986: Money for paddle crabs and land-based salmon. *Catch* 13: 5
- Armstrong, J. H. 1985: Aspects of the biology of the swimming crab, *Ovalipes catharus* (White, 1843), in the Otago region. Unpublished MSc thesis, University of Otago, Dunedin.
- Armstrong, J. H. 1986: Paddle crabs in Otago waters - a possible fishery? *Catch* 13: 19–20.
- Armstrong, J. H. 1988: Reproduction in the paddle crab, *Ovalipes catharus* (Decapoda: Portunidae), from Blueskin Bay, Otago, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 22: 529–536.
- Berrill, M., & Arsenaault, M. 1982. Mating behaviour of the green shore crab *Carcinus maenas*. *Bulletin of Marine Science* 32: 632–638.
- Cameron, M. L. 1984: The paddle crab industry in New Zealand: development of the US West Coast market. Winston Churchill Fellowship Marketing Study, June 1984. Ministry of Agriculture and Fisheries, Wellington, New Zealand. 38 p.
- Campbell, A. 1985: Application of a yield and egg-per-recruit model to the lobster fishery in the Bay of Fundy. *North American Journal of Fisheries Management* 5: 91–104.
- Castillo, R., & Negre-Sadargues, G. 1995. Effect of different dietary carotenoids on the pigmented pattern of the hermit crab *Clibanarius erythropus* Latreille (Crustacea: Decapoda). *Comparative Biochemistry and Physiology* 111A: 533–538.
- Clark, M. R. 1978: Aspects of the population biology of the swimming crab *Ovalipes catharus* (White, 1843) (Crustacea; Decapoda; Portunidae) in the Plimmerton area, Wellington. Unpublished BSc (Hons). Zoology Department, Victoria University, Wellington. 115 p.
- Davidson, G. W. 1994: The respiratory physiology of the New Zealand paddle crab, *Ovalipes catharus*. Unpublished PhD thesis, University of Canterbury, Christchurch, New Zealand. 133 p.
- Davidson, G. W., & Taylor, H. H. 1995: Ventilatory and vascular routes in a sand-burying swimming crab, *Ovalipes catharus* (White, 1843) (Brachyura: Portunidae). *Journal of Crustacean Biology* 15: 605–624.
- Davidson, R. J. 1986: Mussel selection by the paddle crab *Ovalipes catharus* (White): Evidence of flexible foraging behaviour. *Journal of Experimental Marine Biology and Ecology* 102: 281–299.
- Davidson, R. J. 1987: Natural food and predatory activity of the paddle crab, *Ovalipes catharus*. Unpublished MSc thesis, University of Canterbury, Christchurch, New Zealand. 110 p.
- Davidson, R. J., & Marsden, I. D. 1987: Size relationships and relative growth of the New Zealand swimming crab *Ovalipes catharus* (White, 1843). *Journal of Crustacean Biology* 7: 308–317.

