DEPARTMENT OF BIOLOGY
UNIVERSITY OF ICELAND

Stock assessment and population dynamics of the deep-sea red crab *Chaceon maritae* (Brachyura, Geryonidae) off the Namibian coast.

BY

LOUISE LE ROUX

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L. le Roux:[*] Institute of Biology, University of Iceland, Grensásvegur 12, 108
Reykjavík, Iceland, June 1997.

ABSTRACT

Chaceon maritae has been exploited off the Namibian coast since 1973. Catches and CPUE of the fishery were fairly high throughout the 1980s, with a sudden drop occurring between 1988 and 1991. Catches and CPUE remained on a relatively low level since, indicating a large decline in the population. In the light of this apparent decline of the population, growth was investigated from tagging experiments done in the 1990s and compared to growth models determined in the 1980s. Results from growth studies showed that percentage growth increments were generally smaller in the 1990s, although not significantly for males. However, growth studies showed that intermoult periods for males were shorter than in the 1980s.

Stock assessment techniques previously used, such as tag-recapture proved to be unreliable in recent years. Several reasons for the biases in population estimates from tag-recapture are investigated. They include misreporting of tag returns, migration of females and variable catchability of female crabs. Length based cohort analysis and prediction modes were investigated as alternative stock assessment techniques for *C. maritae*. The growth rate of *C. maritae*, investigated by means of a Gulland and Holt plot, showed that growth did not follow a Von Bertalanffy growth equation and standard length based cohort analysis had to be adapted to fit growth dynamics. Cohort analysis confirmed the heavy decline of the population in the 1990s. Prediction models also showed that Yield per Recruit was higher in the 1990s, indicating faster growth. Results from cohort analysis showed that the spawning stock biomass had already declined in 1983, possibly causing the decline in catches and CPUE in later years when recruits are expected to enter the fishery.

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[*] Present address: National Marine Information and Research Centre (NATMIRC), P.O. Box 912, Swakopmund, Namibia.

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INTRODUCTION

1.1 Distribution and general biology of *Chaceon maritae*

Chaceon maritae is a brachyuran crab of the family Geryonidae. Geryonid crabs are true deep-sea crabs and are found in all oceans except in the eastern Pacific above Chile (Manning 1990). C. *maritae* is widely distributed along the West African coast and occurs from Spanish Sahara (23°35'N) southwards to Namibia (Melville-Smith & Bailey 1989). Along the Namibian coast, *C. maritae* is distributed from about 27°S northwards to the Cunene border with Angola (Melville-Smith 1988a).

In Namibian waters *C. maritae* occurs in a narrow bathymetric zone, with an inshore boundary between 340 and 380m, and an offshore boundary between 924 and 970m (Melville-Smith & Bailey 1989). In Angolan waters, most crabs were caught deeper than 300m, thus *C. maritae* also seem to have an inshore boundary around 300m in Angola (Dias & Seita Machado 1973). The *C. maritae* population in Namibia has the highest abundance in the northern regions, 17° - 19°S (Beyers 1994). From exploratory fishing in Angola, it is evident that the abundance of *C. maritae* in Angolan waters is highest in southern Angola (Dias & Seita Machado 1973). Thus, the *C. maritae* population is shared by Namibia and Angola with the highest densities around the Angola/Benguela front.

Sexual zonation has been reported for *C. maritae* by Beyers & Wilke (1980) and Melville-Smith (1987b, 1988b & 1989a), with females generally occurring shallower (<500m). This type of sexual zonation has also been reported for other geryonid crabs (Hastie 1995).

In general the size of male crabs decreases with depth. A similar pattern has been observed for females down to depths of 600m (Beyers & Wilke 1980). Thus, settlement of larvae seems to occur in deep water and crabs subsequently migrate up slope. An inverse relationship between size and depth has also been observed for other geryonids, and larval settlement of e.g. *Chaceon quinquedens* is thought to occur at depths of around 1 000m (Hastie 1995). In Namibian waters, the largest males occur mainly in the southern area (south of 20°S) of their distribution (Melville-Smith 1988a).

Mating locations have not been determined for *C. maritae*, but studies on other geryonids showed that mating takes place in deep water (Hastie 1995). Mating in *C. maritae* takes place during female ecdysis, and females are capable of storing sperm until ovulation occurs (Melville-Smith 1987b). It has not been reported how long females are capable of storing sperm, but it is likely that multiple spawning can occur from one mating, since few females continue moulting once maturity is reached.

All male crabs larger than 80mm CW (carapace width) were found to be sexually mature and the smallest male crab observed to have mated was 76mm CW (Melville-Smith 1987b). Beyers and Wilke (1980), found the size at maturity for female *C. maritae* to be 62mm CW. Melville-Smith (1987b) used three methods to determine size at sexual maturity for females and obtained the following values: 50% maturity at 84mm CW, 96mm CW, and 100mm CW. He found no females smaller than 70mm CW to be mature.

Only a few studies on food consumption of *C. maritae* have been done. Beyers and Wilke (1980) found that the incidence of empty stomachs was higher in females than males and stomach contents consisted mainly of small crustaceans and unidentifiable digested food. They concluded that food ingestion rate was low, probably as a result of limited food availability. Melville-Smith and Bailey (1989) reported that *C. maritae* consumed a wide variety of prey and that small molluscs and polychaete worms were frequently observed in stomach contents. Food abundance from photography observations was generally higher in shallower waters (350-500m) (Melville-Smith & Bailey 1989). Other geryonid crabs were also reported to have a varied diet (Hastie 1995).

Melville-Smith (1987b, 1988a) found no seasonal variation in catch rates or reproductive patterns for *C. maritae*. However, seasonal reproductive patterns and seasonal variations in catches have been reported for several other geryonids (Erdman *et al.* 1990, Hastie 1995).

1.2 History of the fishery

The deep-sea red crab, *C. maritae*, fishery off the Namibian coast started in 1973 when three Japanese fishing vessels caught 3 800 tonnes of whole mass crab (Beyers & Wilke 1980). In 1974 fishing effort increased to 17 vessels, and after that declined again (Fig. 1.1). A Namibian based company entered the fishery in 1976 with one vessel, and was operating with two vessels from 1977 to 1979. The Namibian based company processed only crabs larger than 115mm CW and ceased operating towards late 1979, because of uneconomic yields (Beyers & Wilke 1980, Melville-Smith 1988a). Catch statistics for the Japanese fishing vessels have only been reported since 1980.

The highest catch reported in the history of this fishery was 10 000 tonnes of whole mass crab, landed in 1983 (Fig. 1.2). In the period 1984 to 1988 catches varied between 6 000 and 8 000 tonnes of whole mass crab. In the 1990s catches declined to a level of 2 000 to 4 000 tonnes of whole mass crab per annum (Fig. 1.2). Fishing effort in terms of number of traps per year increased from 1980 to 1983 and declined again towards 1986. Fishing effort increased again and in 1990 the highest fishing effort was recorded. Fishing effort then once again declined towards 1995 (Fig. 1.2). Overall, there is no apparent trend in effort from 1980 to 1995, while at the same time there is a decline in catches in recent years. This is a clear indication that there has been a decline in the Namibian *C. maritae* population.

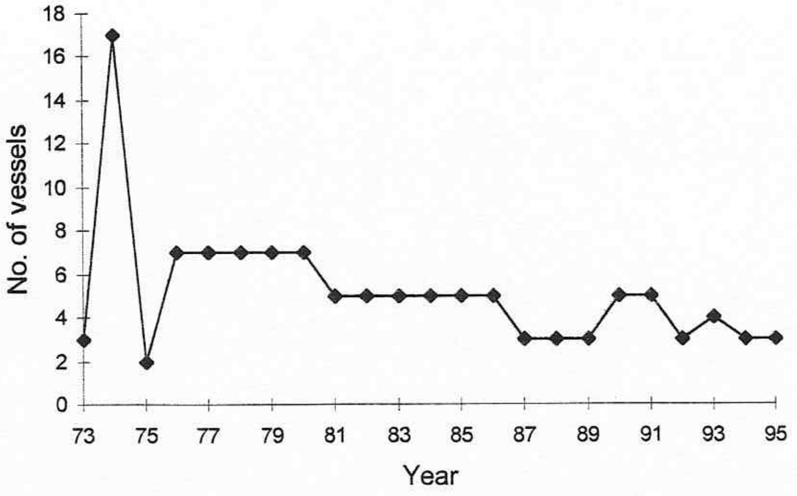


Figure 1.1: The number of vessels in the deep-sea red crab, *C. maritae*, fishery off the Namibian coast from 1973 to 1994.

No catch limits were imposed on the fishery from 1973 to 1988. A total allowable catch (TAC) of 6 000 tonnes of whole mass crab was introduced in 1989. The TAC then declined to 3 000 tonnes of whole mass crab in 1995 (Fig. 1.2).

All crabs caught on commercial fishing vessels are processed. Although there is a minimum legal size limit of 85mm CW as stated in the Fisheries Regulation Act of 1993 (Anon. 1993), this is not imposed on the fishery due to practical difficulties. If animals under the legal size limit are thrown overboard, they would probably not survive, since they would have to move through a large column of water before reaching the bottom and would probably be killed by predators. In the 1990s each vessel was restricted to a maximum of 3 000 crab pots and was not allowed to fish shallower than 500m from 1993 to 1994 (Beyers 1994). The 500m depth restriction was changed to 400m since.

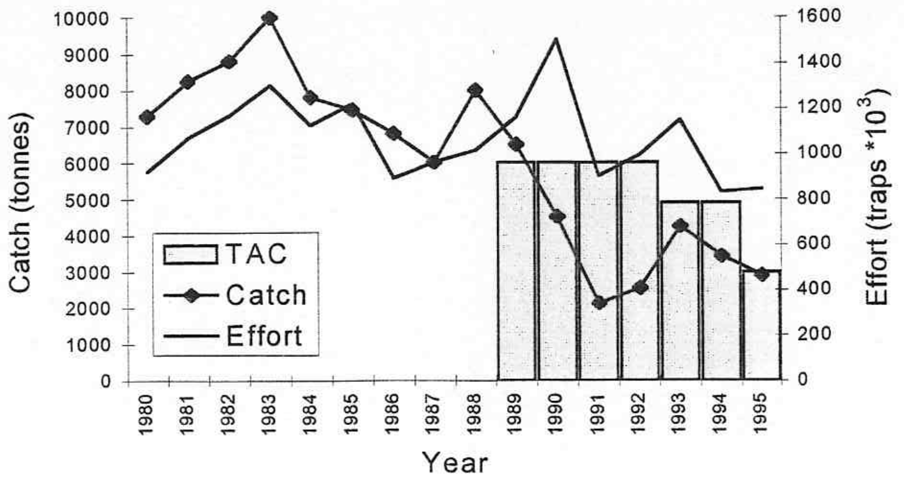


Figure 1.2: Catch and effort of the deep-sea red crab, *C. maritae*, from 1980 to 1994. Values for 1980 to 1989 are estimated from Melville-Smith (1989b). TAC = Total allowable catch.

Catch per unit effort (CPUE) of the Namibian red crab fishery has been fairly stable from 1980 to 1985, with a slight declining trend. Between 1986 and 1988/1989 some fluctuations in CPUE were observed and after 1989, CPUE dropped to levels of 2-3 kg per trap in the 1990s (Fig. 1.3). Melville-Smith (1989b) attributed the fluctuations in CPUE form 1986 to 1988 to a depletion of the brood stock which would lead from density dependent recruitment to environmentally dependent recruitment. The latter form of recruitment would then give rise to variable year classes which would cause the fluctuations in CPUE.

If CPUE trends are evaluated from 1980 to 1995, it is apparent that there is no clear trend in CPUE from 1980 to 1988 (Fig. 1.3). From 1988 to 1990 there is a large decline in CPUE. It is possible that a downward trend in CPUE in the earlier years of the fishery was masked by trap saturation.

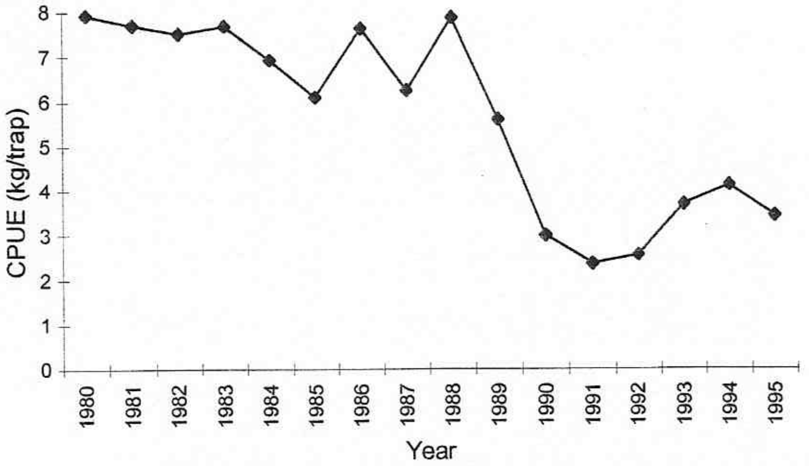


Figure 1.3: Catch per unit effort of the deep-sea red crab, *C. maritae*, fishery off the Namibian coast. Values for 1980 to 1989 were estimated from Melville-Smith (1989).

1.3 Fishing gear

C. maritae is exploited by Japanese style beehive traps on longlines. In the 1990s up to 600 traps, spaced 18m apart, were used on a longline. The traps have a conical plastic collar at the top which serves as an entrance (Beyers & Wilke 1980). The dimensions of the traps are as follows: height - 60 cm, diameter (top) - 78 cm, diameter (bottom) - 136 cm, diameter (plastic collar) - 60 cm.

From 1973 to 1987 no minimum mesh size of traps was imposed on the fishery. A minimum mesh size of 90 mm was introduced in 1987. However, all vessels were using 90 mm mesh on traps, except one vessel which used traps with 60 mm mesh during 1985 and early 1986 (Melville-Smith 1988a).

Traps are baited with hake (*Merluccius* sp.) heads and whole horse mackerel (*Trachurus* sp.). Longlines are usually left in the water for 24 to 120 hours. Soaking times longer than 120 hours sometimes occur if vessels have to call into port for some reason.

1.4 Stock assessment

Yield models for crustacean stocks can be divided into two categories: (i) the conceptual approach, which utilises either implicitly or explicitly dynamics of growth, recruitment, and mortality, and (ii) the empirical approach which uses analysis of a time series of population estimates and one or more environmental factors. The conceptual models can then be once again divided into surplus production models and analytical models (Cobb & Caddy 1989).

Stock assessment in crustacean stocks rely heavily on catch and effort data because of difficulties in ageing (Cobb & Caddy 1989). Many crustacean stocks are assessed by models relying on CPUE data such as various surplus production models (e.g. Phillips & Brown 1989) and the Leslie method based on declining CPUE throughout the fishing season (e.g. Bailey & Elner 1989). Most crustacean stock assessment, however, rely on some kind of yield model, usually a Beverton and Holt Yield per Recruit model, which has been modified to fit dynamics of the particular fishery (e.g. Brander & Bennett 1989, Campbell 1989, Ehrhardt & Restrepo 1989). In few cases analytical models such as cohort analysis have been used for assessment of crustacean stocks (e.g. Brander & Bennett 1989, Greenberg *et al.* 1991, & Zheng *et al.* 1995). In the case of the Norway lobster where Jones length based cohort analysis has been used, a standard Von Bertalanffy growth equation was used (Brander & Bennett 1989). The standard Von Bertalanffy growth equation, however, does not always describe crustacean growth over the entire life span very effectively, particularly for long lived species and/or where growth changes markedly or stops at maturity (Cobb & Caddy 1989).

C. maritae has previously been assessed by the following techniques:

(i) Trawl survey (Beyers & Wilke 1980)
(ii) Underwater photography (Melville-Smith 1983, 1988b)
(iii) EFA (effective fishing area) (Melville-Smith 1986)
(iv) Tag-recapture (Melville-Smith 1988b, Beyers 1994)
(v) Thompson and Bell Yield per Recruit (Y/R) (Melville-Smith 1988a)
(vi) Surplus production models (Le Roux 1993).

Of the first four methods Melville-Smith (1988b) determined photography and tag-recapture as the best methods to assess *C. maritae*. Melville-Smith (1988b) showed that trawling underestimates the population and the technique of EFA overestimates the population. The Y/R models run by Melville-Smith (1988a) only used males in the analysis and utilised catch curve analysis for obtaining mortalities. These yield models

(Melville-Smith 1988a) indicated that the age at first capture was too high. The Schaefer and Pella-Tomlinson surplus production models were used to estimate the population in 1993. The estimates were of the same order as found by tagging in 1991/1992 (Beyers 1994, Le Roux 1993). However, surplus production models utilizes catch and effort data, which can be heavily biased (Hilborn & Walters 1992). The sudden drop in CPUE (1988-1991) also poses difficulties in fitting the models.

In recent years, assessment of *C. maritae* using tag-recapture results proved to be insufficient, e.g. in 1993 it is known that not all tag-returns were reported. It also recently became known that a substantial number of tagged crabs were recaptured in Angola. Tag-recaptures from Angola were only reported on two occasions in 1995 and 1996.

1.5 Crustacean growth

Growth in crustaceans can generally be described in terms of growth increments at each moult and the duration of successive intermoult periods (Fig 1.4) (Mauchline 1977 & Hartnoll 1982). Growth rates of many crustaceans are obtained by length frequency analysis, but this method proved to be difficult for large crustaceans such as crabs and lobsters (Mauchline 1977). Attempts to measure geryonid growth by length frequency analysis proved to be unsuccessful due to the lack of polymodality in length frequencies (Hastie 1995). Growth of larger crustaceans is thus often described from tagging experiments. Since tag returns are generally low, estimates of growth rates are derived from cumulative results. This introduces variation in the data due to differences in growth rates between years (Mauchline 1977).

Increments at moulting can be described by regression equations relating postmoult size to premoult size, called the Hiatt growth diagram (Mauchline 1976, 1977). The main criticism of the Hiatt growth diagram is that it examines postmoult size as a contained measurement and is thus highly correlated with premoult size (Mauchline 1977). Increase in size is generally described as a relative size increment, usually as a percentage of the size at moulting, termed the growth factor (Mauchline 1977, Hartnoll 1982). Linear plotting of successive growth factors as a function of body size usually results in an exponential curve where data on juveniles are included (Mauchline 1977). However, there does not seem to be a functional form that is intrinsically the best line to fit (Botsford 1985).

Information on intermoult period is more difficult to obtain than information on size increments. Two general ways of obtaining information on intermoult period are from laboratory studies and from tagging experiments (Hartnoll 1982). Intermoult period generally lengthens with an increase in length. Mauchline (1977) states that intermoult period plotted against body length generally results in an exponential curve. However, there is no *a priori* reason for favouring any particular relationship (Hartnoll 1982).

Crustacean growth is thus generally described by two regressions: one describing the increase of the intermoult period, the other describing the growth factor against body size, which is not always declining with increase in body size (Mauchline 1977, Hartnoll 1982).

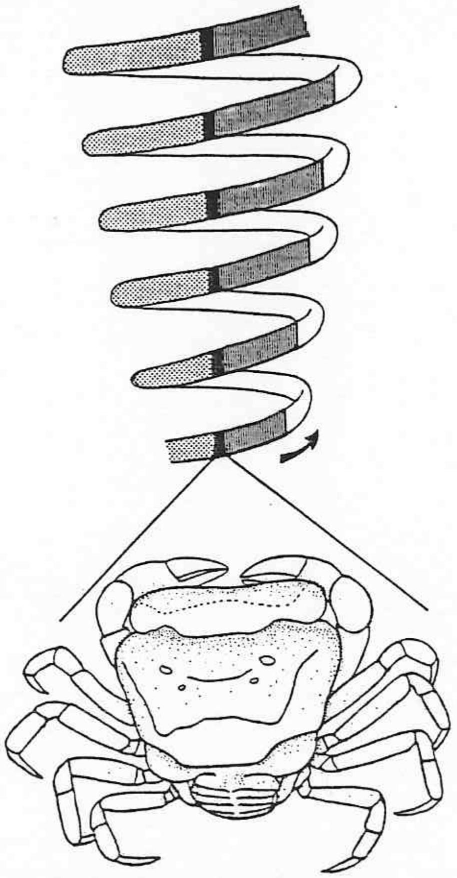


Figure 1.4: A diagram of crustacean growth depicting successive cycles of moulting. Any cycle includes: proecdysis (dotted area), ecdysis = moulting (solid black area), metecdysis (lined area), and anecdysis = intermoult period (clear area). (From Bliss 1990).

1.6 Objectives of this study

The objectives of this study were:

- to describe growth in the 1990s for both male and female *C. maritae*. A re-evaluation of growth was thought necessary, since the population is lower than in the 1980s when growth of *C. maritae* was described by Melville-Smith (1989a).

- to compare growth in the 1990s with growth in the 1980s, since it is likely that growth has changed due to a density dependent effect.

- to describe a relationship of intermoult period and CW for females as well as males. Only the intermoult period for male *C. maritae* is known (Melville-Smith 1989a).

- to analyse the relationship between sex ratio and depth objectively and to evaluate whether depth restrictions are effective in protecting female *C. maritae*.

- to analyse CPUE data from 1990 to 1995 for any sign of seasonality, since seasonality in both reproductive patterns and catches have been reported for other geryonids.

- to evaluate the effectiveness of tag-recapture as a method of stock assessment and to investigate possible biases.

- to investigate alternative methods of stock assessment for *C. maritae*, such as length based cohort analysis and prediction models. Although cohort analysis and prediction models were developed for finfish, an attempt is made to adapt these models to fit the growth dynamics of *C. maritae*.

2 METHODS

2.1 Sampling from commercial catch

Length frequency samples of *C. maritae* were obtained on board commercial crab fishing vessels at sea. Random samples of *C. maritae* were taken while longlines were being hauled. Each sample consisted of six standard sized baskets, as used on the commercial fishing vessels, filled with crab. Sample size varied with the size of crabs in a particular area, and varied from about 400 to 800 crabs per sample. Sampling effort during any particular field trip depended on the number of vessels operating at the time. Generally two samples per vessel were taken during a sampling trip (1993 - 1995). A total 119 876 crabs (82 922 males and 36 949 females) were sampled from 1980 to 1995. Commercial sampling was done approximately every two months throughout the year. Information on position and depth was recorded for each sample.

The following information was recorded for each crab sampled: carapace width (CW), sex, moulting stage, maturity for females and whether females were ovigerous or not. Carapace width was measured to the nearest millimetre below, using stainless steel vernier callipers. The following moulting stages were identified (see Beyers & Wilke 1980):

Hard New: This moulting stage is found in crabs that have recently moulted. The dorsal side of the carapace yields or cracks under slight pressure. The carapace is usually of a light colouration.

Hard: This stage represents the intermoult period. The carapace is of maximum strength and does not yield when pressure is exerted on the dorsal part of the carapace.

Hard Old: This moulting stage is found in crabs approaching a moult. The epimeral suture on the lateral sides of the carapace can be distinctly felt and the newly formed exoskeleton can be seen when breaking a limb.

Soft Old: This moulting stage is found in crabs in the immediate premoult stage. The epimeral suture on the lateral side of the carapace is soft to the touch or has already started to crack. If a limb is broken off the newly formed carapace can be seen. These crabs usually have a dark tan to red carapace.

Soft New: This is the moulting stage of crabs in the immediate post-moult stage. The new carapace has not hardened yet and is soft and jelly-like. These crabs are sampled only if the old carapace that has been shed is present in the sample.

Maturity for females was determined by the degree of opening of the vulvae. Three stages were identified as follows: (i) immature, where the vulvae are in the form of closed slits, (ii) intermediate, where the vulvae are still slit-shaped but partially open, and (iii) mature, where the vulvae are fully opened apertures (Melville-Smith 1987b).

Samples were separated by sex and area, and pooled into five millimetre carapace width (length) class intervals. The mean weight of each length class was determined by integrating the weight length relationship over each length class as follows (pers. comm. J. Beyer):

where:

$$w = q * L^b$$

$$\overline{W}_i = \int_{L_i}^{L_{i+1}} q * L^b * f(L) * dL$$

then:

$$\overline{W}_i = q/(b+1) * 1/(L_{i+1} - L_i) * (L_{i+1}^{(b+1)} - L_i^{(b+1)})$$

where:

w = weight in grams

q = constant = 0.000167 for males and 0.000218 for females (Melville-Smith 1988c)

b = constant = 3.156 for males and 3.056 for females (Melville-Smith 1988c)

$\overline{W}_i$ = mean weight of length class i in grams

L = carapace width in mm

Length frequencies were converted to weight to calculate the sample weight. Total sample weight was then determined per area. The ratio between total sample weight (in kg) per area and total catch (in kg whole mass) was then used to raise samples in each length class to the total catch. The total number of animals caught per length class for each area were then added to determine the annual total number of animals caught in each length class.

Samples were taken from the commercial catch for all years since 1980 except for 1981, 1989 and 1990.

2.2 Catch statistics

Catch statistics were obtained from commercial crab fishing vessels in the form of daily catch logs. The following data were recorded on catch logs for each longline set: date hauled, emersion time (h), position (as grid number, see Fig. 2.1), depth (m), number of traps on the longline, and the amount of each product packed (kg). The amount of each product packed was then converted to whole mass crab by a series of conversion factors calculated by Melville-Smith (1988c).

CPUE was calculated as the total catch in whole mass divided by the total number of traps used.

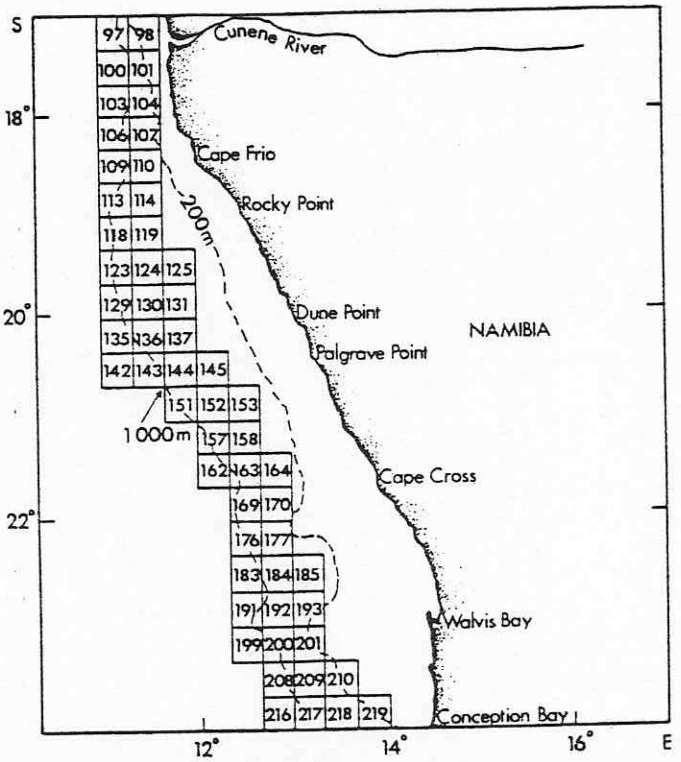


Figure 2.1: The grid system used for reporting catches of *C. maritae* in Namibia (from Beyers 1994).

2.3 Data sources and control

Catch statistics and sampling data for 1980 to 1989 were obtained from SFRI, Cape Town, South Africa. Catch statistics of the *C. maritae* fishery were collected by the Ministry of Fisheries and Marine Resources in Namibia since 1990. Catch statistics were kept on a database at NATMIRC and the calculation of whole mass caught on this database was performed in the same way as at SFRI, thus the data were directly comparable.

Samples from the commercial catch for 1991 and 1992 were under the control of C. J. de B. Beyers (NATMIRC). Since 1993 commercial samples were controlled by the author, who participated in most field trips. During those field trips in which the author could not participate a team of personnel, well trained in sampling *C. maritae*, took part in field trips.

2.4 Tagging

Crabs were collected from commercial crab fishing vessels at sea while a longline was being hauled. Crabs were randomly selected from the longline and immediately transferred to the *R/V Benguela* (1991, 1992 & 1993) or the *R/V Welwitschia* (1994 &

1995), where they were tagged and released. Most crabs were released within 24 hours of being caught. For each batch of crabs released the following information were recorded: position caught, depth caught, date caught, position released, depth released, and date released. For each individual crab tagged, the same information as for sampling were recorded plus the tag number. The following numbers of crabs were tagged and released in each year:

September 1991:	7 281 (tagging experiment of Beyers (1994))
November 1992:	4 541
October 1993:	4 407
December 1994:	3 751
July 1995:	4 442

Prior to tagging, crabs were kept in tanks with running seawater. Coded T-bar tags (Hallprint, Australia) were inserted in the epimeral suture so that the tag was lodged in the branchial cavity, by means of an applicator gun. This proved to be the best method for tagging *C. maritae*, for retaining the tag through moulting (Melville-Smith 1987). Crabs approaching a moult were not tagged, and if any appendages were missing, it was recorded and the crab tagged.

Prior to release, crabs were carefully observed and any dead crabs and broken tags were removed and the tag number recorded. Crabs were released by means of a release cage, which was triggered by a messenger to open at 20 to 30 meters off the bottom.

Crabs were released between 500 and 800m depth in three main regions *i.e.* 18° - 19°S, 19° - 20°S (except 1992), 20° - 21°S (except 1993). Crabs were released at 10' or 20' intervals in each region and randomly distributed between three depth zones: 500-600m, 600-700m, and 700-800m.

Commercial fishermen were asked to return all recaptured crabs. Recaptured crabs were returned to the Ministry of Fisheries and Marine Resources, Namibia with the tag intact and information on the recapture date, catch position, and depth caught.

2.5 Growth

Growth of *C. maritae* was analysed by using tag-recapture results for the period September 1991 to December 1994. Males and females were kept separate in the analysis as they have been shown to have different growth rates (Melville-Smith 1989a). Only crabs that showed an increment of more than 5mm were used in the analysis. Differences of 5mm and less in the size of crabs when recaptured, were considered to be measurement error. It was clear from the data which crabs have moulted, since they usually showed a large increment in size at moulting (see Appendix A, Fig. A1). Since 1991, a total of 1 515 crabs were recaptured, of which 115 males and 77 females had moulted.

General models for crustacean growth were used to analyse growth in *C. maritae* (Mauchline 1976, 1977, Hartnoll 1982). The percentage carapace width increment or growth factor was regressed against premoult CW. Crabs that had moulted more than once could be identified from this plot and were excluded from the regression analysis. Mauchline (1977) proposed a log/linear regression for decapod crustaceans, where the log (percentage growth increment) is regressed against premoult CW. The log/linear and linear/linear regressions were compared by comparing the coefficients of determination (r^2) and visually examining residual plots. Mean percentage growth increments were also calculated for males and females, and these values were analysed for a significant difference using Student's t-test. Before the t-test was employed, an F-test for equal variances was done (Zar 1996).

A Hiatt growth diagram was constructed by regressing the postmoult CW (L_R) against premoult CW (L_T). Only crabs that had moulted once were used in this regression. The slope of the Hiatt growth diagram is expected to change near the point of sexual maturity (Sommerton 1980). Sommerton's (1980) method was used to determine this point of intersection of the two regressions. This procedure started with an initial parameter estimate, which was then improved by iteration until some criterion of precision was found. One of the regression lines was constrained to intersect the other at some specified value of premoult CW (L^*). L^* was then allowed to be a parameter to be estimated along with other parameters. This straight line model can be expressed as follows:

$$L_R = a + bL_T + \varepsilon_i \qquad L_T \leq L^*$$

$$L_R = L_R^* + d(L_T - L^*) + \varepsilon_i \qquad L_T > L^*$$

where $L_R^* = a + bL^*$, a, b, and d are free parameters and ε_i is an error term. This model was then fit in an iterative fashion. Some initial value of L^* was chosen and estimates of the slopes and intersections of the two lines were obtained by linear regression. L^* was then increased by one millimetre and the parameters re-estimated, until a value of L^* was found which minimises the residual sum of squares pooled over both lines (Sommerton 1980).

The regressions for percentage growth increment and the Hiatt growth diagrams were compared to those found by Melville-Smith (1989a). The slopes and intercepts were compared to those of Melville-Smith (1989a) by employing the Student's t-test (Zar 1996). The slopes of the two Hiatt growth diagrams for male *C. maritae* found by Sommerton's method were also compared using the Student's t-test (Zar 1996).

The intermoult period was modelled by regressing the average number of days at large with moulting once against premoult CW. The number of days at large is defined as the total number of days from the date of tagging to the date of recapture. Data of crabs that have moulted once were sorted and the average days at large was calculated for each 1mm CW class interval where data were available. Thus a new dataset was generated for the analysis of intermoult period. A log/linear plot was also tested as proposed by Mauchline (1977), and the regressions of the two plots compared.

A growth model for male *C. maritae* was then constructed by using the regressions for growth factor and intermoult period. Since data for juvenile crabs were not available, comparable data for the species *C. quinquedens*, as determined by Van Heukelem *et* *al.* (1983) were used as an initial estimate of age at a certain size. *C. quinquedens* and *C. maritae* have similar size ranges and similar depth distributions and growth is thus considered to be comparable (also see Melville-Smith 1989a). A growth model using the Hiatt growth diagram was also constructed.

2.6 Analysis of sex ratios by depth

Data from samples of commercial catches from 1994 to 1996 were used in the analysis of sex ratios. Sample sizes for this period ranged from 300 to 1 000 crabs, with only one sample (n = 93) being smaller. A total of 44 samples (= 23 506 crabs in total) was taken during this period. The proportion of males and the depth of each sample were used to investigate the relationship between depth and sex ratio in *C. maritae*.

Since the data were proportions and thus from a binomial distribution, an arcsine transformation was applied to the data as follows:

$$p' = \ln(\text{arcsine}\sqrt{p}\,)$$

where p = proportion of males (Zar 1996). The arcsine transformed data were then regressed against depth (D) in metres.

The data were also fitted to a logistic curve where: $p = 1/(1 + e^{a-b*D})$. A linear transformation of the logistic curve is then:

$$\ln(1/p-1) = a - b*D$$

and ln(1/p-1) was then regressed against depth to determine the parameters a and -b.

The coefficients of determination (r^2) and the residual plots of the two regressions were compared to determine the best fit.

2.7 Seasonality

CPUE data per month from 1990 to 1995 were used to investigate whether there was any sign of seasonality in commercial catches of *C. maritae*. Data were grouped by month and year. Analysis of variance (ANOVA) was run on the data, to determine whether there was any significant difference in the data. Two-factor analysis of variance without replication (Zar 1996) was applied to the data.

2.8 Population estimates from tag-recapture

2.8.1 *Petersen method*

Crabs tagged in November 1992, October 1993, December 1994, and July 1995 were used in the assessment of *C. maritae*. Only crabs recaptured within one year of tagging were used in the assessment.

An estimate of *C. maritae* stock size was calculated by Bailey's modification of the Lincoln index (Ricker 1975) by the following equation:

$$\hat{N} = T^*(C + 1)/(R + 1)$$

where

$\hat{N}$ = population size in numbers
T = number of animals tagged
C = catch in numbers
R = number of tags returned

and the 95% confidence limits of $\hat{N}$were estimated by Pearson's formula (Ricker 1975):

$$x + 1.92 \pm 1.96^* \sqrt{x+1}$$

where x is the number of tag returns (R). The upper and lower limits for R were calculated and the subsequent population number was then accordingly calculated.

2.8.2 *Estimating emigration*

The above method was used by Melville-Smith (1988b) and Beyers (1994). Both abovementioned authors assumed that immigration and emigration counteracted each other. Another term describing emigration was introduced to estimate population size more accurately (Gatz & Loar 1988). This can be calculated as follows:

$$\hat{E}_m = R_A/R_T$$

Where $\hat{E}_m$ = proportion emigrated, R_A = number of tag-recaptures in Angola, and R_T = total number of tag-recaptures = $R_N + R_A$ (where R_N is the number of tag-recaptures in Namibia). The population number was then recalculated as:

$$\hat{N} = T_N(C + 1)/(R_N + 1)$$

where $\hat{N}$ = population size in number in Namibian waters, C = catch in number in Namibian waters, and $T_N = T - T^*\hat{E}_m$ and estimates the number of tagged animals still present in Namibian waters.

Confidence limits were then calculated as above by Pearson's formula.

2.8.3 *Migration*

A thorough analysis of migration was considered beyond the scope of this study. However, a preliminary analysis of movements of *C. maritae* was done to investigate what influence movements of animals might have on the population estimates from tag-recapture. Mostly animals recaptured in Namibian waters were used, and recaptures from Angola were used only in 1995.

All crabs for which recapture information was available were pooled and the distance moved were calculated by the following formula (Stefánsson 1991):

$$D_{AB} = \sqrt{(\phi_A - \phi_B)^2 + (\lambda_A - \lambda_B)^2 * \cos^2((\phi_A + \phi_B)/2)}$$

where D_{AB} = distance in nautical miles, and (ϕ_A, λ_A) and (ϕ_B, λ_B) are latitude and longitude of locations A and B. The differences in the above equation are calculated in minutes.

Males and females were kept separate in the analysis.

Tag and recapture positions were also plotted by means of Arc View GIS (Anon. 1996) to investigate direction of movement. Only crabs tagged in the regions 18°-19°S and 19°-20°S were plotted, since crabs tagged in these regions have the potential to emigrate out of Namibian waters.

2.9 Cohort analysis and prediction models

2.9.1 *Growth parameters and natural mortality*

Tag-recapture results were used to determine the carapace width at the time of tagging (L_T) and carapace width at recapture (L_R), and number of days at large.

To investigate the growth dynamics of *C. maritae*, growth rate of individual crabs was regressed against the mean carapace width (Gulland and Holt plot, Sparre & Venema 1992). Mean daily growth rate was then calculated from the tag-recapture data and multiplied by 365 to determine mean annual growth rate (r). The regression equation is as follows:

$$dL/dt = a + b * \overline{L}$$

where:

$$dL = L_R - L_T$$

$$dt = \text{number of days at large}$$

$$\overline{L} = (L_R + L_T)/2$$

Literature on other decapod crustaceans was consulted for likely values of natural mortality for both males and females. Natural mortality of *C. maritae* males was suggested to be between 0.05 and 0.15 per year (Melville-Smith 1988).

2.9.2 *Cohort analysis*

Preliminary results from the Gulland and Holt plot indicated that growth in *C. maritae* could not be described by the traditional Von Bertalanffy growth equation. Traditional length based cohort analysis models (Sparre & Venema 1992) was thus adapted to fit the growth dynamics of *C. maritae*. The mean annual growth rate (r), was incorporated into the standard length based cohort analysis as follows:

a) $\Delta t_i = (L_{i+1} - L_i) / r$

b) Last N_{Li+1} = Last $N_{Li} * e^{-Z\Delta ti}$

c) Last $N_{Li} = C_{(Li, Li+1)} / [(F_t / Z_{(Li, Li+1)}) * (1 - e^{-Z\Delta ti})]$ where F_t is a guesstimate

d) $N_{Li} = N_{Li+1} * e^{M\Delta ti} + C_{(Li,Li+1)} * e^{M\Delta ti/2}$

e) $F_{(Li, Li+1)} * \Delta t_i = \ln(N_{Li}/N_{Li+1}) - M\Delta t_i$

therefore:

$F_{(Li, Li+1)} = 1/\Delta t_i * \ln(N_{Li}/N_{Li+1}) - M$

where:

Δt_i = the time spent in length class *i*
L_i = Carapace width in mm at the beginning of the *i*th length class
F_t = Terminal fishing mortality
N_{Li} = Number of crabs attaining length L_i
$C_{(Li, Li+1)}$ = Number of crabs caught between lengths L_i and L_{i+1}
$F_{(Li, Li+1)}$ = Fishing mortality of crabs between lengths L_i and L_{i+1}
M = Natural mortality (constant)
$Z_{(Li, Li+1)}$ = Total mortality = $F_{(Li, Li+1)} + M$

The mean number of crabs in the population has to be calculated to be able to determine the mean biomass of crabs. The mean number of crabs was calculated and weighted by the time (Δt_i), spent in a particular size class (Sparre & Venema 1992).

The annual mean number of animals in each size class was calculated as follows:

$$\overline{N}_{(Li, Li+1)} * \Delta t_i = (N_{Li} - N_{Li+1}) / Z_{(Li, Li+1)}$$

and the total annual mean number of animals ($\overline{N}$) was then given by

$$\Sigma \overline{N}_{(Li, Li+1)} * \Delta t_i$$

The annual mean biomass in each size class, $\overline{B}_{(Li, Li+1)} * \Delta t_i$, was correspondingly calculated by multiplying $\overline{N}_{(Li, Li+1)} * \Delta t_i$ with the average weight, $\overline{W}_i$. The total annual mean biomass was then given by

$$\Sigma \overline{B}_{(Li, Li+1)} * \Delta t_i$$

Cohort analysis was first run with a range of values for F_t, while keeping M constant and the effect on the mean annual population number was investigated. Cohort analysis was then run with a range of values for natural mortality for males and females, respectively.