- Dersan Kour, V. R., & Subramoniam, T. 1992. Carotenoid metabolism during embryonic development of a marine crab, *Emerita asiatica* (Milne-Edwards). *Invertebrate Reproduction and Development* 21: 99–106.
- Dunham, P. J. 1978. Sex pheromones in Crustacea. *Biological Reviews of the Cambridge Philosophical Society* 53: 555–583.
- Haddon, M. 1988: Impact of paddle crabs on shellfish. *Catch* 15: 9–11.
- Haddon, M. 1989: Growth of the New Zealand paddle crab *Ovalipes catharus*, and the replacement of lost claws. *N. Z. M. S. S. Newsletter* 31: 7.
- Haddon, M. 1994: Size-fecundity relationships, mating behaviour, and larval release in the New Zealand paddle crab, *Ovalipes catharus* (White 1843) (Brachyura: Portunidae). *New Zealand Journal of Marine and Freshwater Research* 28: 329–334.
- Haddon, M. 1995: Avoidance of post-coital cannibalism in the brachyurid paddle crab *Ovalipes catharus*. *Oecologia* 104: 256–258.
- Haddon, M., & Wear, R. G. 1987: Biology of feeding in the New Zealand paddle crab *Ovalipes catharus* (Crustacea, Portunidae). *New Zealand Journal of Marine and Freshwater Research* 21: 55–64.
- Haddon, M., & Wear, R. G. 1993: Seasonal incidence of egg-bearing in the New Zealand paddle crab, *Ovalipes catharus* (Crustacea: Brachyura), and its production of multiple egg batches. *New Zealand Journal of Marine and Freshwater Research* 27: 287–293.
- Haddon, M., Wear, R. G., & Packer, H. A. 1987: Depth and density of burial by the bivalve *Paphies ventricosa* as refuges from predation by the crab *Ovalipes catharus*. *Marine Biology* 94: 25–30.
- Hartnoll, R. G. 1982: Growth. *In*: Abele, L. G. (Ed.) *The biology of Crustacea*, Vol. 2. Embryology, morphology, and genetics. pp. 111–196. Academic Press, New York.
- Hartnoll, R. G., & Dalley, R. 1981: The control of size variation within the instars of a Crustacean. *Journal of Experimental Marine Biology & Ecology* 53: 235–239.
- Kung, H. T. 1973: Some aspects of the biology of the swimming crab *Ovalipes catharus* (White, 1843) in Paremata Harbour, New Zealand. Unpublished MSc thesis, Victoria University, Wellington.
- McLay, C. L., & Osborne, T. A. 1985: Burrowing behaviour of the paddle crab *Ovalipes catharus* (White, 1843) (Brachyura: Portunidae). *New Zealand Journal of Marine and Freshwater Research* 19: 125–130.
- Ministry of Fisheries 1995: A guide to New Zealand's Marine Recreational Fishing Rules. Challenger and central fisheries management areas. Ministry of Fisheries. Wellington.
- NZFIB 1996: The New Zealand seafood industry economic review 1994–1996. New Zealand Fishing Industry Board, Wellington. 65 p.
- Osborne, T. A. 1987a: Life history and population biology of the paddle crab, *Ovalipes catharus*. Unpublished PhD thesis, University of Canterbury, Christchurch, New Zealand. 156 p.
- Osborne, T. A. 1987b: Seasonal distribution and movements of the paddle crab *Ovalipes catharus* in Canterbury coastal waters. *Mauri Ora* 14: 43 – 55.
- Paul, L. J. 1986: New Zealand fishes. An identification guide. Reed Meuthen, Auckland, 184p.
- Petit, H., Negre-Sadargues, G., Castillo, R., & Trilles, J-P. 1997. The effects of dietary astaxanthin on growth and moulting cycle of postlarval stages of the prawn, *Penaeus japonicus* (Crustacea, Decapoda). *Comparative Biochemistry and Physiology* 117A: 539–544.
- Richards, R. N. 1992: The structure and function of the gills of the New Zealand paddle crab, *Ovalipes catharus*. MSc thesis, University of Canterbury, Christchurch, New Zealand. 131 p.
- Stead, D. 1983: Paddle crab investigations. *Catch* 83, 10: 14–15.
- Stead, D. 1984: Crab fishery expansion possible. *Catch* 84, 11: 13–14.
- Stevenson, W., & Rees, M. 1968: A revision of the genus *Ovalipes* Rathbun, 1898 (Crustacea, Decapoda, Portunidae). *Records of the Australian Museum* 27: 213–261.
- Sullivan, M., & Lang, G. 1995: Fisheries Law, Brooker's, Wellington.
- Taylor, H. H. 1990: Pressure-flow characteristics of crab gills: Implications for regulation of hemolymph pressure. *Physiological Zoology* 63: 72–89.

- Wear, R. G. 1980: Crustacean culture - its prospects in New Zealand. *In*: Wear, R. G., Dinamani, P, & Hickman, R. W. (Comps.). *Proceedings of the Aquaculture Conference*. pp. 23-27. Fisheries Research Division, *Occasional publication No. 27*.
- Wear, R. G. 1982: Paddle crabs: a potential industry or a pest? *Catch 9*: 16-17.
- Wear, R. G. 1984: Paddle crabs are probable predators. *Catch 11*: 11-13.
- Wear, R. G. 1988a: Paddle crab fishery has potential in NZ. *Catch 15*: 11.
- Wear, R. G. 1988b: Paddle crabs eat small shellfish. *Catch 15*: 12-13.
- Wear, R. G; Fielder, D. R. 1985: The marine fauna of New Zealand: larvae of the Brachyura (Crustacea, Decapoda). *New Zealand Oceanographic Institute Memoir 92*: 1-90.
- Wear, R. G; Haddon, M. 1987: Natural diet of the crab, *Ovalipes catharus* (Crustacea, Portunidae), around central and northern New Zealand. *Marine Ecology (Progress Series) 35*: 39-49.