Since length based cohort analysis assumes equilibrium conditions (Sparre & Venema 1992), CPUE of the *C. maritae* fishery was examined to determine different periods over which catches can be pooled for cohort analysis. It was assumed that periods of similar CPUE were representative of periods of equilibrium.

Samples from commercial catches were raised to the total catch, as described above, to calculate the annual catch in number. In years where no commercial sampling was done, it was assumed that the catch composition was equal to that of the previous or next year and raised to the appropriate catch. No commercial samples were taken in the following years: 1981, 1989, and 1990. Catch composition in 1981 was assumed to be equal to that of 1982, catch composition of 1989 equal to 1988 and catch composition of 1990 equal to 1991.

F-arrays from cohort analysis were examined to determine the most heavily exploited length groups and the average fishing mortality was calculated from these length groups.

The terminal fishing mortality (F_t) was assumed to be equal to the average fishing mortality of the previous three length classes. This is a reasonable assumption, since the oldest animals are not expected to have a difference in catchability or selectivity by the current fishing gear (also see Stefánsson 1994). Cohort analysis was run in an iterative fashion until the above assumption was fulfilled.

Cohort analysis was also run preliminarily on an annual basis to investigate annual population number and biomass trends calculated by the model for comparison to population estimates from tag-recapture. Spawning stock biomass was also calculated from cohort analysis run on an annual basis. The spawning stock biomass was taken to be the biomass of all crabs larger than 85mm CW.

2.9.3 *Prediction models*

The Thompson and Bell prediction model was used and adapted to growth in *C. maritae* in a similar fashion as for cohort analysis. Fishing mortality per length class (F-array) was calculated from cohort analysis. Annual recruitment was put equal to 2000 recruits (1000 males and 1000 females), and the resultant Yield per 2000 recruits was calculated as follows:

a) $\Delta t_i = (L_{i+1} - L_i) / r$

b) First N_{Li} = total annual recruitment = 2 000

c) $N_{Li+1} = N_{Li} * e^{-Z\Delta ti}$ where $Z = Z_{Li} = X*F_{Li} + M$

d) $C_{(Li,Li+1)} = (N_{Li} - N_{Li+1}) * X*F_{Li}/Z_{Li}$

e) $\bar{W}_{(Li,Li+1)} = q/(b+1) * 1/(L_{i+1} - L_i) * (L_{i+1}^{(b+1)} - L_i^{(b+1)})$

f) $\bar{Y}_{(Li,Li+1)} = C_{(Li,Li+1)} * \bar{W}_{(Li,Li+1)}$ and $\sum \bar{Y}_{(Li,Li+1)}$ = total yield

g) $\bar{B}_{(Li,Li+1)} * \Delta t_i = (N_{Li} - N_{Li+1})/Z_{Li} * \bar{W}_{(Li,Li+1)}$ and $\sum \bar{B}_{(Li,Li+1)} * \Delta t_i$ = total biomass

where:

X = F-factor or factor with which F is multiplied
$\bar{Y}_{(Li,Li+1)}$ = Mean yield from length class i to length class $i+1$
$\bar{B}_{(Li,Li+1)}\Delta t_i$ = Mean biomass from length class i to length class $i+1$

The F-array as calculated from cohort analysis was used to calculate a selection/recruitment ogive for both males and females, since there is an obvious relationship between fishing mortality and gear selection (Sparre & Venema 1992). The selection ogive was calculated as follows:

$$S_{(Li,\, Li+1)} = F_{(Li,\, Li+1)} / F_{MAX}$$

where $S_{(Li,\, Li+1)}$ = the fraction of animals retained by the gear currently in use, $F_{(Li,\, Li+1)}$ = fishing mortality in length class i to $i+1$, and F_{MAX} = maximum fishing mortality for all length classes. The parameters L50% and L75%, *i.e.* the lengths at which 50% and 75% of the animals are retained by the gear, were than estimated from the resultant curve.

Knowing the parameters L50% and L75% for the gear currently in use, a new selection ogive was calculated for new values of L50% and L75% (Sparre and Venema 1992), and thus a new F-array as follows:

$$F_{(Li,\, Li+1)}new = F_{MAX} * S_{(Li,\, Li+1)}new$$

where: $S_{(Li,\, Li+1)} = 1/ [1 + e^{(S1 - S2*L(i,\, i+1))}]$

and parameters S1 and S2 of the selection ogive was estimated as follows:

$$S1 = L50\% * \ln(3)/(L75\% - L50\%) \text{ and}$$

$$S2 = \ln(3)/(L75\% - L50\%) = S1/L50\%$$

The F-array calculated for new values of L50% and L75% was then used in the Thompson and Bell prediction model to investigate the effect of an increase in length at first capture on the resultant Yield per Recruit curve.

3 RESULTS AND DISCUSSION

3.1 Growth

From the plot of percentage growth factor against premoult CW, it was seen that only one male crab had moulted twice within the period of tag-returns (Fig. 3.1). This individual was excluded from the regression analysis. The equations fitted for the regressions were as follows:

$$y = -0.13L_T + 29.59 \text{ for males and } r^2 = 0.28 \ (n = 114)$$
$$y = -0.14L_T + 26.47 \text{ for females and } r^2 = 0.23 \ (n = 77)$$

with the following 95% confidence limits of parameters:

Males:	slope:	[-0.16 , -0.09]
	intercept:	[26.07 , 33.11]
Females:	slope:	[-0.20 , -0.08]
	intercept:	[21.66 , 31.28]

Equations for the log/linear plots were as follows:

$$\ln(y) = -0.0076L_T + 3.57 \text{ for males and } r^2 = 0.31$$
$$\ln(y) = -0.011L_T + 3.58 \text{ for females and } r^2 = 0.27$$

with the following 95% confidence limits of parameters:

Males:	slope:	[-0.0098 , -0.0055]
	intercept:	[3.37 , 3.77]
Females:	slope:	[-0.015 , -0.0068]
	intercept:	[3.25 , 3.92]

where y = % growth increment or growth factor and, L_T = premoult CW.

All regressions of percentage growth factor were significant at a 99% level ($P < 0.001$) and the log/linear plots for both males and females had a higher significance than the linear/linear regressions. However, visual examination of the residuals of the log/linear plot did not indicate a better fit than the linear/linear regression (Appendix A, Figures A2 & A3).

T-tests (Appendix A, Table A2) showed that the slope and intercept for the regression for males were not significantly different from that found by Melville-Smith (1989a) (P = 0.61 for the slope and P = 0.23 for the intercept). For females, however, both the slope and the intercept were found to be significantly different from Melville-Smith (1989a) (P = 0.047 for the slope and P = 0.0008 for the intercept).

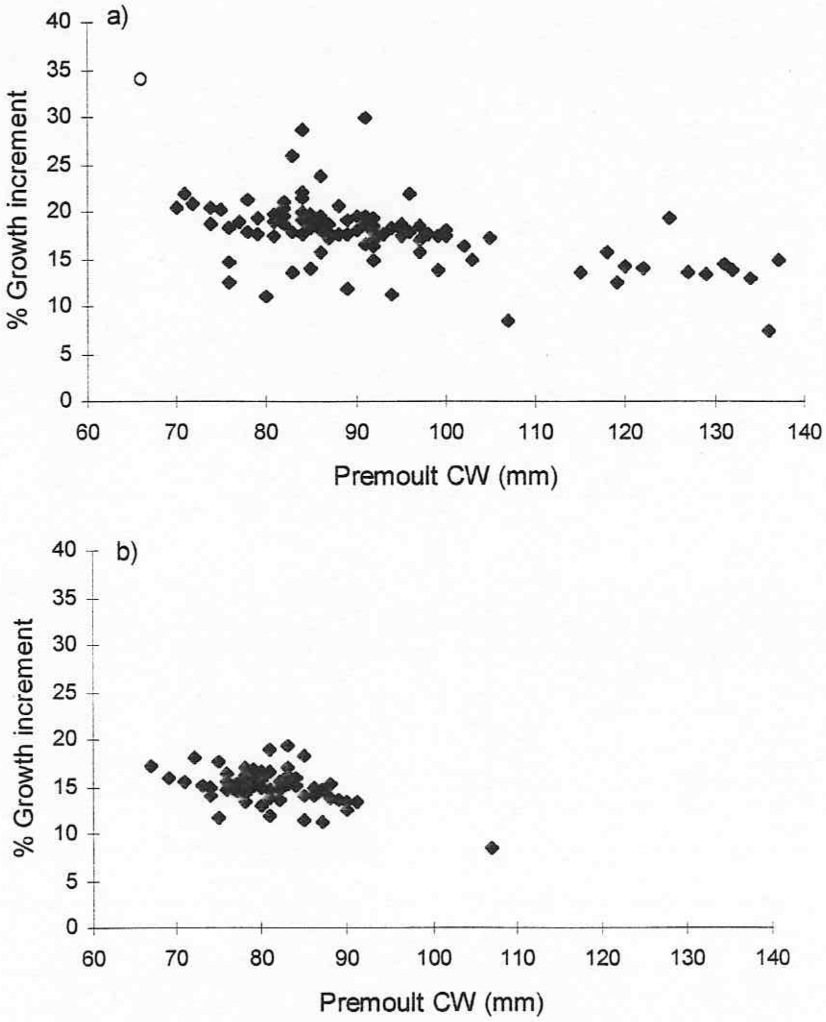


Figure 3.1: Plot of percentage growth increment for male(a) and female (b) *C. maritae* against premoult carapace width. The open circle represents one male which had moulted twice.

Mean values calculated for percentage growth increments were 17.99 (n = 114, SD = 3.62) for males and 15.037 (n = 77, SD = 1.71) for females. An F-test indicated that the variances for males and females were significantly different (P = 3.38E-11), thus a t-test for unequal variances was employed. A one-tailed t-test indicated that mean percentage growth increment for females was significantly smaller than that of males (P = 1.39E-12).

In the Hiatt growth diagram for *C. maritae* males the point of intersection was found to be at 88mm premoult CW (L^* = 88mm CW), as determined by Sommerton's (1980) method. Melville-Smith (1989a) found this intersection point to be 93mm CW. The intersection point occurs near the point of sexual maturity, around 80mm CW (Melville-Smith 1987b). Two regressions were thus done, one for males ≤88mmCW and one for males >88mmCW. The regression equations were found to be:

≤88mmCW: $L_R = 1.04L_T + 15.96$ and $R^2 = 0.60$ ($n = 59$)
>88mmCW: $L_R = 1.01(L_T - L^*) + 107.83$ and $R^2 = 0.92$ ($n = 55$)

with the following 95% confidence limits of parameters:

slope (≤88mmCW):	[0.82 , 1.27]
intercept (≤88mmCW):	[-2.48 , 34.41]
slope (>88mmCW):	[0.96 , 1.07]

The 95% confidence limits for the intercept of the regression equation for males larger than 88mmCW could not be determined, since this is a fixed point determined by an iterative method.

It is expected that immature crabs grow slightly faster, since no energy has to be put into reproduction. However, results from Sommerton's method indicate that the increase in carapace width is very similar between immature and mature male crabs. The slopes of the two regressions were compared using a t-test, and it was found that the slopes were not significantly different ($P = 0.65$). It was thus decided to use a single Hiatt growth diagram for male crabs (Fig. 3.2a). The regression equation was as follows:

$$L_R = 1.016L_T + 18.44 \text{ and } r^2 = 0.93 \ (n = 114)$$

with the following 95% confidence limits of parameters:

slope:	[0.97 , 1.07]
intercept:	[13.62 , 23.26]

During the study time no mature females were found to be in the soft moulting stage just before ecdysis. Although some female crabs have been observed to moult after maturity is reached in the laboratory, there is probably such an extended time before the second mature moult, that crabs might never reach it (Melville-Smith 1990).

Thus, for practical purposes it can be assumed that females stop growing once maturity is reached. The female Hiatt growth diagram (Fig. 3.2b) was thus described by a single linear relationship (also see Melville-Smith 1989a). The regression equation for the female Hiatt growth diagram was as follows:

$$L_R = 1.002L_T + 14.11 \text{ and } r^2 = 0.92 \ (n = 77)$$

with the following 95% confidence limits of parameters:

slope:	[0.93 , 1.07]
intercept:	[8.50 , 19.72]

The slopes of the Hiatt growth diagrams for males as calculated by Sommerton's method were found not to be significantly different from those of Melville-Smith (1989a) ($P = 0.29$ for $CW \leq L^*$, and $P = 0.96$ for $CW > L^*$). The intercept of the regression for male crabs smaller than L^* was also found not to be significantly different ($P = 0.23$) from that found by Melville-Smith (1989a). For the female Hiatt growth diagram both the slope and the intercept were found not to be significantly different from those found by Melville-Smith (1989a) ($P = 0.51$ for the slope and $P = 0.35$ for the intercept) (Appendix A, Table A2).

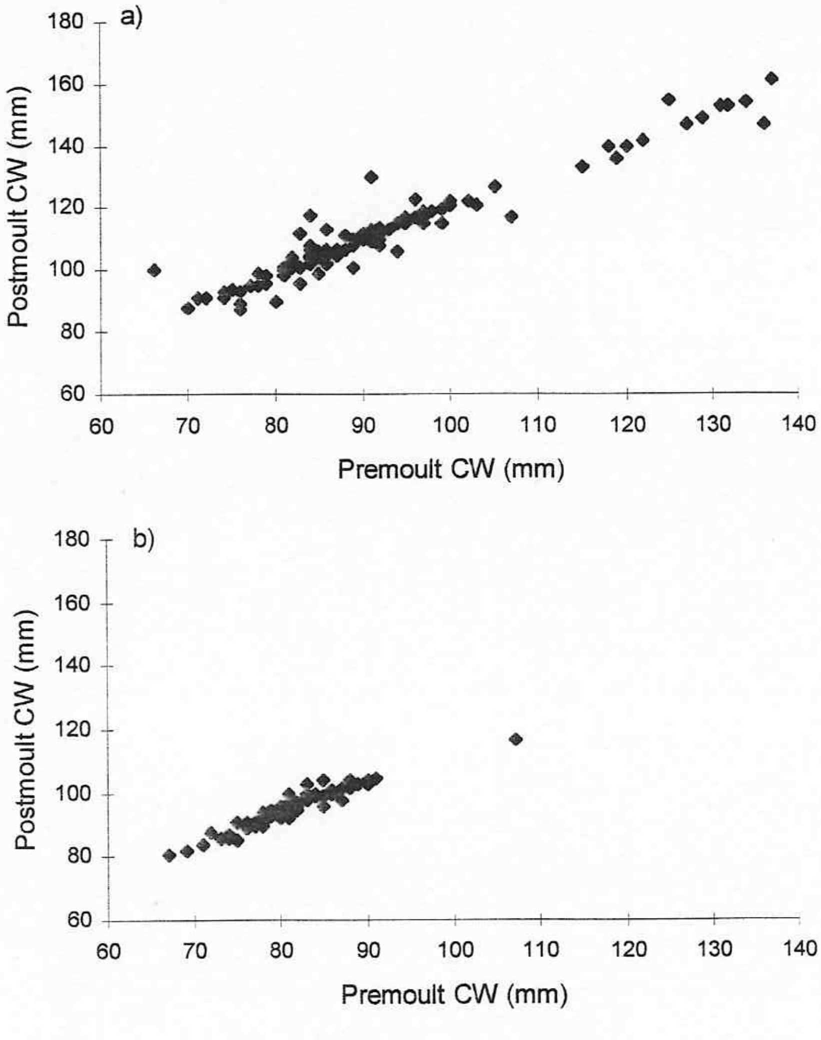


Figure 3.2: Hiatt growth diagrams for male (a) and female (b) *C. maritae.*

The average number of days at large for male crabs that had moulted once were regressed against premoult CW to determine the relationship between size and intermoult period (Fig. 3.3). A log/linear regression was also performed on this data. The following equations were found for male crabs:

$$y = 7.23L_T + 21.20 \text{ and } R^2 = 0.39 \ (n = 42)$$

with the following 95% confidence limits for parameters:

slope: [4.33 , 10.14]
intercept: [-267.17 , 309.56]

and

$$\ln(y) = 0.0103L_T + 5.53 \text{ and } R^2 = 0.31$$

with the following 95% confidence limits for parameters:

slope: [0.0054 , 0.015]
intercept: [5.05 , 6.01]

where y = average number of days at large with moulting once.

Both regressions were significant at a 99% level and the linear/linear regression had a higher significance. Residual plots of the regressions also showed a slightly better fit for the linear/linear regression (Appendix A, Fig. A4).

From the plot of average number of days at large against premoult carapace width for females, there were four datapoints that were obvious outliers (Fig. 3.3). These outliers were datapoints where the average number of days at large was more than 600. It was thus decided to exclude all datapoints where average days at large was more than 600. The following regression equation was found:

$$y = 2.19L_T + 136.08 \text{ and } R^2 = 0.07 \ (n = 19)$$

with the following 95% confidence intervals of parameters:

slope: [-1.86 , 6.24]
intercept: [-204.36 , 476.51]

where y = average number of days at large with moulting once.

The regression for female intermoult period was found not to be significant ($P = 0.27$), thus it can be concluded that the intermoult period for females does not increase with size. The average intermoult period for females was then calculated and found to be 319.16 days (n = 19, and s.e. = 14.71). Thus, intermoult period for females varied around one year regardless of size.

A growth model for male crabs was then constructed by using the linear/linear regressions for both growth factor and intermoult period (Table 3.1 & Fig. 3.4a). Another growth model was constructed using the equation for the male Hiatt growth diagram and the linear/linear regression for intermoult period (Table 3.2 & Fig. 3.4b).

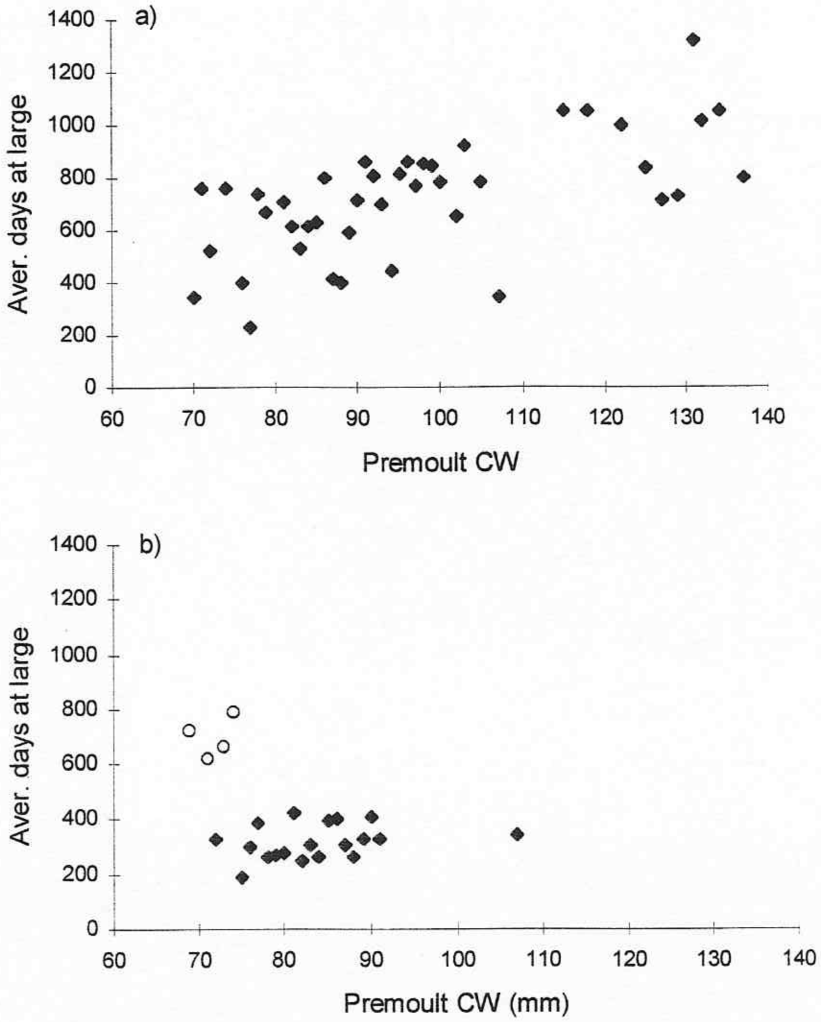


Figure 3.3: Average number of days at large with moulting once for male (a) and female (b) *C. maritae* plotted against premoult CW (mm). Open circles are datapoints which were excluded from the analysis for females.

Table 3.1: A growth model for male *C. maritae* as calculated from growth factors and intermoult periods. The age given at 22 mm CW is that of *C. quinquedens* (Van Heukelem *et al.* 1983), and was used only as a relative starting point.

Instar no.	Age (years)	Carapace width
6	***1.39***	***22***
7	2.00	27.90
8	2.76	35.17
9	3.69	44.01
10	4.83	54.59
11	6.21	66.98
12	7.88	81.13
13	9.85	96.82
14	12.16	113.62
15	14.81	130.92
16	17.80	148.00
17	21.11	164.11

Table 3.2: A growth model for male *C. maritae* as calculated from the Hiatt growth equation and intermoult periods. The age given at 22 mm CW is that of *C. quinquedens* (Van Heukelem *et al.* 1983), and was used only as a relative starting point.

Instar no.	Age (years)	Carapace width
6	***1.39***	***22***
7	2.26	40.80
8	3.50	59.90
9	5.13	79.32
10	7.15	99.05
11	9.57	119.11
12	12.39	139.49
13	15.62	160.21
14	19.27	181.27

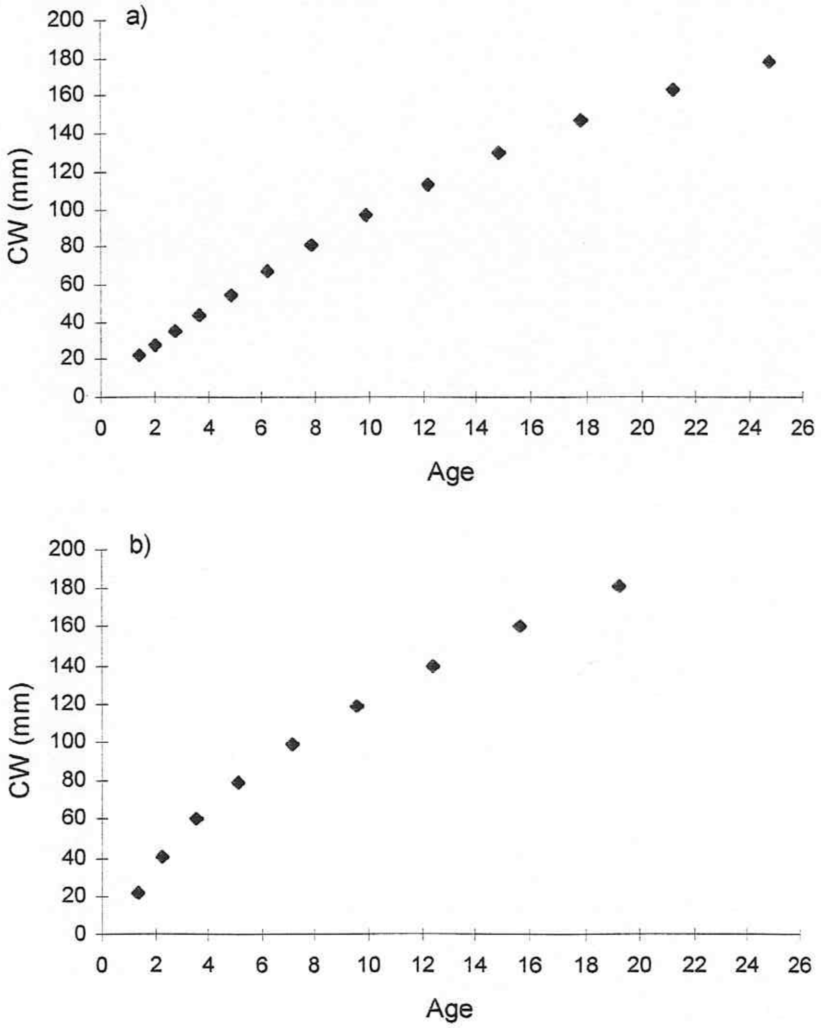


Figure 3.4: Carapace width (mm) at age for male *C. maritae* using two functions of growth increment: a) percentage growth increment and (b) Hiatt growth diagram.

3.2 Discussion *(Growth)*

Hartnoll (1982) reported a mean growth increment of 22% for larval decapods, and that this value tend towards 25-26%. These values compare well with the values of the intercepts found in this study, which was assumed to be representative of larval growth (29.6% for males, and 26.4% for females). Hartnoll (1982) also reported that the slopes of regressions of log(%growth increment) on size tended to be shallow for species which attain a fairly large size and/or where growth was limited by a terminal moult. *Cancer magister* and *Cancer pagurus* e.g. reached maximum carapace widths of 190mm and 149mm, respectively, with the slopes for the log(%growth increment) function being 0.0018 and 0.002, respectively (Hartnoll 1982). These values for the slope compared well with the slope for males (0.0076) found here. Female *C. maritae* were found to have a steeper slope than males, as is to be expected, since they attain a smaller maximum size. The maximum size for male *C. maritae* is around 165mm CW, and the maximum size for females is around 130mm CW, although very few females grow larger than 100mm CW (also see Melville-Smith 1988a).

Hartnoll (1982) reported numerous cases where growth increments were smaller in females than males. This is probably due to a large proportion of available resources being used for reproduction in females. A smaller change in the growth factor regression is expected for males at puberty than for females (Hartnoll 1982). In the data presented here there was no obvious change in the regression for females *C. maritae* at puberty (Fig. 3.1), which is to be expected if females do not continue moulting once maturity is reached. Although it is possible for females to moult after maturity, this probably occurs rarely (see Melville-Smith 1990, Fig. 3.2).

Hiatt growth diagrams are generally difficult to interpret and mathematically not satisfactory, since the premoult size is contained within the postmoult size, which produces a great deal of correlation (Hartnoll 1982, Zar 1996).

Intermoult period for males was modelled differently from Melville-Smith (1989a). He used the following data to model the intermoult period: maximum number of days at large without moulting, maximum number of days at large with moulting once, number of days at large before the first double moult, and confirmed intermoult periods. He also assumed that the intermoult period should (i) not be less than the maximum number of days at large without moulting, and (ii) not be more than the number of days at large before recording the first double moult. The relationship of intermoult period and CW found by Melville-Smith (1989a) were $y = 0.006\ e^{-0.018x}$, where y = 1/(intermoult period) and x = carapace width.

C. maritae was not believed to have an annual moulting cycle (Melville-Smith 1989a). Therefore, the average number of days at large for crabs that have moulted once was believed to be a good indicator of intermoult period from the present tag-recapture data. The average number of days at large were used to overcome the following two artefacts which can be caused by the time of recapture:

(i) Although only crabs in hard or hard new moulting stages were tagged, the possibility exists that they can moult and be recaptured shortly afterwards. This is caused by the fact that *C. maritae* does not seem to have an annual moulting season. This would cause intermoult period to be underestimated.

(ii) Crabs can be recaptured a long time after ecdysis took place, and would thus result in an overestimate of intermoult period.

The growth model for male *C. maritae*, as calculated in Table 3.1, indicated that growth was similar to that calculated by Melville-Smith (1989a) for crabs up to 113mm CW, but larger crabs seemed to grow faster than reported by Melville-Smith (1989a). This was probably due to the fact that intermoult periods calculated here were shorter than that indicated by the function of intermoult period reported by Melville-Smith (1989a), especially for larger crabs. Melville-Smith (1989a) used the function of percentage growth increment and premoult carapace width to calculate the growth model for males, which was comparable to Table 3.1. The number of instars (17) found for male crabs (Table 3.1) compared well with the 16 instars found by Melville-Smith (1989a), which is typical for brachyurans (Hines 1990).

According to the mesh selectivity as reported by Melville-Smith (1986), the growth model (Table 3.1) indicated that crabs recruit to the fishery at an age of about six to eight years. This was slightly less than the seven to nine years determined by Melville-Smith (1989a) from a tagging study in the 1980s.

Using the Hiatt growth diagram in the growth model resulted in faster growth of male crabs. According to this they would recruit to the fishery at about three to five years of age. However, this model was considered to be less reliable due to difficulties in interpretation of the Hiatt growth diagram as stated earlier (also see Mauchline 1977, Hartnoll 1982, Botsford 1985).

Apart from *C. maritae*, growth in other geryonid crabs had only been measured directly in one other species, *C. quinquedens*. Growth increments in captive female *C. quinquedens* within the size range 73-94mm CW, were 8-21% and showed no correlation with premoult size (Hines 1990). *C. quinquedens* juveniles, reared in the laboratory, showed that larval growth was temperature dependent and crabs would require 5-6 years to grow to 114mm CW (Van Heukelem *et al.* 1983). Field tagging studies of *C. quinquedens* indicated slow growth with potentially long intervals between moults of larger crabs. In a tagging study on *C. quinquedens* by Lux *et al.* (1982) some males of 130 to 140mm CW and some females >110mm CW did not moult for 6 to 7 years. The study by Lux *et al.* (1982) also indicated higher moult frequency for females and small crabs. According to the function of intermoult period and carapace width, intermoult periods for *C. maritae* males of 140mm CW were around three years.

3.3 Analysis of sex ratio's by depth

Comparison of the two regressions done for the analysis of sex ratio by depth showed that the logistic curve fitted the data better than the linear curve fitted to arcsin transformed data (Table 3.3 and Figures 3.5 & 3.6). The coefficient of determination (r^2) for the logistic curve was higher than that of the linear regression and the residuals from the linear curve also showed signs of non-linearity for large crabs (Appendix A, Fig. A5).

The logistic curve showed that commercial catches taken at 500 and 550m consisted of 50% and 60% males respectively, *i.e.* 50% and 40% females.

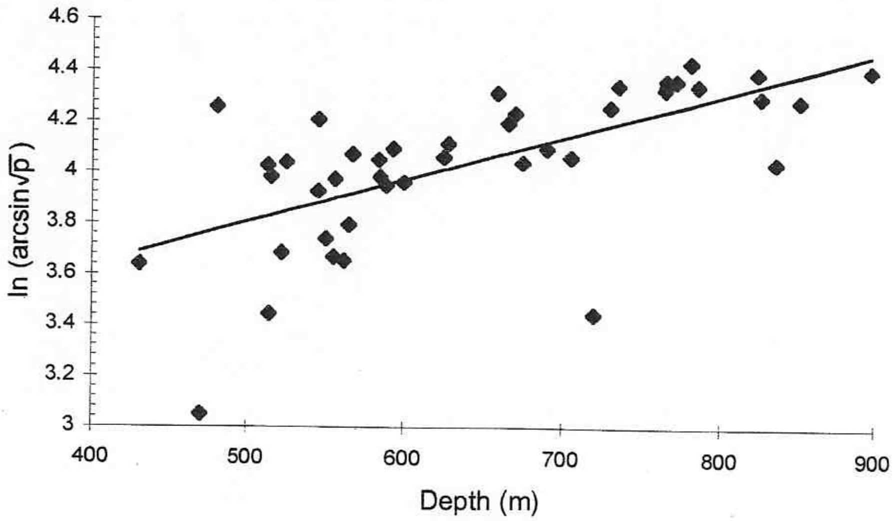


Figure 3.5: Linear regression of arcsine transformed data of proportion males in commercial catches against depth for *C. maritae* off the Namibian coast.

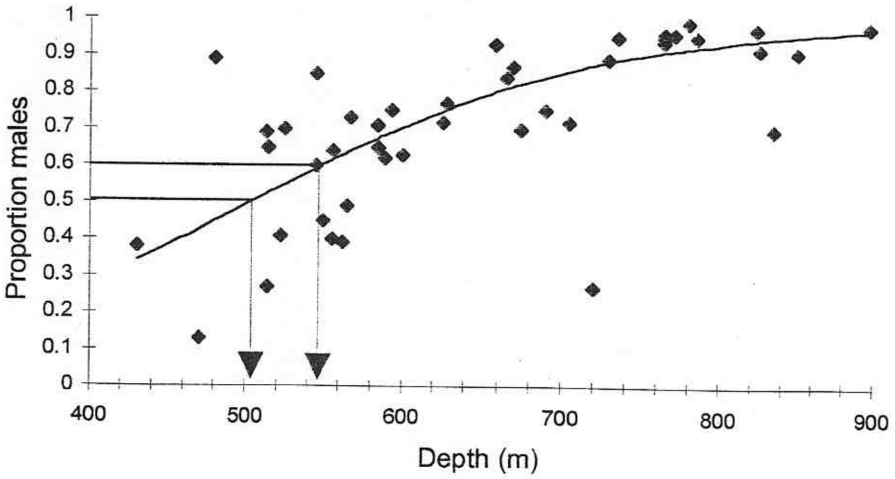


Figure 3.6: A logistic curve fitted to proportion of males in commercial catches plotted against depth for *C. maritae* off the Namibian coast.

Table 3.3: A summary of results from the analysis of sex ratio by depth for *C. maritae* by means of a linear regression and a logistic curve.

Curve	n	r^2	a	**95% confidence limits**	b	**95% confidence limits**
Linear	44	0.43	2.98	2.59 - 3.37	0.0017	0.0011 - 0.0023
Logistic	44	0.54	4.50	2.83 - 6.18	-0.0090	-0.12 - -0.0064

3.4 Seasonality of CPUE

Results from ANOVA run on CPUE data per month (Fig. 3.7) showed that there was no significant difference in CPUE data per month (Table 3.4). However, CPUE data between years were significantly different from each other (Table 3.4).

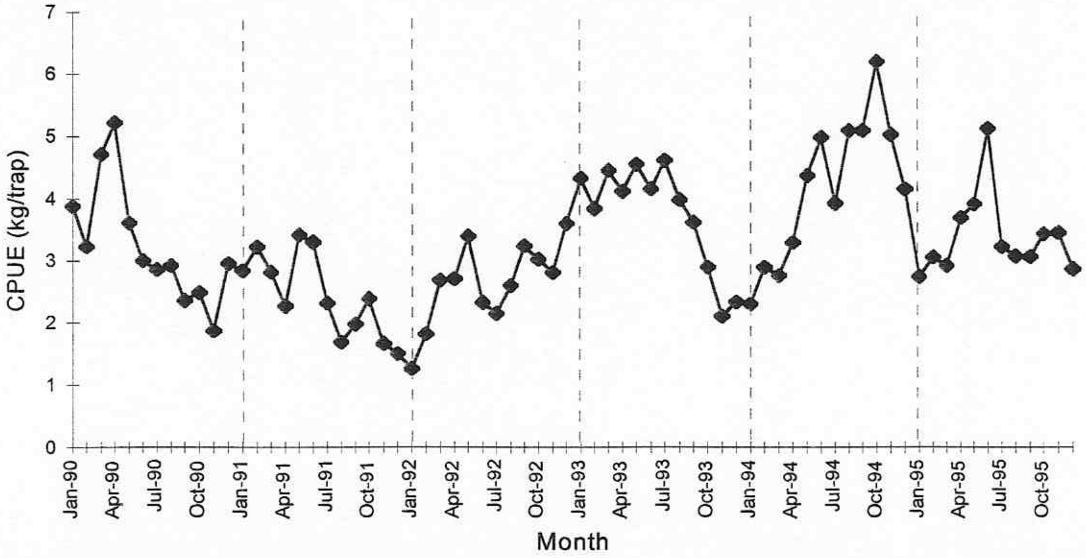


Figure 3.7: CPUE per month from 1990 to 1995 for the deep sea red crab, *C. maritae*, fishery off the Namibian coast.

Table 3.4: Summary results of two-way ANOVA without replication run on monthly CPUE data from 1990 to 1995 of the *C. maritae* fishery off Namibia.

Year	**N**	**Sum**	**Average**	**Variance**
1990	12	39.10	3.26	0.93
1991	12	29.42	2.45	0.45
1992	12	31.61	2.63	0.45
1993	12	44.98	3.75	0.73
1994	12	50.05	4.17	1.38
1995	12	40.52	3.38	0.42
Month	**N**	**Sum**	**Average**	**Variance**
Jan	6	17.35	2.89	1.22
Feb	6	18.07	3.01	0.44
Mar	6	20.34	3.39	0.86
Apr	6	21.30	3.55	1.11
May	6	23.25	3.88	0.24
Jun	6	22.88	3.81	1.26
Jul	6	19.07	3.18	0.90
Aug	6	19.35	3.22	1.38
Sep	6	19.35	3.23	1.19
Oct	6	20.42	3.40	2.01
Nov	6	16.91	2.82	1.60
Dec	6	17.39	2.90	0.86
ANOVA				
Source	**SS**	**df**	**MS**	**P**
Year	25.49	5	5.10	3.87184E-05
Month	8.01	11	0.73	0.46
Error	39.92	55	0.73	
Total	73.42	71		

3.5 Tag-recapture

3.5.1 *Petersen method*

Population estimates were obtained for the following tag-recapture periods: November 1992 - November 1993, October 1993 - October 1994, December 1994 to December 1995, and July 1995 to July 1996. The results of 1993/1994 have to be interpreted with caution, as it is known that not all recaptures were reported. This would result in an overestimate of the population. The number of animals tagged and returned are given in Table 3.5. Density and population estimates of fully recruited crabs (>75 mm CW) for these periods are given in Table 3.6 (Also see Fig. 3.8).

Table 3.5: Number of deep-sea red crab, *C. maritae*, tagged and recaptured off the Namibian coast per year for three regions.

Region	Year	No. Tagged	No. Recaptured	% Recaptured
18° - 19°S	92/93	2296	97	4.22
	93/94	2306	62	2.69
	94/95	1746	27	1.55
	95/96	2298	36	1.57
19° - 20°S	92/93	0	0	0
	93/94	2101	99	4.71
	94/95	1507	35	2.32
	95/96	1853	113	6.10
20° - 21°S	92/93	2244	66	2.94
	93/94	0	0	0
	94/95	498	5	1.00
	95/96	291	7	2.41

Table 3.6: Density and population estimates with 95% confidence limits of fully recruited deep-sea red crab, *C. maritae*, as calculated by the Petersen method for three regions off the Namibian coast.

Region	Year	Population (millions)	95% confidence limits	Density (crabs.ha^{-1})
18° - 19°S	92/93	95.11	78.11 - 115.76	904.88
	93/94	116.65	91.31 - 148.87	1109.78
	94/95	181.59	126.19 - 260.09	1727.63
	95/96	108.97	79.30 - 149.34	1036.70
19° - 20°S	92/93	-----	-----	-----
	93/94	91.33	75.16 - 110.95	325.80
	94/95	113.29	82.10 - 155.91	404.16
	95/96	29.39	24.48 - 35.27	104.84
20° - 21°S	92/93	12.42	9.79 - 15.73	43.43
	93/94	-----	-----	-----
	94/95	60.60	28.58 - 116.58	211.98
	95/96	13.93	7.21 - 25.47	48.73

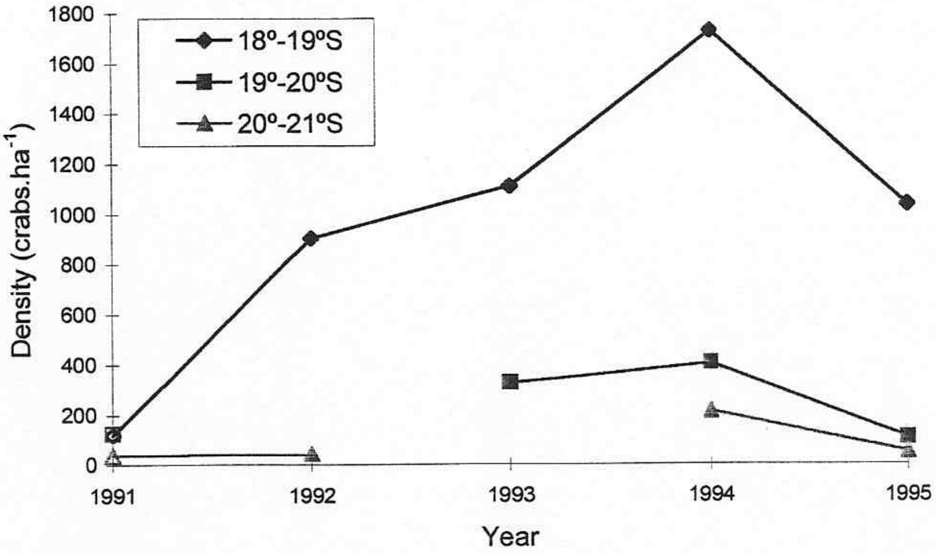


Figure 3.8: Density of *C. maritae* as determined by tag-recapture. The estimates of 1991 is from Beyers (1994).