Table 1: Reported landings (t) of paddle crab for calendar years 1977–86, and fishing years 1986–87 to 1997–98. Data sources are: FSU = Fisheries Statistics Unit; TCEPR = Trawl, Catch, Effort and Processing Return; CELR = Catch, Effort and Landing Return; CLR = Catch Landing Return; QMR = Quota Management Report; LFRR = Licensed Fish Receivers Return; - = data not available; * = data from 1986–87 fishing year. () = data likely to be underestimated. Fishing year = 1 October to 30 September.

Year	FSU Inshore	FSU Deepwater	FSU Total	TCEPR Estimated	CELR Estimated	CELR Landed	CLR	CELR Land+CLR	QMR	LFRR	Best estimate
1977	0.8	-	0.8	-	-	-	-	-	-	-	0.8
1978	3.7	-	3.7	-	-	-	-	-	-	-	3.7
1979	2.7	-	2.7	-	-	-	-	-	-	-	2.7
1980	9.0	-	9.0	-	-	-	-	-	-	-	9.0
1981	42.4	-	42.4	-	-	-	-	-	-	-	42.4
1982	65.1	-	65.1	-	-	-	-	-	-	-	65.1
1983	110.1	-	110.1	-	-	-	-	-	-	-	110.1
1984	243	-	243	-	-	-	-	-	-	-	243
1985	306	-	306	-	-	-	-	-	-	-	306
1986	202	-	202	-	-	-	-	-	-	*169.4	202
1987-88	-	-	-	-	-	-	-	-	-	164.1	164.1
1988-89	-	-	-	-	(25.9)	(19.3)	(0.075)	(19.3)	-	204.0	204.0
1989-90	-	-	-	1.090	290.8	231.4	0.127	231.5	(3.7)	249.8	249.8
1990-91	-	-	-	0.853	197.7	183.4	0.024	183.4	17.0	172.0	183.4
1991-92	-	-	-	0.020	289.0	264.4	0.172	264.5	29.0	256.4	264.5
1992-93	-	-	-	2.260	312.8	308.2	0.188	308.3	24.7	290.8	308.3
1993-94	-	-	-	0	424.0	416.7	6.038	422.7	55.7	397.0	422.7
1994-95	-	-	-	0	405.6	396.6	0.050	396.7	35.6	394.4	396.7
1995-96	-	-	-	20.070	465.9	346.9	55.904	402.8	39.7	380.9	402.8
1996-97	-	-	-	21.380	331.4	384.0	26.387	410.4	20.1	306.3	410.4
1997-98	-	-	-	0.040	333.9	438.5	10.760	449.3	19.0	354.3	449.3

Table 2: Reported paddle crab landings (t) by Quota management Area (QMA) and fishing year. Source = $CELR_{\text{landing}} + CLR$. QMAs are shown in Figure 1.

Year	QMA 1	QMA 2	QMA 3	QMA 4	QMA 5	QMA 6	QMA 7	QMA 8	QMA 9	unspec.	Total
1989-90	20 140	56 735	37 997	406	552	0	93 697	21 952	0	0	231 479
1990-91	33 756	37 469	26 053	0	6 030	0	68 394	11 681	0	0	183 383
1991-92	96 482	31 764	31 393	18	161	0	83 194	21 498	0	0	264 510
1992-93	175 163	14 109	35 883	0	28	0	58 637	24 513	0	0	308 333
1993-94	277 093	17 823	45 868	0	155	0	49 373	26 778	5 650	0	422 740
1994-95	236 621	5 813	35 873	4	22	0	71 536	46 451	326	0	396 646
1995-96	182 796	4 740	17 776	278	1 140	54 904	81 873	58 261	206	806	402 780
1996-97	169 479	24 919	38 217	0	1 074	25 075	106 087	44 398	21	1 162	410 432
1997-98	196 697	125 038	18 183	27	12 529	8 230	62 643	25 543	22	347	449 259
Total	1 388 227	318 410	287 243	733	21 691	88 209	675 434	281 075	6 225	2 315	3 069 562