3.5.2 *Estimating emigration*

Fishermen reported a substantial amount of recaptures being made in Angolan waters (pers. comm., K. Otani, General Manager, Nissho Iwai Corporation). They said that especially high recaptures were made during 1991 to 1992, and that since 1993, recaptures in Angola declined and approximately 20 to 30 recaptures were made in one fishing trip (3 - 4 months). Unfortunately, data on tag-recaptures from Angola have only been reported on two occasions in 1995 and 1996. From October to December 1995, 78 tag-recaptures were reported from one vessel and for July to September 1996, 29 tag-recaptures were reported from the same vessel. Tag-recaptures in Namibian waters for the period of October to December 1995, amounted to only 25 recaptures per vessel on average. There is also an artisenal fishery for *C. maritae* in Angola, but no tag returns have been received from this fishery. Thus far all reported tag-recaptures from Angola were females.

For crabs tagged in 1995/1996, 35 crabs from the area 18° - 19°S, and 15 crabs from the area 19° - 20°S, were recaptured in Angola. Population estimates, taking these estimates of emigration to Angola into account for 1995/1996 are presented in Table 3.7. This still does not represent all tag returns from Angola, since these were tag-recaptures from only one fishing trip for one vessel in Angola. Although these estimates did not represent total emigration to Angola, the population estimate for 18° - 19°S was reduced by about 49%, while the population estimate for 19° - 20°S was reduced by 12%.

Table3.7: Population estimates, with an estimate of emigration to Angola taken into account, for fully recruited deep-sea red crab, *C. maritae*, in two regions off the Namibian coast.

Region	Year	Population (millions)	95% confidence limits	Density (crabs.ha^{-1})
18° - 19°S	95/96	55.25	40.21 - 75.72	525.65
19° - 20°S	95/96	25.95	21.61 - 31.14	246.84

3.5.3 *Migration*

Preliminary analysis of movements showed that *C. maritae* has the ability to move substantial distances. From Fig. 3.9 it can be seen that 94% of males and only 60% of females tagged during the period 1992-1995 moved between 0 and 5 nautical miles from their tagging locations, within one year of recapture. However, 6% of males and 40% of females moved more than 50 nautical miles from their tagging locations. Thus, crabs either stayed near their tagging locations or moved substantially from their tagging location. This pattern is similar to movements of crabs tagged in 1991 (Appendix B, Fig. B10), although only 12% of females moved further than 50 nautical miles in this year.

The maximum distance moved within one year for males was 120 nautical miles and that for females was 180 nautical miles. These were three females recaptured in January 1996 after 196, 197, and 200 days, respectively, in Angola. From Fig 3.9 it was also clear that more females tended to move from their tagging locations while males tended to stay close to their tagging locations. It was also clear that females moved further than males. G-tests (Zar 1996) confirmed that there was not an equal ratio between males and females staying at their tagging locations (P = 2.02E-11) and that there was not an equal ratio of males and females moving further than 50 nautical miles (P = 8.73E-10).

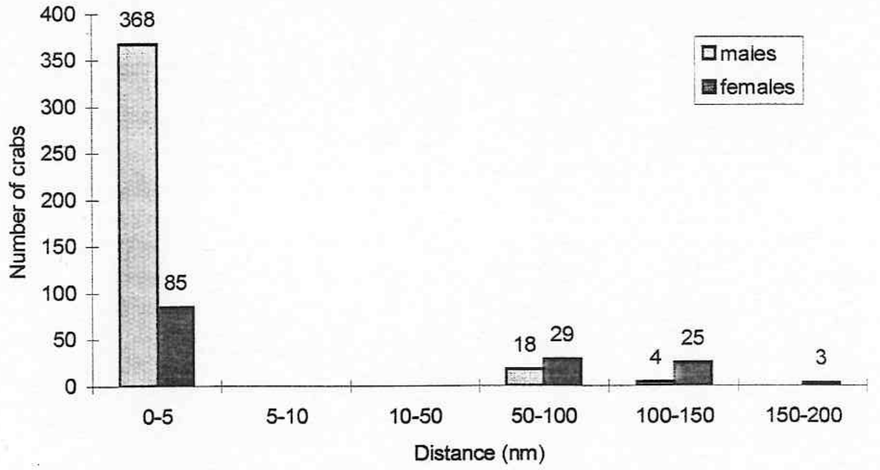


Figure 3.9: Frequency distribution of distances moved within one year of tagging for male and female *C. maritae*.

From plots of movements of crabs tagged in the region 18°-19°S (Appendix B, Figures B1 to B4) it was seen that a substantial proportion of crabs can move out of Namibian waters. From these figures it was also seen that females tended to move in a northerly direction. For crabs tagged in 1995 (Appendix B, Fig. B5) it was clear that a substantial number of female crabs did emigrate out of Namibian waters and that females recaptured in Namibian waters did not move very far from their tagging location, except for one female recaptured at around 20°S. From crabs tagged in the area 19°-20°S, it was also clear that a substantial number of crabs tagged in 1991 and

1993 (Appendix B, Figures B6 & B7) could potentially migrate into Angolan waters or extreme northern Namibian waters (*i.e.* north of 18°S) where fishing effort is generally low (unpublished data). This was not so apparent for crabs tagged in the same region in 1994. However, emigration of a substantial number of females out of Namibian waters was once again observed for crabs tagged in 1995, where data from Angola were available (Appendix B, Fig. B8).

The data on movements of *C. maritae* (Fig. 3.9) indicated that population estimates from tag-recapture in Namibian waters were mostly biased by females moving out of the area of recapture. Catches also consisted mainly of males e.g. in the area 18°-19°S catches consisted of 60-70% males for the 1992 to 1994 tagging experiments and 85% males in 1995. It was thus decided to recalculate population number only for males, since this was less likely to be biased (Table 3.8, Fig. 3.10).

Table 3.8: Density and population estimates with 95% confidence limits of fully recruited male *C. maritae*, as calculated by the Petersen method for three regions off the Namibian coast.

Region	**Year**	**Population (millions)**	**95% confidence limits**	**Density (crabs.ha^{-1})**
18° - 19°S	92/93	54.99	44.83 - 67.42	523.15
	93/94	46.17	33.87 - 62.87	439.24
	94/95	51.59	26.69 - 94.31	490.86
	95/96	80.16	57.28 - 111.80	762.65
19° - 20°S	92/93	-----	-----	-----
	93/94	67.87	54.74 - 84.11	242.12
	94/95	83.46	59.64 - 116.40	297.73
	95/96	16.49	13.47 - 20.17	58.83
20° - 21°S	92/93	11.84	9.21 - 15.20	41.43
	93/94	-----	-----	-----
	94/95	48.89	23.06 - 94.04	171.00
	95/96	9.47	4.70 - 17.76	33.13

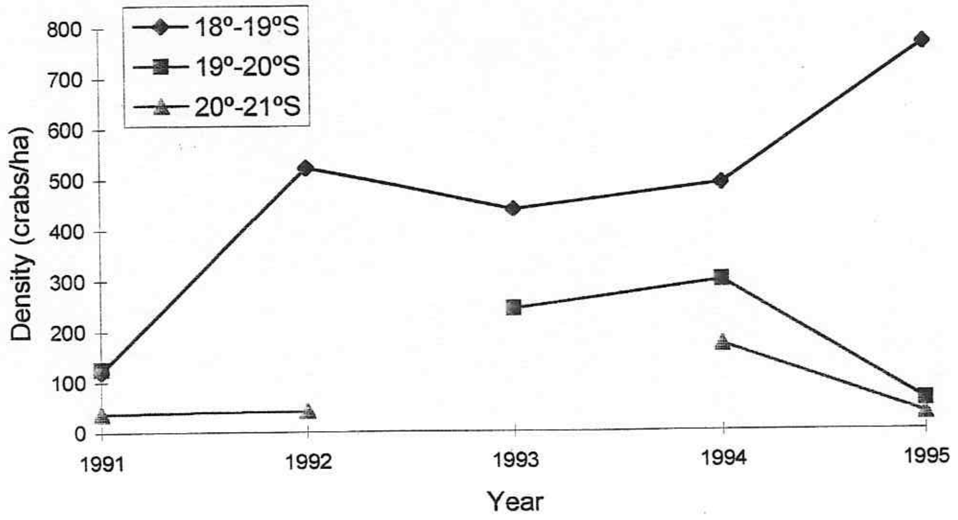


Figure 3.10: Densities of male *C. maritae* as determined by tag-recapture. Densities of 1991 is that of the total population from Beyers (1994).

3.6 Discussion *(Tag-recapture)*

The simplicity and potential precision of methods for assessing populations, such as the Petersen method, makes them popular amongst fish biologists. However, vast errors can occur in population estimates if assumptions of the method are violated (Gatz & Loar 1988).

Assumptions of the Petersen method are that the population is closed, all members of the population have equal catchability and that no tags are lost or unreported. If births and immigration occur, one can calculate the estimated population size during the time of recapture, but not if deaths and emigration occur. Another implicit assumption of the Petersen method is that the catchable population is the total population, and thus only the portion of the population subject to mark and recapture can be estimated (Gatz & Loar 1988).

Standard formulae for estimating the variance or confidence limits of the Petersen population estimate, only estimate the magnitude of error caused by random sampling during the period of recapture. These errors thus indicate nothing as to the magnitude or direction of errors possible when assumptions are violated (Gatz & Loar 1988).

Gatz and Loar (1988) showed that a small ratio of recaptured animals (R) to total animals caught (C) can result in large errors. A ratio of R/C lower than the true R/C would also result in larger errors than overestimates of R/C.

In a marine environment it is difficult to adhere to some of the assumptions behind the Petersen method (Beyers 1994). Beyers (1994) assumed the following:

(i) Tag loss only became significant at ecdysis and only a small number of animals were expected to moult during the 12 month period of recapture.
(ii) It was assumed that all recaptures were reported, since only a few vessels took part in the tagging programme and crabs caught are handled individually.
(iii) Tagging mortality was assumed to be insignificant, since only crabs in a good condition were released.
(iv) Although tagged animals were not randomly distributed, it was assumed that released crabs distributed themselves rapidly in a random fashion after release (also see Melville-Smith 1988b).
(v) It was assumed that immigration and emigration counteracted each other, although Beyers (1994) stated that the 500m depth restriction on fishing might have biased the results.
(vi) Natural mortality was ignored, since it was assumed that this would affect tagged and untagged crabs equally.
(vii) Recruitment into the fishery was ignored.

Beyers (1994) reported the following densities of *C. maritae* in Namibian waters from a tagging experiment conducted in 1991/1992:

Region	Density (crabs.ha^{-1})
17°15'-18°S	227.5

18° - 19°S	119.1
19° - 20°S	125.0
20° - 21°S	37.0

with an average of 98.4 crabs.ha^{-1} for the whole region. Melville-Smith (1988b) found a density of 50.5 crabs.ha^{-1} in the region 19°40'S to 20°10'S, which is comparable to the density in the region 20° to 21°S as found by Beyers (1994). Most population estimates from tag-recapture from 1992 onwards resulted in far higher densities (Table 3.5), than that found by Beyers (1994). For 92/93 only the density found in the region 20°-21°S was comparable to Beyers (1994). For 93/94 and 94/95 none of the densities calculated were comparable to that found by Beyers (1994). For 95/96, densities found in the regions 19°-20°S and 20°-21°S were comparable to that found by Beyers (1994). If emigration to Angola was taken into account, the density estimate in the regions 18°-19°S and 19°-20°S still resulted in much higher estimates than that found by Beyers (1994).

Substantial emigration of crabs out of Namibian waters can create obvious biases in stock estimates if not taken into account when assessing the crab stock by tag-recapture. Tag-recaptures over the last three years were low, in comparison with 1991/1992. Factors that can contribute to low tag returns include:

- Emigration of crabs out of Namibian waters: In the area 18°-19°S there was a substantial discrepancy in population estimates from 92/93 onwards, compared to the estimates of Beyers (1994) (Fig. 3.8). This is also the region which will be mostly affected by emigration of crabs out of Namibian waters, and thus low tag-returns from this region in Namibian waters would result in too high population estimates. Reports from fisherman in Angolan waters were that tag-recaptures declined from 1993 onwards (pers. comm. K. Otani). This decrease was an absolute decrease in tag-returns, since this only involved one fishing vessel. In terms of population size the decline in tag-returns in Angolan waters can be interpreted as an increase in the population there, which might be due to immigration from Namibian waters. Crabs in the regions 18°-19°S and 19°-20°S can emigrate out of Namibian waters (Fig. 3.9 and figures in Appendix B), and data from 1995 showed that a substantial number of females did emigrate out of Namibian waters (Appendix B, Figures B5 & B9).

- Emigration of crabs out of the fishing area: Melville-Smith (1987a) showed that female *C. maritae* tended to move to shallower waters. Since, fishing in Namibian waters was restricted to waters deeper than 400 or 500m, animals migrating to shallower waters would not be recaptured and thus had effectively emigrated out of the tagged population (also see Beyers 1994).

- Misreporting of tag-returns: It is known that not all recaptures for 93/94 were reported. Unfortunately no estimate of non-reported tags can be provided.

The factors mentioned above, could all have contributed to a low R/C ratio and would have resulted in overestimates of the population size in Namibian waters.

From the preliminary analysis of movements of crabs (Fig. 3.9 & Appendix B, Fig. B10) the pattern of movements was similar for crabs tagged in 1991 and crabs tagged in 1992-1995. Although, in 1991, 88% of female crabs tended to move less than 5 nautical miles, compared to only 60% for other years of tagging. Thus, from preliminary analysis of migration it did seem that there was an increased emigration of especially female crabs out of the area. However, the fact that tag-recaptures from Angola were not reported for crabs tagged in 1991 could have biased these results.

Apart from movements of female crabs, tag-recapture results could also have been biased by the following factors resulting from features of the female *C. maritae* population:

- The fishery consist mainly of males and few females are caught in the area assessed (500-800m) (Fig. 3.6).
- Higher moulting frequency. Growth models showed that females were expected to moult within one year and thus tag-loss at ecdysis was more likely for females than males.
- Difference in catchability. Female crabs were expected to have a lower catchability than male crabs (Miller 1990).

Thus, it is probably more realistic to estimate the male population only, and densities in the area assessed (500-800m depth) is expected to be mostly representative of male crabs due to sexual segregation. Male crabs are also the most important in the fishery.

Assessment of the male population only showed similar trends in densities as the whole population, except for the area 18°-19°S (Tables 3.6 & 3.8). The total population trend (Fig. 3.8) showed a peak in 1994, and declined towards 1995 for all areas. Densities calculated for the male population only, showed an increasing trend in density in the area 18°-19°S. This could have been caused by a low R/C ratio due to the high number of males caught in this area in 95/96, which might result in larger errors.

The numbers of animals tagged in each area after 1991 were similar to that of Beyers (1994). If the *C. maritae* population in Namibia had increased since 1991 as is suggested by the data, one would expect the R/C ratio to decrease. This factor plus the effects of emigration and other features of the female population, could have magnified the decrease in R/C and a too low R/C ratio is prone to large errors (see Gatz & Loar 1988).

Lux *et al.* (1982) showed that *C. quinquedens* tended to stay close to their tagging locations, but that crabs were capable of moving up to 90km. Movements in *C. quinquedens*, however, were mainly up and down the slope rather than longshore (Lux *et al.* 1982).

Where data from Angolan recaptures were available, crabs did not seem to be caught on their migration route. For the area 18°-19°S (Appendix B, Fig. B5) no tagged crabs were caught between 18°S and the Angolan border. This might have been due to a generally low fishing effort in this area (unpublished data). However, the same pattern was apparent for crabs tagged in the area 19°-20°S (Appendix B, Fig. B9), and although fishing effort is relatively high in the area 18°-19°S (unpublished data), tagged crabs were not caught on their migration route.

3.7 Cohort analysis and prediction models

3.7.1 *Growth parameters and natural mortality*

Data for input into the Gulland and Holt plot were examined before doing the regression. From the growth model proposed for deep-sea red crab intermoult periods for the size range of male crabs examined here, were more than one year. Thus, for males, all crabs which were recaptured within less than 300 days of tagging were excluded from the regression. For female *C. maritae*, all crabs recaptured more than 600 days after tagging were excluded, as the intermoult period for females was assumed to be around one year.

In the Gulland and Holt plots for both males (n = 106) and females (n = 66) the slopes were found not to be significantly different from zero (P = 0.75 for males and P = 0.90 for females) (Fig. 3.11). This implied that growth in *C. maritae* was linear, and thus did not conform to the general Von Bertalanffy growth model. The mean annual growth rates (r) of males and females were found to be 9.88 mm/year (S.D. = 2.92) and 19.49 mm/year (S.D. = 6.24), respectively.

A general value of natural mortality reported for long-lived crabs and lobsters was around 0.1 (Cobb & Caddy 1989). A natural mortality of around 0.1 was also reported for *Cancer pagurus* (Edwards 1989). Melville-Smith (1988a) reported on other values of natural mortality in the literature, e.g. 0.1 and 0.02 for *Homarus americanus*, 0.1 for *Jasus edwardsii*, and 0.14 for *C. pagurus*.

Since females grew at almost double the rate of males, it was not realistic to assume the same natural mortality for both sexes. In general faster growing animals are expected to have a higher natural mortality (Sparre & Venema 1992). Females also moulted at more regular intervals than males which can be a contributing factor to natural mortality, since crustaceans in a soft shell state are more vulnerable to predation (Cobb & Caddy 1989). It was assumed that the natural mortality for females lies in the range of 0.15 to 0.25. This can be compared to values for natural mortality reported in the literature for Decapoda with similar growth rates. Some values of natural mortality reported are: 0.23 for *Panulirus cygnus* (Phillips & Brown 1989), and 0.2 for *Cancer magister* (Methot 1989).

3.7.2 *Cohort analysis*

Length based cohort analysis assumes equilibrium conditions or a constant parameter system (Sparre & Venema 1992). CPUE data were examined to determine periods of relatively similar CPUE's (see Fig. 1.3). CPUE for the period 1980 to 1984 were fairly similar, while CPUE between 1985 to 1989 showed some fluctuations. There was a heavy drop in CPUE after 1989 and CPUE remained on a fairly low level since. Thus three periods, *i.e.* 1980-1984, 1985-1989, and 1990-1995, were identified and were assumed to be in equilibrium. Cohort analysis was thus done for these three periods. Size frequency distributions for the three periods are presented in Fig. 3.12 (also see Appendix A, Figures A6 and A7).

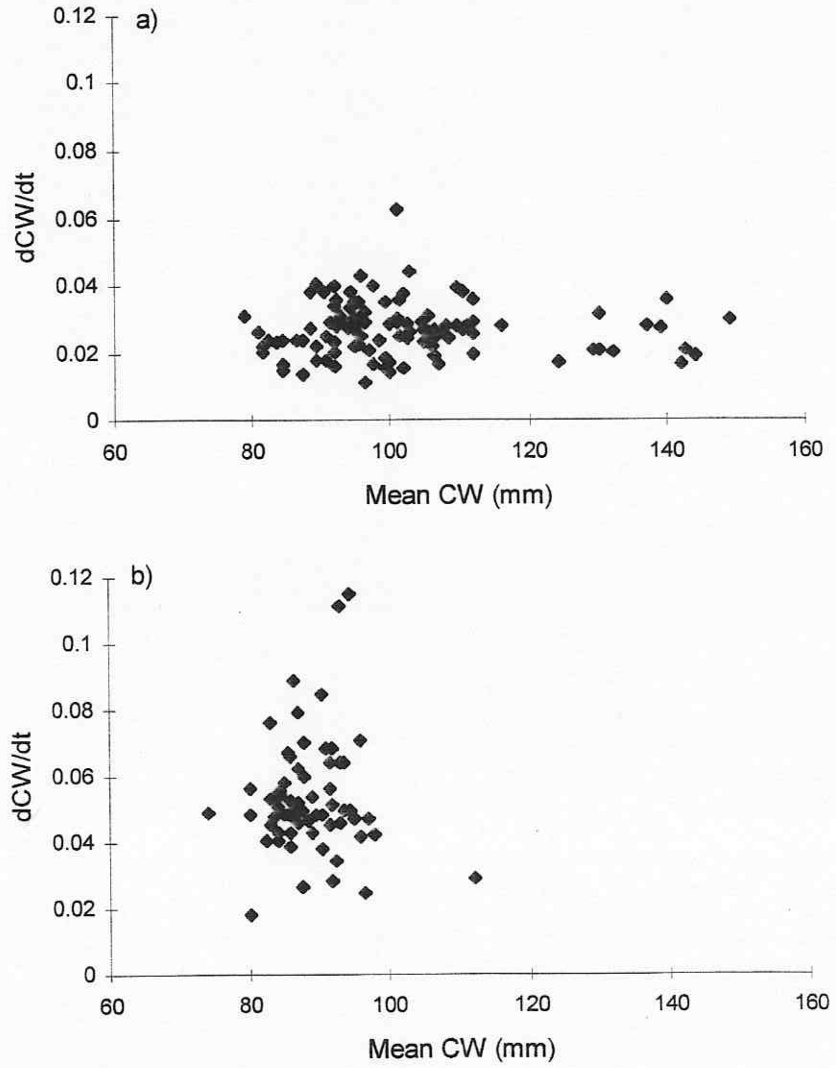


Figure 3.11: Gulland and Holt plots for male (a) and female (b) *C. maritae*.

Annual mean population number were plotted against F_t to examine the effect of F_t (Appendix A, Fig. A8). Very small values of F_t had the most effect on the population number, while higher F_t values had less effect and resulted in a lower population number.

For 1980-1984 a female plus group was formed at 102.5 mm CW, since very few females larger than this were caught, and no plus group was formed for males. For 1985-1989 plus groups were formed for both males and females. A male plus group was formed at 147.5 mm CW. From examining the catch structure for this period (Appendix A, Figures A6 & A7), it can be seen that some larger females were caught than in the previous period. However, females larger than 97.5mm CW still only constituted 6% of the total female catch. It was thus decided to form a plus group at 102.5mm CW. For 1990-1995 females larger than 97.5mm CW only formed 3% of the total female catch and a plus group was also formed at 102.5 mm CW.

Preliminary runs of cohort analysis showed that the F-array for female *C. maritae* always resulted in a dome shaped curve, thus the assumption of F_t being equal to the average fishing mortality of the oldest animals did not hold. This made it more difficult to decide objectively on an F_t value for females. Since the F-array for females always produced a dome shaped curve, the F_t value would be expected to be lower than the fishing mortalities of the oldest animals. For 1980-1984, it was assumed that F_t was equal to half of the average fishing mortality of the previous two length classes. For subsequent periods (1985-1989 and 1990-1995) it was assumed that F_t for females (as calculated for 1980-1984) would increase by the same amount as F_t for males.

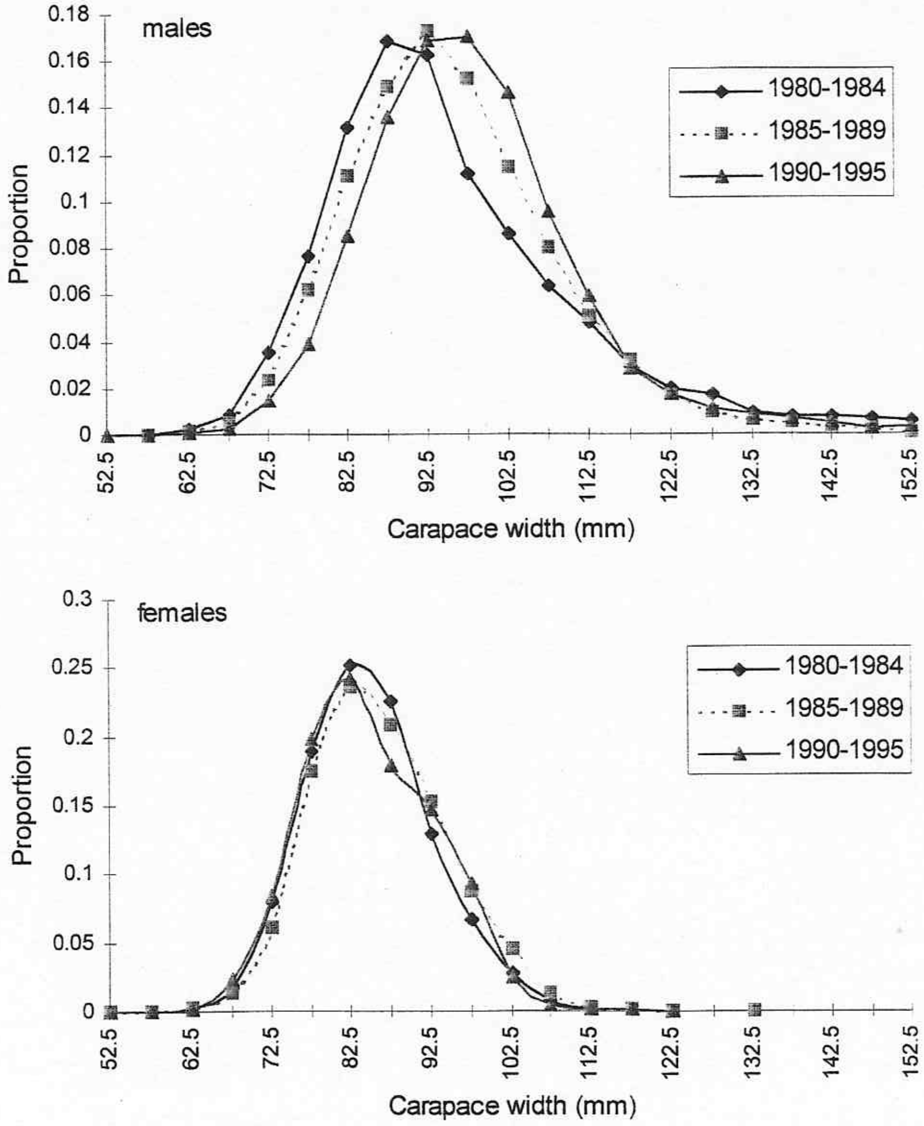


Figure 3.12: Size frequency distribution of male and female *C. maritae* off the Namibian coast for three periods: 1980-1984, 1985-1989, and 1990-1995.

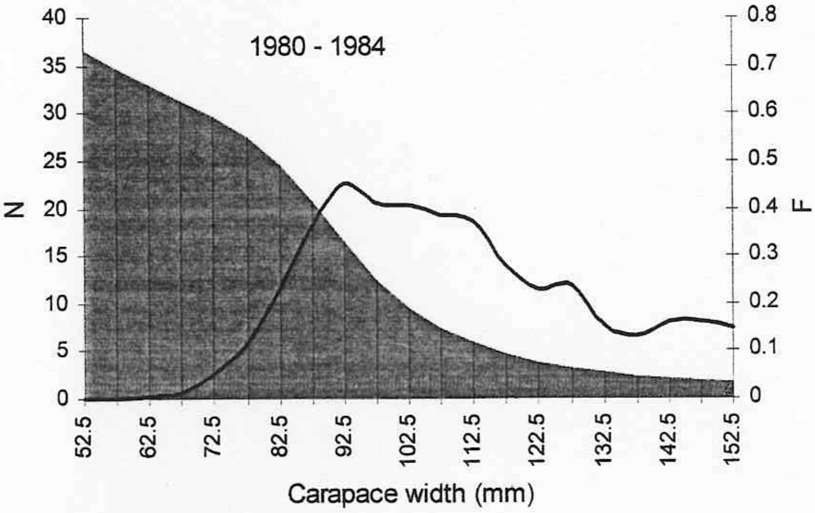
The length groups that were most heavily exploited were 82.5mm to 132.5mm CW for males, and 77.5mm to 97.5mm CW for females for all periods examined (Figures 3.13 & 3.14). (Note that lengths given here represent mid-lengths of length classes.)

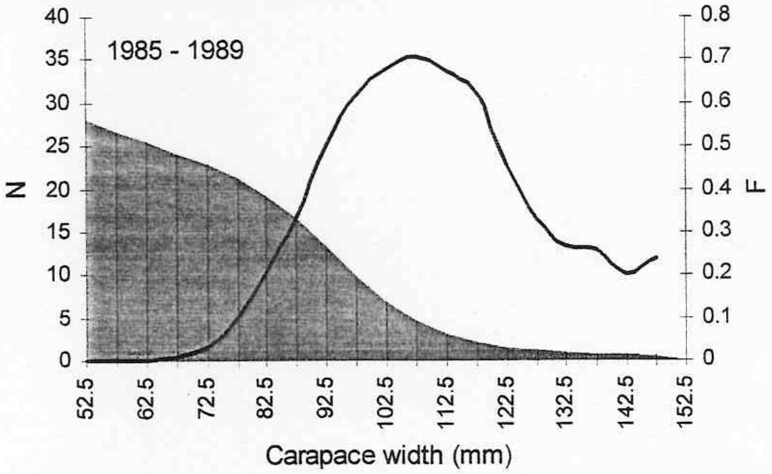
Results showed that there was a 20% to 30% reduction in population size from 1980-1984 to 1985-1989, and that fishing mortalities for males were substantially higher and fishing mortalities for females were lower in the latter period. The population estimate then decreased by over 50% in the last period (1990-1995) analysed, with fishing mortalities for males being similar and fishing mortalities for females being higher than those for 1985-1989 (Table 3.9 & Figures 3.13 & 3.14).

If the reduction of the population was looked at in terms of biomass, results showed that biomass was reduced by 30% to 40% from 1980-1984 to 1985-1989, and towards 1990-1995 the biomass reduced by over 50%.

Table 3.9: Results from cohort analysis for deep-sea red crab, *C. maritae*, for three periods, 1980 to 1984, 1985 to 1989, and 1990 to 1995.

Years		**Mm = 0.05** **Mf = 0.15**	**Mm = 0.1** **Mf = 0.2**	**Mm = 0.15** **Mf = 0.25**
1980 - 1984	$\sum \bar{N}$ (millions)	155.29	186.61	234.02
	$\sum \bar{B}$ (tonnes)	27 497.68	33 493.38	42 707.87
	Mean F (males)	0.39	0.32	0.24
	Mean F (females)	0.86	0.81	0.74
	Ft (males)	0.2	0.15	0.11
	Ft (females)	0.39	0.36	0.33
1985 - 1989	$\sum \bar{N}$ (millions)	125.35	144.71	169.91
	$\sum \bar{B}$ (tonnes)	19 169.47	21 820.85	25 301.44
	Mean F (males)	0.56	0.49	0.42
	Mean F (females)	0.69	0.63	0.58
	Ft (males)	0.3	0.24	0.19
	Ft (females)	0.49	0.45	0.41
1990 - 1995	$\sum \bar{N}$ (millions)	55.14	63.78	75.50
	$\sum \bar{B}$ (tonnes)	8 954.24	10 147.28	11 838.98
	Mean F (males)	0.55	0.48	0.42
	Mean F (females)	1.06	1.007	0.93
	Ft (males)	0.32	0.27	0.21
	Ft (females)	0.51	0.48	0.43





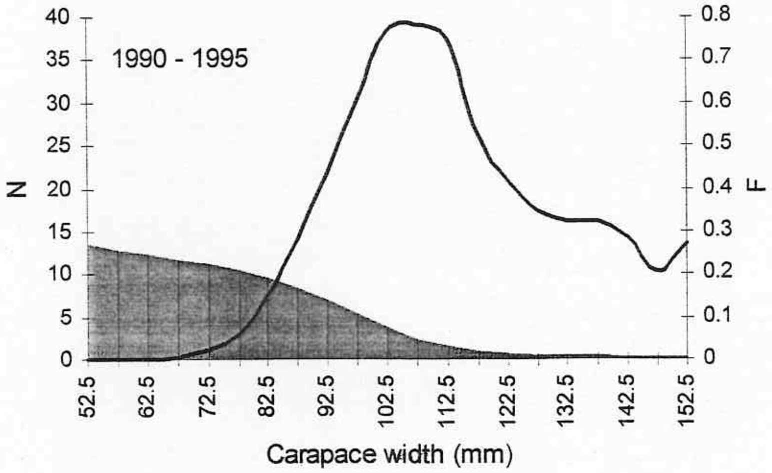


Figure 3.13: Population number (N = area chart) and fishing mortalities (F = line chart) of male *C. maritae* for three different periods. Results depicted here were calculated with M = 0.1.

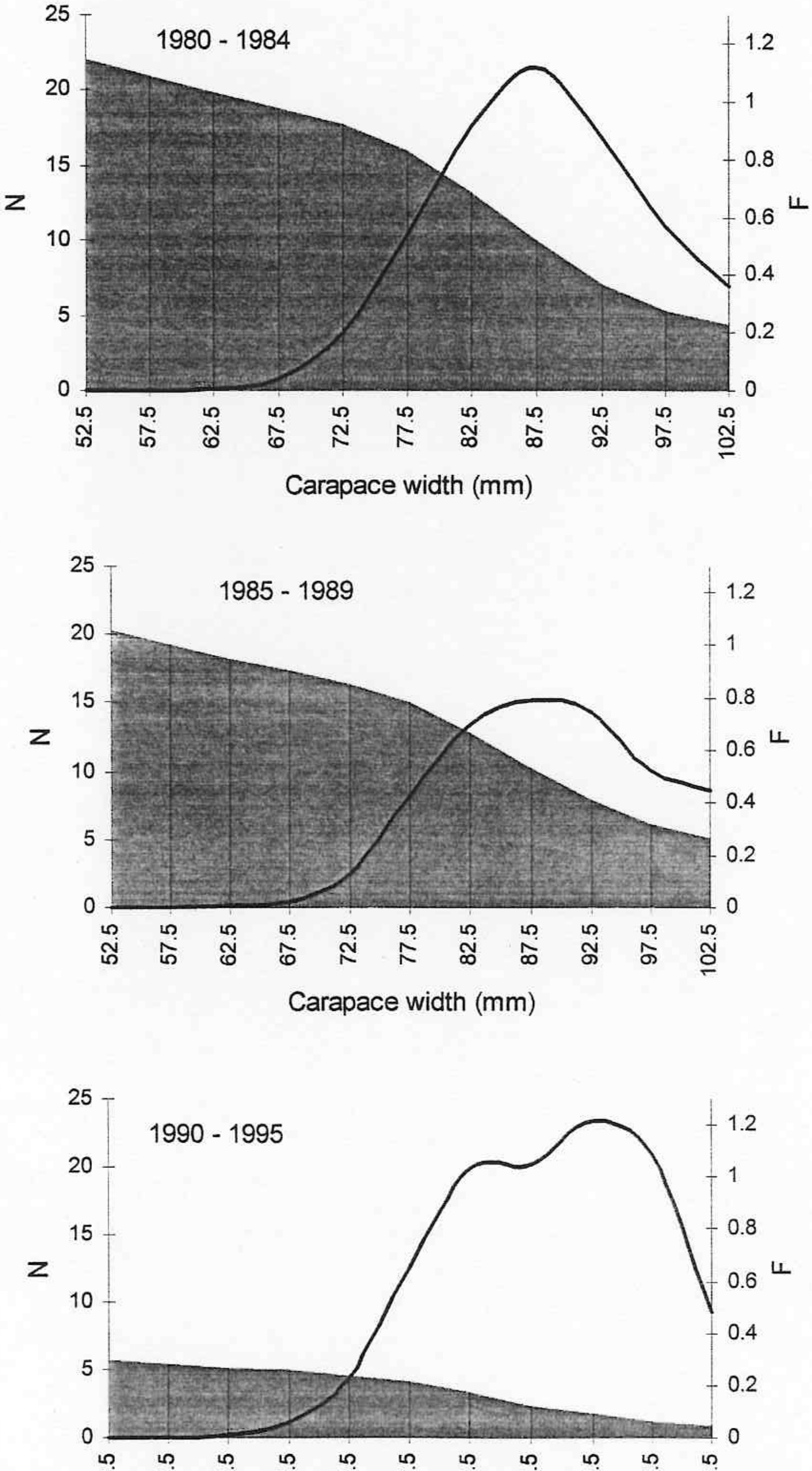


Figure 3.14: Population number (N = area chart) and fishing mortalities (F = line chart) of female *C. maritae* for three different periods. Results depicted here were calculated with M = 0.2.

Cohort analysis, run on an annual basis, indicated that the population number and biomass of *C. maritae* showed some fluctuations, but the general trend from 1983 onwards was downward (Figures 3.15 & 3.16). Fig. 3.15 show two periods of reduction in population number of *C. maritae*, 1983 to 1987, and the most substantial reduction in the population being from 1989 to 1991. If one considers the spawning stock biomass, however, another pattern emerges, with the largest reduction being from 1982 to 1984 (Fig. 3.17).

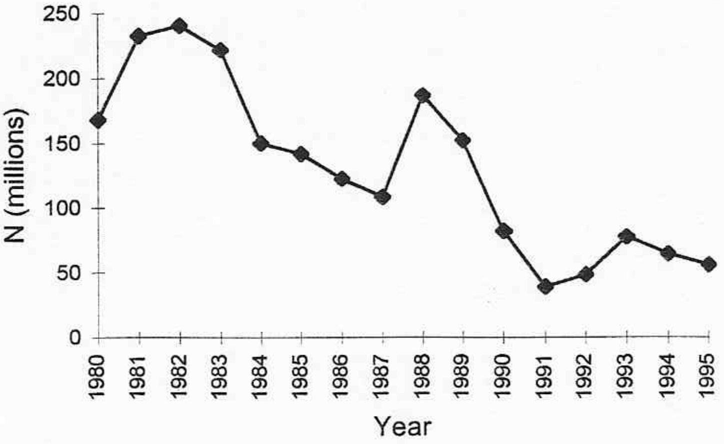


Figure 3.15: Mean annual population number of *C. maritae* as calculated by cohort analysis run on an annual basis from 1980 to 1995.

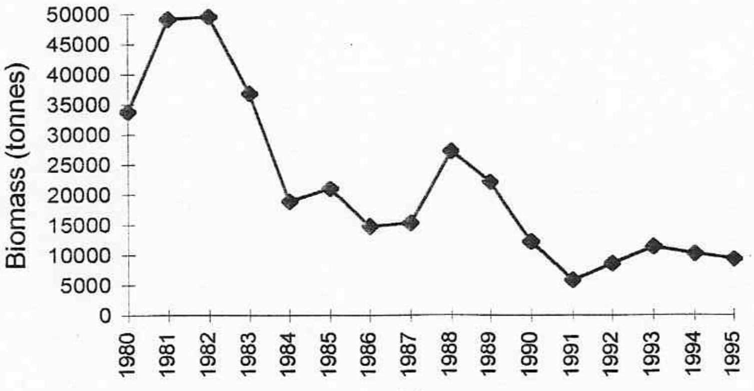


Figure 3.16: Mean annual biomass estimate of *C. maritae* as calculated by cohort analysis run on an annual basis from 1980 to 1995.

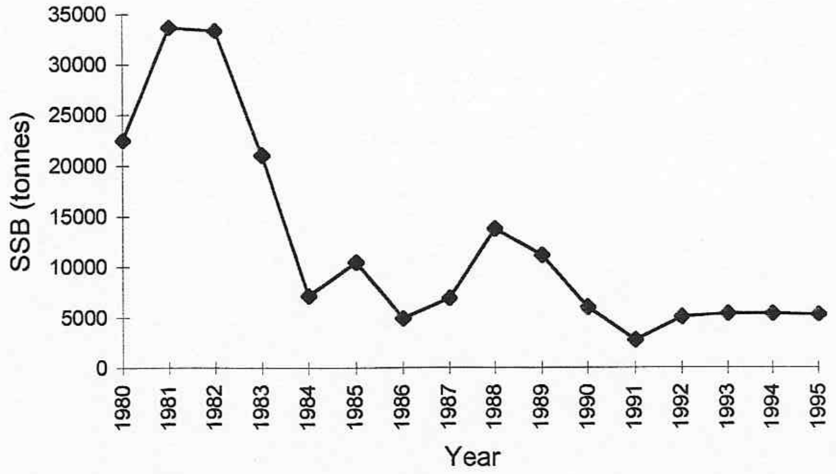


Figure 3.17: Spawning stock biomass (SSB) of *C. maritae* as calculated from cohort analysis run on an annual basis.

3.7.3 *Prediction models*

Results from the Thompson and Bell prediction models showed that *C. maritae* was exploited around MSY levels for the smallest M and below MSY for other values of M for 1980-1984. Fishing mortalities during this period were higher than the optimum level of exploitation at $F_{0.1}$, except for the largest M (Table 3.10). Yield analysis of the second period, 1985-1989, showed that the stock was exploited above MSY levels for the smallest M, and below MSY levels for other values of M. However, fishing mortalities from 1985-1989, were higher than $F_{0.1}$ at all levels of M (Table 3.10). For the last period of assessment, the stock was exploited above MSY levels for all values of M, except for the largest value of M. Fishing mortalities for this period were above the $F_{0.1}$ level for all values of M (Table 3.10).

The Yield per Recruit (Y/R) curves (Fig. 3.18) showed that Y/R was similar in the first two periods analysed and higher in the last period (1990-1995). The higher Y/R in the last period analysed indicated that the overall growth rate of the population was higher. The higher growth rates in the 1990s were probably due to a density dependent effect, since the population was substantially lower in the 1990s than the 1980s (Table 3.9).