Table 3: Estimates of paddle crab brood fecundity from Wellington, Canterbury, and Otago waters. Drained body weight was defined by Haddon (1994) as blotted total weight minus the pleopods and eggs. Bwg = body weight in grams.

Source		Sample			Brood fecundity		Relationship
Region	Source	n	Mean	Range	Mean	Range	
Wellington	Kung (1973)	9	65.6	56 - 75	601 863	448 000 - 722 000	$F = 15,613 \times CW - 423,531$
	Haddon (1994)	30	79.12	46 - 107	293 360	82 000 - 638 000	$F = 17,950.9 \times e^{0.3325 \times CW}$
	Haddon (1994)					drained body weight	$F = 25,630.76 + 2552.12 \times BWg$
Canterbury	Osborne (1987a)	42	-	48 - 115	-	100 000 - 1 200 000	$F = 1.62 \times (CW)^{2.07}$
Otago	Armstrong (1985)	6	101.6	88 - 112.7	1 753 718	931 000 - 2 122 807	$F = 44,041 \times CW - 2,724,000$

Table 4: Parameters used in the egg per recruit model (*see* Section 4.3.4), egg production for each instar (E_m) and total egg production (E_t) for Pegasus Bay and Tasman Bay (from Osborne 1987a). S_m , proportion of sexually mature females in instar m ; D_m , extrusion factor (essentially the number of broods per season) for instar m ; Q_m , mean number of late stage eggs per female (brood size) in instar m ; N_m , number of females in instar m .

	Instar	Mean size	S_m	D_m	Q_m	N_m	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
							$E_t = 1.56 \times 10^9$

Table 5: Instar parameters, size increment between instars' and increment as percentage of premoult size for crabs from Little Akaloa Bay and Brighton Beach, Pegasus Bay. Size and increment measurements in mm CW. *, mean values constrained. (from Osborne 1987a).

	2	3	4	5	6	7	8	9	10	11	12	13
Juveniles												
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	-							
Males												
X					37.6	49.4	63.8	78.4	93.2	108.1	*122	
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	12.9	-
Females												
X					36.8	48.8	63.1	76.3	88.8	99.1	109.4	
S.D.					3.27	3.9	4.56	4.83	*4.5	*4.5	4.55	
increment					9.9	12	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	-

Table 6: 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. *, mean values constrained. (from Osborne 1987a).

	2	3	4	5	6	7	8	9	10	11	12	Instar 13
Juveniles												
X		12.1	16.5	21.5	28.5							
S.D.		0.51	0.85	1.06	1.38							
increment		4.4	5	7	-							
% increment		36.4	30.3	32.6	-							
Males												
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	27.6	27.1	27.3	23.9	19.4	14.4	-
Females												
X						36.6	45.2	55.5	69.7	83	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	-

Table 7: Mortality estimates between instars in Pegasus Bay and Tasman Bay, based on the proportion of each instar in the natural population (P_m) and the duration of each instar in days (I_m) (see Section 4.10). N_m , number of individuals in instar m , (), values of mortality assigned where the calculated values were aberrant. (from Osborne 1987a).