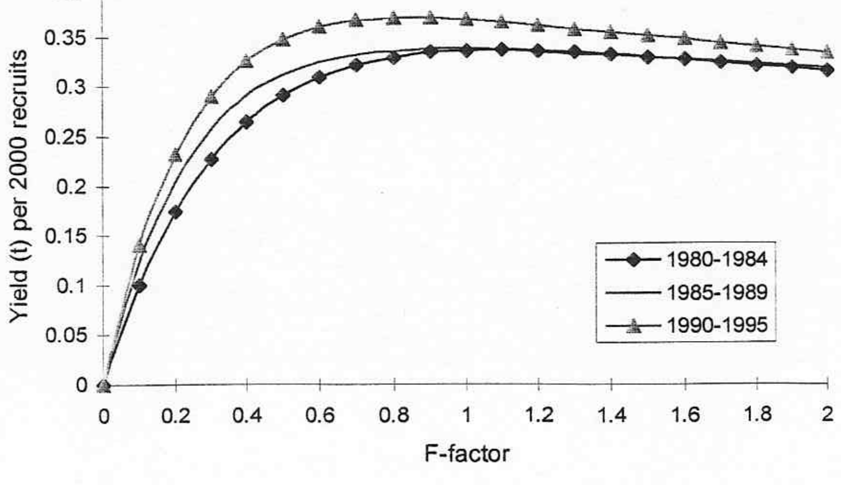


Figure 3.18: Yield per 2000 recruits for *C. maritae* for three different periods. The Yield per recruit curve was calculated at M(males) = 0.05 and M(females) = 0.15.

The selection ogive parameters were calculated from cohort analysis (1990-1995) with natural mortality for males and females being 0.1 and 0.2, respectively (Fig. 3.19). The current L50% and L75% as calculated from the F-array from cohort analysis results were as follows:

L50% (males):	91mm CW
L75% (males):	97mm CW
L50% (females):	77mm CW
L75% (females):	81mm CW

Table 3.10: Fishing mortalities for *C. maritae* off the Namibian coast at MSY and $F_{0.1}$ as calculated from the Thompson and Bell prediction model for three periods at various values of natural mortality. Mm = natural mortality for males and Mf = natural mortality for females.

		Fishing mortality		
M		**1980-1984**	**1985-1989**	**1990-1995**
	$F_{current}$	0.39	0.56	0.54
Mm = 0.05	$F_{0.1}$	0.25	0.28	0.25
Mf = 0.15	**MSY**	0.40	0.53	0.41
	$F_{current}$	0.32	0.49	0.49
Mm = 0.1	$F_{0.1}$	0.27	0.31	0.28
Mf = 0.2	**MSY**	0.46	0.59	0.44
	$F_{current}$	0.25	0.42	0.42
Mm = 0.15	$F_{0.1}$	0.28	0.34	0.30
Mf = 0.25	**MSY**	>0.5	0.72	0.51

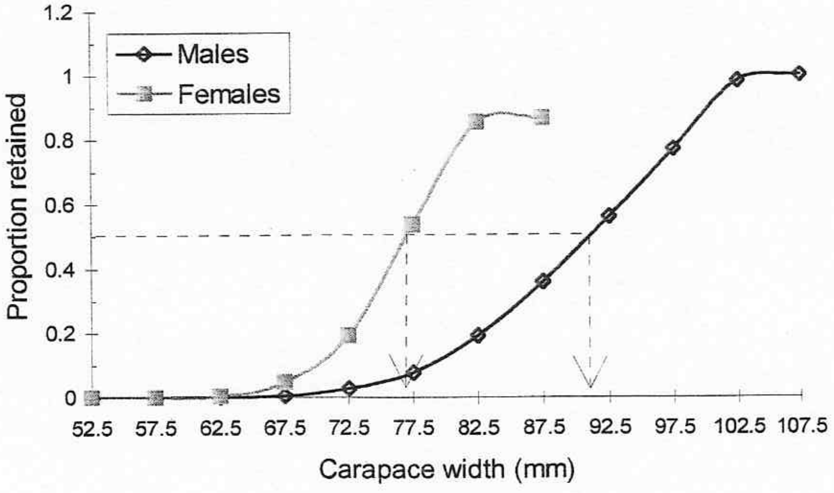


Figure 3.19: Selection/recruitment ogive as calculated from the F-array from cohort analysis for both male and female *C. maritae*.

New F-arrays were calculated for both males and females with the following parameters:

L50% (males):	100mm CW
L75% (males):	106mm CW
L50% (females):	85mm CW
L75% (females):	90mm CW

The resulting Thompson and Bell curve showed that by increasing the length at first capture for both males and females, Y/R can be increased by 13% to 35% (Fig. 3.20a). If L50% and L75% for females were increased and that of males kept at the present level, not much would be gained in Y/R (Fig. 3.20b).

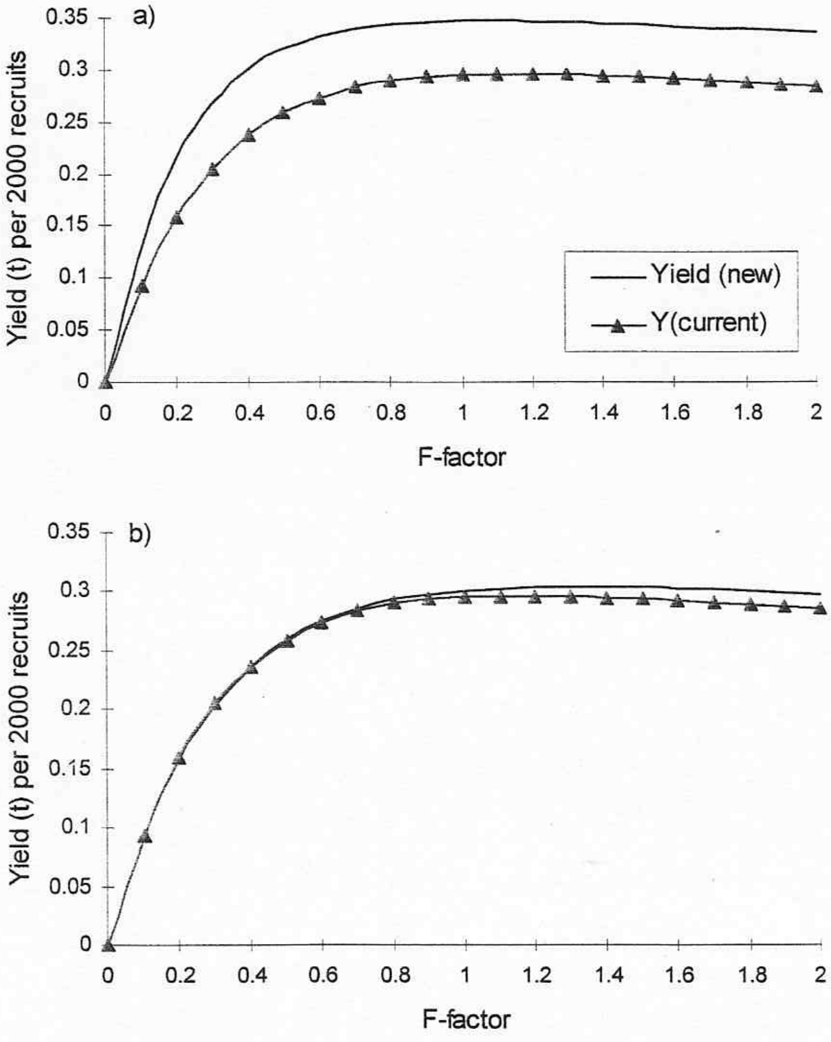


Figure 3.20: Yield per 2 000 recruits of *C. maritae* with new values of L50% and L75% for (a) both males and females, and (b) only for females. Yield curves were calculated with M = 0.1 for males and M = 0.2 for females.

3.8 **Discussion** *(Cohort analysis and prediction models)*

Analytical models such as cohort analysis offer an age-based approach to population dynamics and were originally developed for finfish assessment, where individual age can be determined. Since ageing in crustaceans is not directly possible, population size structure is often substituted for age structure (Cobb & Caddy 1989).

For stock assessment purposes such as length based cohort analysis, a model for mean length at age is needed and the Von Bertalanffy growth equation usually provides an adequate fit for the exploited part of the population. The Von Bertalanffy growth equation is usually estimated from modal progressional analysis or from growth increments using the Gulland and Holt plot where it is feasible to split length frequencies into components believed to represent age groups. However, for decapod crustaceans the Von Bertalanffy growth equation often does not describe growth adequately, due to the discontinuous nature of crustacean growth (Cobb & Caddy 1989).

Measuring growth by tag-recapture, which is often the only measure available for investigating growth in crustaceans, poses a problem. In tag-recapture experiments, individual growth rates are measured and the assumption that tags and the tagging process itself do not affect growth has to be made. Growth from tag-recapture data does not describe mean size at age and is rather a formulation of how an individual is growing. Thus, it has to be assumed that all individuals in the population grow according to the same Von Bertalanffy growth equation (also see Wang & Thomas 1995 & Wang *et al.* 1995). However, if the dataset of growth obtained from tag-recapture is sufficiently large, one would expect to arrive at a model of average growth of the population.

The growth model for male crabs (Fig. 3.4) seemed to represent a Von Bertalanffy type of growth. However, the range of crabs caught in the fishery included crabs in the range 60 to 150mm CW. For this size range of crabs, linear growth can probably be safely assumed for practical purposes. Using the average growth rate from a wide range of crabs and assuming a linear function for growth, thus avoided the assumption of the same Von Bertalanffy growth equation for all crabs in the population. Since the slopes of the Gulland and Holt plots (Fig. 3.11) were not significantly different from zero, it can be assumed that individual crabs have growth rates that vary randomly around a constant value (r). A linear growth function based on average moult increments was also proposed for *Paralithodes camtschaticus* (Zheng *et al.* 1995).

Crustaceans may remain at the same size for relatively long periods of time. Many models based on the population structure by size or moult group are beginning to be used for crustaceans. Many ecological processes in crustaceans are size rather than age dependent. Mortality due to predation and fishing is size selective, thus a size specific mortality function is important when considering effects of fishing or predation. Fecundity, growth, feeding behaviour, and habitat selection are also processes which are size dependent in crustaceans (Cobb & Caddy 1989).

If figures 3.13 and 3.14 are compared, it can be seen that for all periods of assessment, the sex ratio at the smallest length classes (52.5mm CW) deviated from a 1:1 ratio. This deviation from a 1:1 sex ratio was even more pronounced in the last period, 1990-1995. This indicated that females might have suffered from higher mortalities in the last period of assessment, which might be due to increased emigration of females to Angolan waters.

Analysis of sex ratio's by depth indicated that catches taken at depths shallower than 500m consisted of 50% or more females, and that sex ratios in deeper waters were biased towards males. The area where 50% or more females were caught (400-500m) is very small, compared to the area where the rest of the population occur and it is thus highly unlikely that 50% of the female population occur shallower than 500m. The 500m depth restriction would thus not be the most effective measure for protecting the female population. It was also possible to get a catch consisting of mostly females at a depth of around 700m (Figures 3.5 & 3.6).

It is difficult to distinguish between catchability and distribution as causes for observed sex ratio's from trap catches (Miller 1990). In decapod crustaceans males usually have a higher catchability than females, mainly due to a difference in food consumption. The observed difference in sex ratio's from *C. maritae* catches might be due to catchability differences between males and females. Observations from other decapod crustaceans caught in traps indicated that food consumption in females was less than in males and that ovigerous females fed less than females that were not ovigerous. Differences in sex ratio's in decapod crustaceans can also be caused by factors such as migration, moulting cycles, mating cycles, and distributional differences between the sexes (Miller 1990).

The moult cycle also influences catchability, with catchability being lowest directly before and after a moult (Miller 1990). In the growth studies presented here, it was clear that females moulted more often than males, which would thus contribute to a lower catchability for females and partly explain the observed sex ratio at the smallest length classes.

Females were also believed to have a higher natural mortality than males. If it is assumed that juvenile females also had a higher natural mortality than juvenile males, one would expect a discrepancy in sex ratio at the smallest length classes in the fishery.

In length based cohort analysis a constant parameter system is assumed. Length based cohort analysis is critically dependant on having a length frequency from a population at equilibrium or represents an average distribution over some period of time for which recruitment and exploitation rates have been stable on average, with no significant trends in either (Hilborn & Walters 1990).

If catch and CPUE (Figures 1.2 & 1.3) were considered together as an indication of the exploitation rate (i.e. CPUE is assumed to be a rough index of abundance), no significant trends in either were observed for the three periods defined for cohort analysis.

Recruitment is more difficult to determine for *C. maritae*. However, if length frequencies were considered (Appendix A, Figures A6 & A7) there did not seem to be any indication of variable year classes entering the fishery. It has to be kept in mind though, that for Geryonidae, it was hypothesised that good recruitment events were rare and that one good year class can sustain the population for years or even decades to come (Hines 1990 & Hastie 1995).

In the model presented here for *C. maritae*, it was assumed that natural mortality was equal for all length classes. This assumption is obviously unrealistic and poses a problem in generally used analytical models. It is generally believed that small animals would be exposed to a higher natural mortality due to predation (Sparre & Venema 1992), and in the case of crustaceans also due to a higher moulting frequency (Cobb & Caddy 1989). In the case of *C. maritae* the range of crabs caught by the commercial fishery did not include small crabs where natural mortality is expected to be high. Thus, it is acceptable to assume constant natural mortality for most of the length classes in the analysis.

In some cases a bowl shaped curve of natural mortality can be assumed, since older animals are also expected to have higher natural mortality due to senescence (e.g. Zheng *et.al* 1995). In this study, M in the largest length classes was assumed to be constant and equal to that of other length classes, due to a lack of any better estimate.

The growth factor introduced in cohort analysis, representing linear growth has one disadvantage. A model of linear growth implies that there is no measure which slows down growth in larger animals such as L_∞ in the Von Bertalanffy growth equation. This might be achieved by either introducing some kind of L_∞ or by increasing natural mortality in the largest length classes. This can also be achieved by weighting Δt_i by the intermoult period which increased with length for male *C. maritae* and would effectively slow down growth in larger animals. For females however some kind of L_∞ must be introduced, since moulting was believed to be annual and females showed some kind of terminal moult.

The shape of the F-arrays for males (Fig. 3.13) showed that fishing mortality on larger animals decreased from the first to the latter two periods. For 1980-1984 fishing mortality was more or less evenly distributed over length classes 87.5mm to 112.5mm CW, after which it gradually declined towards 152.5mm CW. For 1985-1989 fishing mortalities showed a dome shaped curve, with fishing mortalities for length classes larger than 117.5mm CW declining sharply to 152.5mm CW. In the last period of assessment, 1990-1995, the dome shaped curve of fishing mortality was even more pronounced and here fishing mortality started declining from 112.5mm CW.

The change in the shape of the F-array curves for the three periods is possibly due to a change in fishing effort in the area where the largest males occur. However, the largest animals have the highest value (pers. comm. K. Otani) and would thus be most desired by fisherman. Large males occur only in the southern part of the distribution and if the abundance of large males declined and catches became economically unviable, one would expect less fishing, and thus a lower fishing mortality in the area of their distribution. A decrease in the abundance of large animals in the population was already apparent at the end of the 1970s, when vessels that processed only large animals ceased operating due to uneconomic yields. The indication of a decrease in abundance of large males, however, was not reflected in the size distribution of males (Fig. 3.12), which indicated that males in the population were getting larger. This increase in size can be wrongly interpreted as an indication of a healthy population. The increase in size in males over the three periods can probably be ascribed to declining recruitment, resulting in the absence of small animals in the population. Length frequencies of females did not show an increase in size for the three periods. However, females do not grow as large as males and one would expect a similar size distribution if a terminal moult occurs.

The female *C. maritae* F-arrays did not vary very much and were dome shaped for all three periods (Fig. 3.14). The curve for the period 1985-1989 was slightly flatter than other periods and can be ascribed to more larger females being caught during that period. Fishing mortalities for large females generally started declining around the size at maturity. This decline is to be expected, since a higher incidence of ovigerous females would lead to a lower catchability of these length classes (also see Miller 1990). Thus, it is probably not economically viable to exploit large females due to low catchability.

From the first to the second period analysed average annual biomass declined faster than average annual population number. The faster decline of biomass indicated that there were still recruits coming into the fishery, but that the parent stock was declining, probably due to heavy exploitation. This is supported by the higher average fishing mortality for males from 1985-1989. Although fishing mortalities for females were lower during this period (1985-1989), they generally only made up around 30% of the catch, and thus the impact of fishing was expected to be mainly seen in the male population. For the last period analysed, population number and biomass declined at about the same rate, indicating a reduction in both recruitment and the parent stock.

During the last period of assessment several environmental factors, apart from fishing could have affected recruitment. The following major environmental events took place in the northern Benguela region off Namibia (O'Toole & Shannon 1997):

- 1991-1992: an eighteen month long cool period from mid 1991, with pronounced upwelling off Namibia and Angola.
- 1993-1994: Major poleward movement of oxygen poor water on the shelf at the occurrence of so-called black-tides.
- 1995: A *Benguela Niño* in the northern and central Benguela, characterised by poleward flow and widespread warming.

Other events occurring in the northern Benguela worth mentioning is temperature anomalies, with 1987 being a cool year and 1988, 1989, and 1990 being warm years. Another *Benguela Niño* occurred in 1984 (O'Toole & Shannon 1997). The main features of circulation in the northern Benguela system are as follows (Appendix B, Figure B11, O'Toole & Shannon 1997):

- Offshore flow in a north westerly direction.
- Cyclonic circulation around the Angola Dome and periodic intrusion of tropical water.
- Wind driven surface currents (mainly in a northerly direction) and a poleward undercurrent.
- Poleward flowing Angola Current in extreme north.

Melville-Smith (1990) hypothesised that female *C. maritae* migrate into central or northern Angolan waters before becoming ovigerous. Larvae would then migrate to the surface and be transported southward by the Angola Current to settle in highest densities between the seasonal boundaries of the Angola/Benguela front.

It is probable that spawning of *C. maritae* can take place in the southern part of their distribution and that larvae are transported northward by the Benguela current, since ovigerous females have been observed in the area 20°-21°S (unpublished data).

Melville-Smith & Bailey (1989) reported on environmental causes of the depth distribution of *C. maritae* and came to the following conclusions:

(i) Dissolved oxygen was considered unlikely to be a major factor in *C. maritae* distribution, since crabs were caught at depths where the dissolved oxygen level was as low as $0.45\ \mathrm{ml.l^{-1}}$. The shelf region around 18°S, where *C. maritae* is abundant, is characterised by a semi-permanent cell of oxygen deficient water and crabs therefore need to be resistant to these low oxygen levels. However, Beyers & Wilke (1980) did show a good positive correlation between dissolved oxygen and *C. maritae* catch.
(ii) Temperature was considered to be an important factor affecting the inshore limit of distribution of *C. maritae*. Temperatures recorded between 300 and 400m depth, declined sharply, and *C. maritae* is generally found in waters of less than 10°C off the Namibian coast.
(iii) The offshore distribution of *C. maritae* was considered to be limited by topographical features rather than hydrological features.

Major environmental events such as a *Benguela Niño* and temperature anomalies are probably the most likely ones to affect *C. maritae*. Temperature is also known to affect the catchability of decapod crustaceans, with increasing temperatures generally resulting in higher catch rates (Miller 1990). However, one would expect an increase in catchability due to higher temperatures only to be valid within the range of temperatures tolerable to the species in question.

If the aforementioned major environmental events are compared to catches and CPUE of *C. maritae* in Namibian waters, it seems that in years where *Benguela Niños* occurred, catches and CPUE were lower than the previous year (Figures 1.2 & 1.3), although one would expect CPUE to increase due to a higher catchability. However, the inshore distribution of *C. maritae* off the Namibian coast is considered to be limited by high temperatures, and thus major warming events may increase temperatures beyond the tolerable range for *C. maritae* and thus affect the population negatively. A declining trend in catches and CPUE (Figures 1.2 & 1.3) of *C. maritae* is also apparent during warmer years (1988-1990). The lowest catches and CPUE, however, were recorded during a major cooling event in the northern Benguela (1991 and 1992). A decline in catch and CPUE was also recorded in 1987, which was a cold year. This is to be expected if catchability of crabs decline at lower temperatures.

One would also expect major events such as *Benguela Niños* to affect recruitment of *C. maritae*, since larvae would be transported far beyond their expected area of settlement by the southward intrusion of warm, nutrient poor Angolan waters.