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

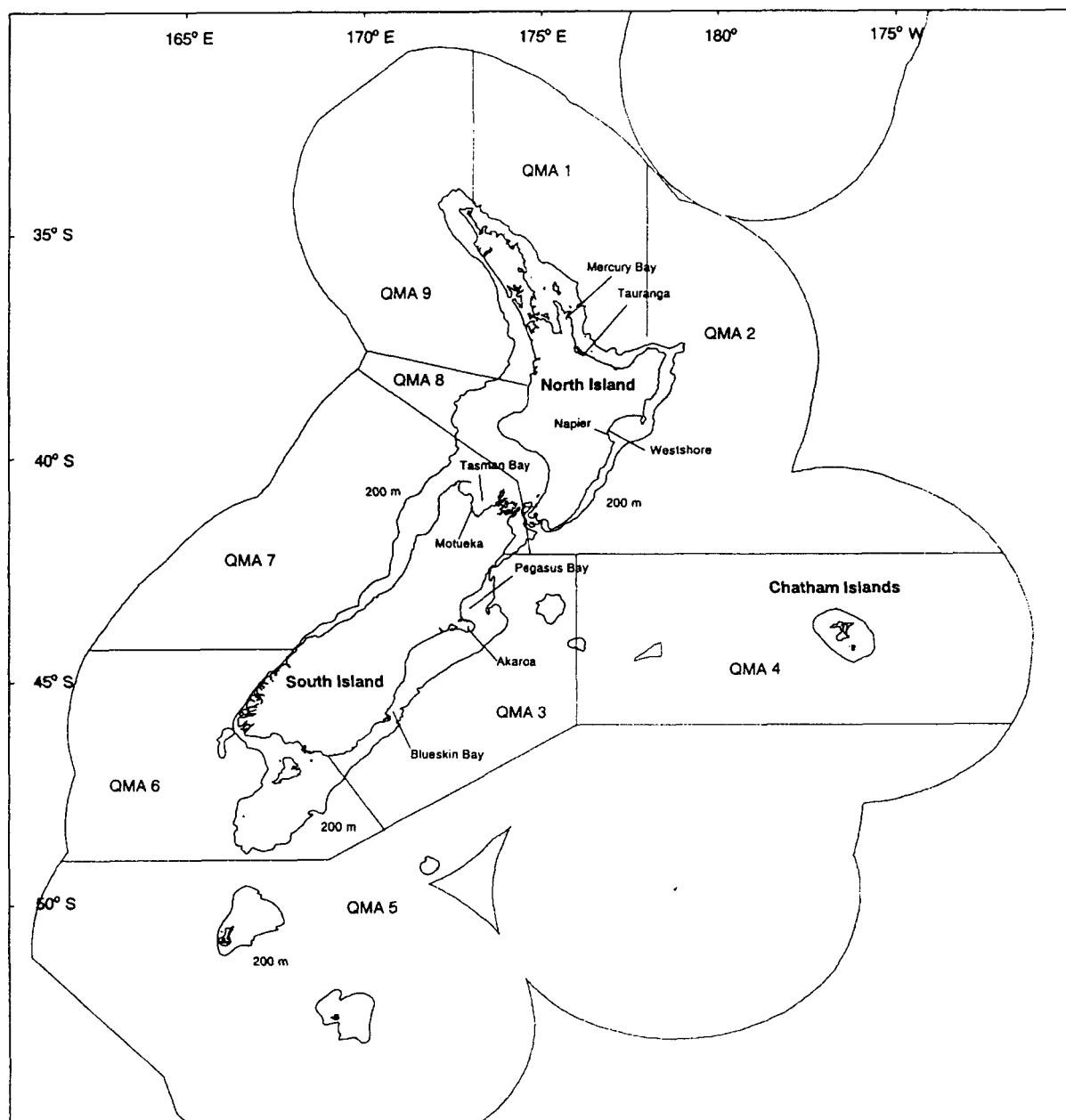


Figure 1: Map of the New Zealand Exclusive Economic Zone (EEZ), Quota Management Areas (QMA), and places mentioned in the text.

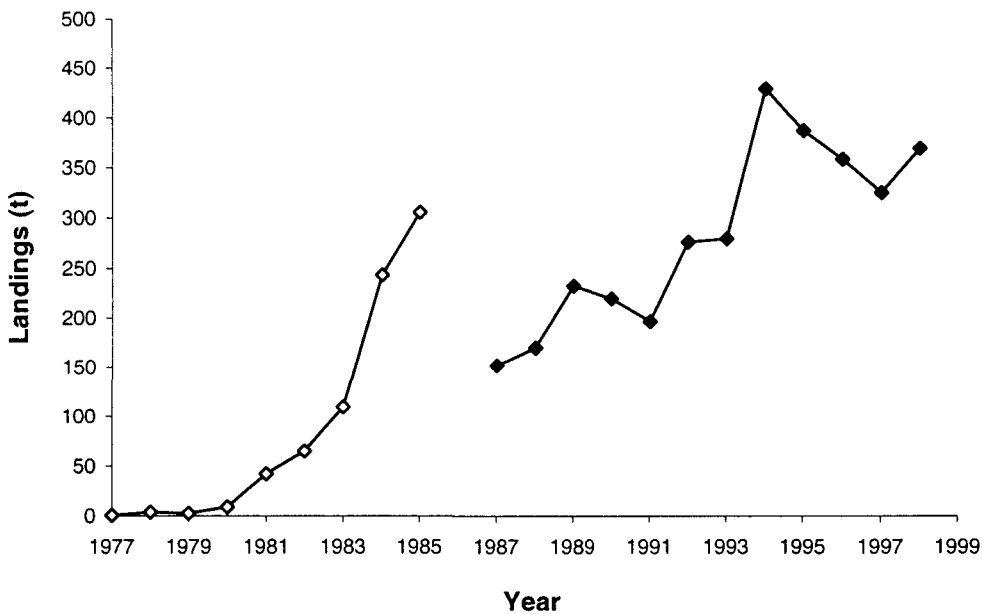


Figure 2: Estimated annual landings (t) of paddle crabs by calendar year. Data are from FSU (1977–85) and LFRR (1987–98) sources.

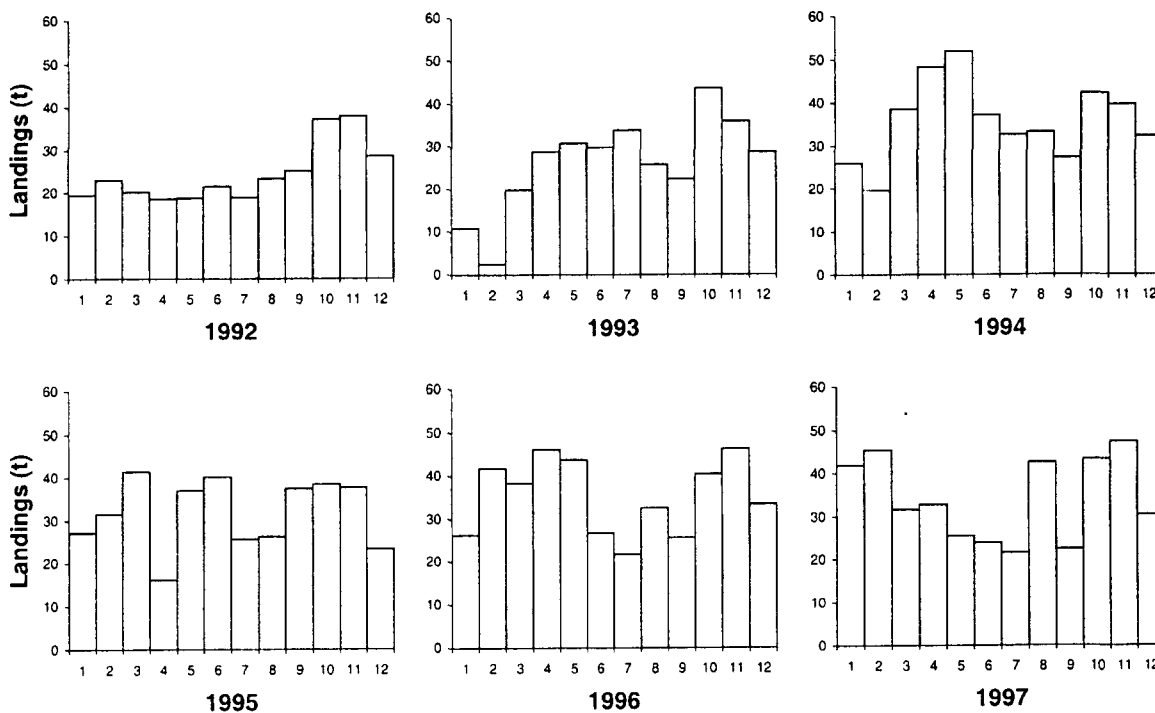


Figure 3: Monthly variation in paddle crabs landings (t). Data source, $CELR_{landed} + CLR$.

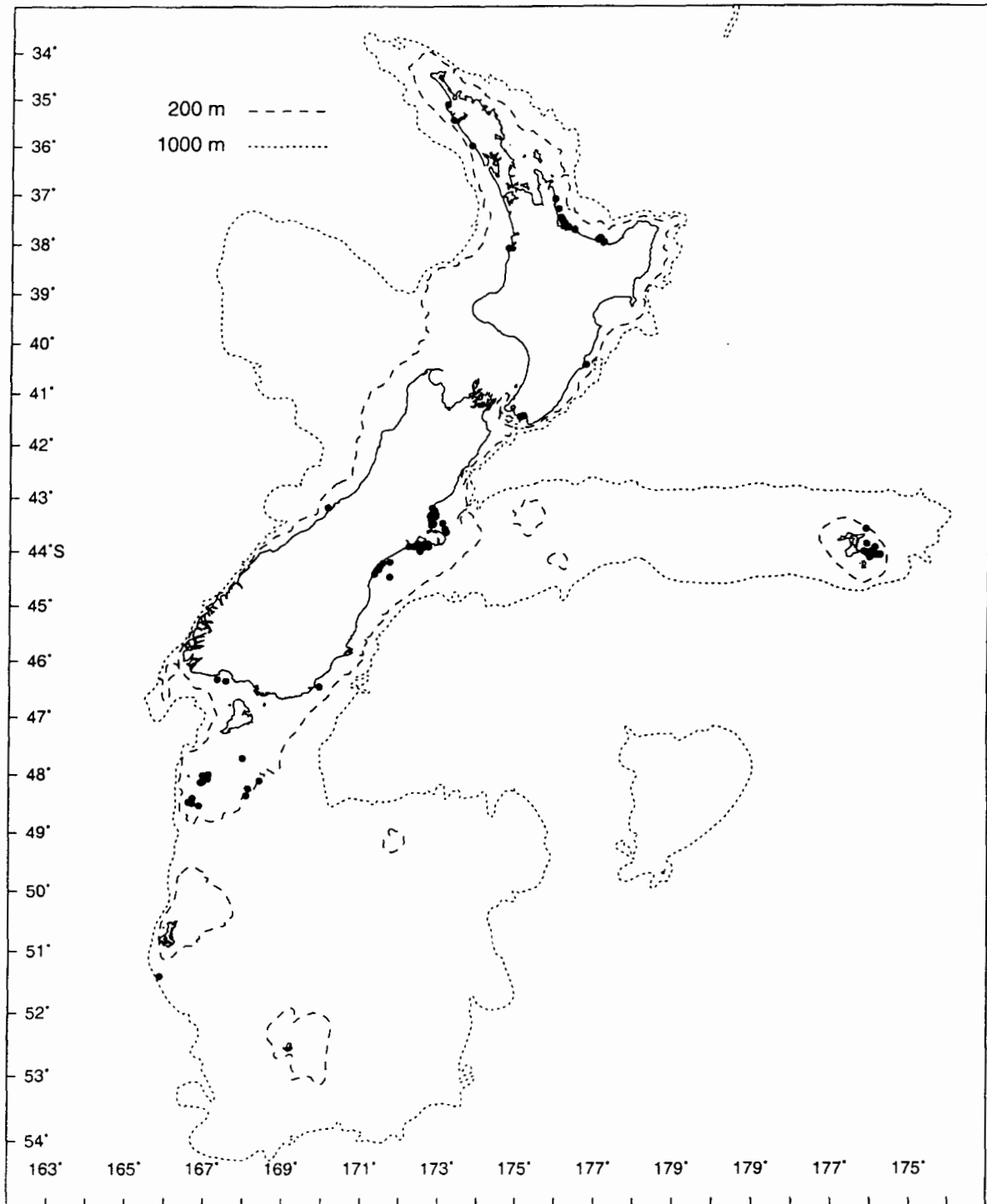


Figure 4: Positions of paddle crabs (PAD) caught by research tows recorded from the research trawl survey database.