Dissolved oxygen did not seem to have negative effects on catch rates of *C. maritae*, since in the two years (1993 and 1994) where there was a major intrusion of oxygen poor waters into the northern Benguela, catches and CPUE increased (Figures 1.2 & 1.3).

It was assumed that *C. maritae* recruit into the fishery between six to eight years of age. Thus, if the 1984 *Benguela Niño* affected larvae, one would expect to see the influence on the fishery after a period of six to eight years, *i.e.* in 1989 to 1990. From Figures 1.2 and 1.3 a major decline in catches and CPUE is apparent during these years.

Recruitment into the fishery may also be dependent on the spawning stock biomass and not only on environmental factors, although variation in recruitment from a given stock size can be large (King 1995). The spawning stock biomass already started to decline after 1982, and by 1984 the spawning stock biomass was already substantially reduced (Fig. 3.17). This pattern was obviously not reflected in the catches and CPUE (Figures 1.2 & 1.3) of the *C. maritae* fishery off Namibia. It is possible that the peak in population number observed in 1989 (Fig. 3.15) resulted from recruits from spawning in 1982 or 1983, when the spawning stock was still fairly large. After 1989, however, there is a clear declining trend in population number which could be related to the decline in spawning stock biomass from 1983 onwards.

Apart from environmental factors, heavy fishing on the *C. maritae* stock probably also contributed to the decline in stock size in Namibian waters. Average fishing mortalities for male *C. maritae* calculated for the three periods assessed, ranged from 0.24 to 0.56, with most fishing mortalities being higher than 0.3. This level of exploitation was much too high to sustain a stock consisting of such slow growing, long-lived individuals. Thompson and Bell prediction models showed that fishing mortality was above the optimum level of exploitation ($F_{0.1}$) for all three periods, except for 1980-1984 where the highest level of M was used in calculations. Thus, natural mortality estimates of 0.15 for males and 0.25 for females was probably too high, since it indicated that the stock was exploited below optimum levels.

From 1981 to 1983 population number of the *C. maritae* stock was relatively high (Fig. 3.15). However, spawning stock biomass already started to decline in 1983 (Fig. 3.17). Thus, in 1983 most of the stock consisted of recruits entering the fishery. The heavy fishing in 1983 (whole mass catch = 10 000 tonnes) on a stock consisting mostly of recruits probably contributed to the decline of the stock in later years. If it is assumed that recruits entering the fishery spawn one to two years later, one would expect to see offspring from the 1983 recruits six to eight years later, i.e. 1990 to 1993, where population number was at it's lowest level (Fig 3.15). High catches in the early 1980s probably also contributed to the decline in spawning stock biomass, which became apparent in 1983. Thus, both growth- and recruitment overfishing in the early years of the fishery contributed to the heavy decline in the *C. maritae* stock off Namibia.

Although catches in the 1990s were fairly low, Thompson and Bell prediction models (Table 3.10) showed that the fishing pressure was still too high, and only resulted in the spawning stock biomass being stable from 1992 to 1995 (Fig. 3.17). From selection ogives calculated for the 1990s (Fig. 3.18) the L50% for female *C. maritae* was below the size at sexual maturity, 84mm CW or 96mm CW (Melville-Smith 1987b), thus many females are being caught before being able to spawn. Increasing size at first capture in the fishery would not only increase yield per recruit, but would also be essential for preserving the breeding stock of the population.

4 CONCLUSION

Growth models of *C. maritae* described here were consistent with general patterns of growth for long-lived decapods. The long intermoult periods of large crabs and the higher moulting frequency of small and female crabs were also consistent with growth of other geryonid crabs.

In theory, there are two possible strategies of growth in crustaceans. Ecdysis can occur at regular time intervals and the percentage growth increment decreases with each successive moult. On the other hand, growth increments at each successive moult can be the same, but the intermoult period increases with age. In most crustaceans, growth strategy is a combination of both (King 1995).

Yield per Recruit models indicated that growth in *C. maritae* was faster in the 1990s and one would expect this to be reflected in individual growth. From the growth data presented here, percentage growth increments in the 1990s for both male and female *C. maritae* were smaller than in the 1980s (Melville-Smith 1989a), although the difference was not significant for male crabs. However, data on intermoult period in the 1990s showed that the timing between moults for male crabs was shorter than in the 1980s. A completely different relationship between premoult carapace width and intermoult period was found here than in the 1980s, and there is nothing in the data that suggested that this relationship was the same. Thus, faster growth in the 1990s was achieved by a decrease in intermoult period. It is also expected to have smaller growth increments if there was a decrease in intermoult period.

Analysis of CPUE data did not show any seasonality in catches of *C. maritae*, which is consistent with results from other researchers such as Melville-Smith (1988a). Melville-Smith (1987b) did not find any seasonal pattern in reproductive cycles of female *C. maritae*, and suggested that this was due to the absence of changes in daylength and temperature. However, in some areas annual fluctuations of deep-sea physical/chemical processes do occur and seasonal growth and reproductive patterns have been demonstrated in a variety of benthic invertebrates (Hastie 1995). One would also expect some kind of seasonality if there is an annual moulting cycle in females, as is suggested by the data. Average CPUE data per month did suggest two peaks in CPUE, one in winter (May/June) and a smaller peak in spring (October), although the difference was not significant. Catches, however, consist mainly of males and CPUE data would thus be representative of males rather than females. If seasonality is to be further examined, one should use data on female moulting stages rather than catch data to investigate seasonality.

Females that emigrated to Angola, were not caught on their migration route, indicating that they did not feed while migrating. This indicated that female migration to Angola might be a spawning migration, since ovigerous female decapods are expected to have a low catchability due to a low food consumption (Miller 1990). If there are any seasonal processes in the *C. maritae* population off Namibia, as was suggested by female intermoult periods, one would expect this to be seen in spawning migrations of females. However, data on tag-recaptures from Angola were not enough to grant this kind of analysis. For future investigations of seasonality, sex ratio data should also be examined, since one would expect the migration of females to have an influence on sex ratio.

The population estimate of 72 million found by Beyers (1994) was close to the population estimate found by cohort analysis for 1990-1995 at the highest level of M (Table 3.9). However, this level of M was thought to be too high for *C. maritae*. If estimates of emigration were available, population estimates from tag-recapture in 91/92 (Beyers 1994) would probably be closer to estimates from cohort analysis at lower levels of M.

When comparing population number found by tag-recapture and that found by cohort analysis, tag-recapture methods overestimate the population, even when only males were assessed (Tables 3.6, 3.8 & 3.9). Densities of over 1 000 crabs.ha^{-1} (equivalent to >1 crab.m^{-2}), found in the region 18°-19°S (Table 3.6) was obviously not realistic and much higher catch rates were to be expected if densities were this high. When emigration of animals out of Namibian waters was taken into account, the population estimate from tag-recapture was still higher than the estimate from cohort analysis (Tables 3.7 & 3.9). However, population estimates in Table 3.7 only accounted for recaptures made during one fishing trip in Angola and was still an overestimate. It is not surprising that tag-recapture overestimates the population, since up to 40% of females and 6% of males can potentially emigrate out of the region where they were tagged. Thus, most bias in tag-recapture population estimates would result from females emigrating out of the region where they were tagged and potentially out of Namibian waters. Other factors which might have biased results of tag-recapture, apart from emigration, were the small number of females caught in the area of assessment, a higher moulting frequency in females which could have contributed to tag-loss, and differences in catchability between males and females.

In general all tag-recapture results indicated a higher population number of *C. maritae* off Namibia than in 1991, which was consistent with results from cohort analysis (Fig. 3.15). However, the assumptions of the Petersen method which were violated all contributed to a lower R/C ratio, which might have increased the error of population estimates substantially. Thus, the increase in the population after 1991 from tag-recapture was probably magnified due to errors caused by a low R/C ratio.

The dynamics of *C. maritae* migration should be taken into account when conducting future tag-recapture experiments. Most crabs tended to stay within five nautical miles of their tagging location. When conducting future tagging experiments, the tagging locations should be targeted for subsequent sampling, rather than relying entirely on the commercial fishery for recaptures. Subsequent sampling for recaptures should also be conducted within a shorter period than a year to minimise the possibility of emigration out of Namibian waters. Target fishing on the tagging locations would also minimise the possibility of unreported recaptures. Tag-recapture methods taking emigration into account can potentially provide good estimates of the population under the condition that all recaptures from Angola are reported.

Cohort analysis and prediction models showed that the population had been reduced substantially since 1980, and that fishing mortality was too high in most scenarios of natural mortality. The highest levels of M used in the analysis were probably too high, since it gave the impression that the stock was exploited below MSY levels or even below $F_{0.1}$. If the stock was underexploited in the early 1980s, one would have expected to see either an increased or stable stock in later years.

Preliminary annual cohort analysis showed that a decline in spawning stock biomass already occurred in 1983. This was obviously not reflected in catches and CPUE, and catch rates until 1989 were probably kept up by recruits from years prior to 1983. Although population number had already declined in 1984, CPUE did not show any trend from 1980 to 1989. Population number from 1984 to 1989 could thus have been sufficiently large to saturate traps.

Both recruitment and growth overfishing contributed to the decline in the *C. maritae* stock off Namibia, and major environmental events such as *Benguela Niños* might have affected recruitment.

It is clear that TAC regulations were not effective in managing the stock, since catches were generally below the TAC, except for 1989 and 1995. The generally low catches in the 1990s did, however, seem to keep spawning stock biomass stable since 1992. From the results of sexual segregation it was concluded that a depth restriction of 500m would not be the most effective way of protecting female crabs. Prediction models also showed that both male and female size at first capture need to be increased to increase yield per recruit.

A more effective way to protect females and increase size at first capture for males at the same time, would be to introduce escapement rings in traps. Introducing escapement rings into traps would allow escape of small animals at depth and would overcome practical difficulties of implementing the existing legal size limit.

Length based cohort analysis can potentially provide good indicators of population and biomass trends of *C. maritae*. Compared to tag-recapture, cohort analysis provided more realistic estimates of the population and were more consistent with trends in catches and CPUE. Cohort analysis and prediction model results can probably be improved if an independent estimate for recruitment can be obtained. However, estimating recruitment in geryonids proved difficult (Hastie 1995).

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6 REFERENCES

ANON. 1993. Sea Fisheries Regulation Act of 1993. *Government Gazette, Namibia.*

ANON. 1996. *Arc View GIS: The geographic information system for everyone.* Environmental Systems Research Institute, USA. 350pp.

BAILEY, R. J. F. & R. W. ELNER. 1989. Northwest Atlantic snow crab fisheries: Lessons in research and management. In: Caddy, J. F. (Ed.). *Marine Invertebrate Fisheries: Their assessment and management.* John Wiley & Sons. 752pp.

BEYERS, C. J. DE B. 1994. Population estimates and density of the deep-sea red crab *Chaceon maritae* (Manning and Holthuis) off Namibia determined from tag-recapture. *S. Afr. J. mar. Sci.* **14**: 1-9.

BEYERS, C. J. DE B. & C. G. WILKE. 1980. Quantitative stock survey and some biological and morphometric characteristics of the deep-sea red crab *Geryon quinquedens* off South West Africa. *Fish. Bull. S. Afr.* **13**: 9-19.

BLISS, D. E. 1990. *Shrimps, crabs and lobsters: Their fascinating life history.* Columbia University Press, Morning Side Edition. 242pp.

BRANDER, K. M. & D. B. BENNETT. 1989. Norway lobsters in the Irish Sea: Modeling one component of a multispecies resource. In: Caddy, J. F. (Ed.). *Marine Invertebrate Fisheries: Their assessment and management.* John Wiley & Sons. 752pp.

BOTSFORD, L. W. 1985. Models of growth. In: Wenner, A. M. (Ed). *Crustacean issues 3: Factors in adult growth.* A. A. Balkeema Publishers, Rotterdam, Netherlands. 362pp.

CAMPBELL, A. 1989. The lobster fishery of Southwestern Nova Scotia and the Bay of Fundy. In: Caddy, J. F. (Ed.). *Marine Invertebrate Fisheries: Their assessment and management.* John Wiley & Sons. 752pp.

COBB, J. S. & J. F. CADDY. 1989. The population biology of Decapods. In: Caddy, J. F. (Ed.). *Marine Invertebrate Fisheries: Their assessment and management.* John Wiley & Sons. 752pp.

DIAS, C. A. & J. F. SEITA MACHADO. 1973. Preliminary report on the distribution and relative abundance of deep-sea red crab (*Geryon* sp.) off Angola. *ICSEAF. Colln scient. Pap. int. Commn. SE. Atl. Fish.* **1**: 258-270.

EDWARDS, E. 1989. Crab fisheries and their management in the British Isles. In: Caddy, J. F. (Ed.). *Marine Invertebrate Fisheries: Their assessment and management.* John Wiley & Sons. 752pp.

EHRHARDT, N. M. & V. R. RESTREPO. 1989. The Florida stone crab fishery: A reusable resource? In: Caddy, J. F. (Ed.). *Marine Invertebrate Fisheries: Their assessment and management.* John Wiley & Sons. 752pp.

ERDMAN, R. B., BLAKE, N. J., PERRY, H. M., WALLER, R. S., LINDBERG, W. J., & F. D. LOCKHART. 1990. Annual reproduction in deep-sea brachyuran crabs (*Chaceon* spp.) from the Southeastern United States. In: Lindberg, W. J. & E. L. Wenner (Eds). *Geryonid crabs and associated continental slope fauna: A research workshop report. Florida Sea Grant College Tech. Pap.* **58**: 61pp.

GATZ, J. A. & J. M. LOAR. 1988. Petersen and removal population size estimates: combining methods to adjust and interpret results when assumptions are violated. *Env. Biol. Fish.* **21**(4): 293-307.

GREENBERG, J. A., MATULICH, S. C., & R. C. MITTELHAMMER. 1991. A system-of-equations approach to modeling age-structured fish populations: The case of Alaskan red king crab, *Paralithodes camtschaticus*. *Can. J. Fish. Aquat. Sci.* **48**: 1613-1622.

HARTNOLL, R. G. 1982. Growth. In: Abele, L. G. (Ed.) *The Biology of Crustacea Vol.2: Embryology, Morphology, and Genetics.* Academic Press. London. 440pp.

HASTIE, L. C. 1995. Deep-water geryonid crabs: a continental slope resource. In: Ansell, A. D., Gibson, R. N., & Barnes, M. (Eds). *Oceanography and Marine Biology: an Annual Review.* **33**: 561-584.

HILBORN, R. & C. J. WALTERS. 1992. *Quantitative fisheries stock assessment: Choice, dynamics and uncertainty*. Chapman and Hall, New York. 570pp.

HINES, A. H. 1990. Rapporteur's comments: Commentary on life history and ecology of deep-sea crabs of the family Geryonidae. In: Lindberg, W. J. & E. L. Wenner (Eds). *Geryonid crabs and associated continental slope fauna: A research workshop report. Florida Sea Grant College Tech. Pap.* **58**: 61pp.

KING, M. 1995. *Fisheries biology, assessment and management.* Fishing News Books. Blackwell Science. 341pp.

LE ROUX, L. 1993. Stock assessment of the deep-sea red crab *Chaceon maritae* from tag-recapture data and Surplus Production models. *Internal Report. NATMIRC. Ministry of Fisheries and Marine Resources, Namibia.*

LINDBERG, W. J. & E. L. WENNER (Eds). 1990. Geryonid crabs and associated continental slope fauna: A research workshop report. *Florida Sea Grant College Tech. Pap.* **58**: 61pp.

LUX, F. E., GANZ, A. R., & W. F. RATHJEN. 1982. Marking studies on the red crab *Geryon quinquedens* Smith off southern New England. *J. Shellf. Res.* **2**(1): 71-80.

MANNING, R. B. 1990. Studies on systematics of geryonid crabs. In: Lindberg, W. J. & E. L. Wenner (Eds). *Geryonid crabs and associated continental slope fauna: A research workshop report. Florida Sea Grant College Tech. Pap.* **58**: 61pp.

MAUCHLINE, J. 1976. The Hiatt growth diagram for Crustacea. *Mar. Biol.* **35**: 79-84.

MAUCHLINE, J. 1977. Growth of crabs, shrimps and lobsters - an assessment. *J. Cons. int. Explor. Mer.* **37**(2): 162-169.

MELVILLE-SMITH, R. 1983. Abundance of deep-sea red crab *Geryon maritae* in South West African waters from photography. *S. Afr. J. mar. Sci.* **1**: 123-131.

MELVILLE-SMITH, R. 1986. Red crab (*Geryon maritae*) density in 1985 by the technique of effective area fished per trap on the northern fishing grounds off South West Africa. *S. Afr. J. mar. Sci.* **4**: 257-263.

MELVILLE-SMITH, R. 1987a. Movements of deep-sea red crab (*Geryon maritae*) off South West Africa/Namibia. *S. Afr. J. Zool.* **22**: 143-152.

MELVILLE-SMITH, R. 1987b. The reproductive biology of *Geryon maritae* (Decapoda, Brachyura) off South West Africa/Namibia. *Crustaceana.* **53**(3): 259-275.

MELVILLE-SMITH, R. 1988a. The commercial fishery for and population dynamics of red crab *Geryon maritae* off South West Africa, 1976-1986. *S. Afr. J. mar. Sci.* **6**: 79-95

MELVILLE-SMITH, R. 1988b. Comparative population size estimates for a portion of the red crab *Geryon maritae* stock off the South West African coast. *S. Afr. J. mar. Sci.* **6**: 23-31.

MELVILLE-SMITH, R. 1988c. Product-whole mass conversion factors in the Namibian red crab fishery. *ICSEAF. Colln scient. Pap. int. Commn. SE. Atl. Fish.* **15**(2): 81-86.

MELVILLE-SMITH, R. 1989a. A growth model for the deep-sea red crab (*Geryon maritae*) off South West Africa/Namibia (Decapoda, Brachyura). *Crustaceana.* **56**(3): 279-292.

MELVILLE-SMITH, R. 1989b. Recent trends in the Namibian red crab (*Chaceon maritae*) fishery. *Internal Report, SFRI, Cape Town, South Africa.*

MELVILLE-SMITH, R. 1990. *Chaceon maritae* studies off South West Africa. In: Lindberg, W. J. & E. L. Wenner (Eds). *Geryonid crabs and associated continental slope fauna: A research workshop report. Florida Sea Grant College Tech. Pap.* **58**: 61pp.

MELVILLE-SMITH, R. & G. W. BAILEY. 1989. A preliminary investigation into the possible causes of depth zonation by red crab (*Geryon maritae*), off Namibia. *Sel. Pap. ICSEAF int. Commn SE. Atl. Fish.* **1**: 1-12.

METHOT, R. D. 1989. Management of a cyclic resource: The dungeness crab fisheries of the Pacific coast of North America. In: Caddy, J. F. (Ed.), *Marine Invertebrate Fisheries: Their assessment and management*, John Wiley & Sons. 752pp.

MILLER, R. J. 1990. Effectiveness of crab and lobster traps. *Can. J. Fish. Aquat. Sci.* **47**: 1228-1251.

O'TOOLE, M. J. & L.V. SHANNON. 1997. The changing state of the Benguela Current Ecosystem. *In press*. American Association for the Advancement of Science Meeting, Seattle, USA, 13-18 February 1997.

PHILLIPS, B. F. & R. S. BROWN. 1989. The West Australian rock lobster fishery: Research for management. In: Caddy, J. F. (Ed.), *Marine Invertebrate Fisheries: Their assessment and management*, John Wiley & Sons. 752pp.

RICKER, W. E. 1975. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Bd. Can.* **191**: 382pp.

SOMMERTON, D. 1980. Fitting straight lines to Hiatt growth diagrams: a re-evaluation. *Journ. Cons. Int. Explor. Mer.* **39**: 15-19.

SPARRE, P. & S. C. VENEMA. 1992. Introduction to tropical fish stock assessment. *FAO. Fish. Tech. Pap.* **306**(1): 376pp.

STEFÁNSSON, G. 1994. *Notes on the dynamics of exploited fish populations.* Marine Research Institute, Reykjavík, Iceland. 63pp.

STEFÁNSSON, U. 1991. *Haffræði I.* Prentsmiðjan Gutenberg, Reykjavík. 413pp.

VAN HEUKELEM, W., CHRISTMAN, M. C., EPIFANIO, C. E., & S. D. SULKIN. 1983. Growth of *Geryon quinquedens* (Brachyura: Geryonidae) juveniles in the laboratory. *Fishery Bull., U.S.* **81**(4): 903-905.

WANG, Y. & M. T. THOMAS. 1995. Accounting for individual variability in the Von Bertalanffy growth model. *Can. J. Fish. Aquat. Sci.* **52:** 1368-1375.

WANG. Y., THOMAS, M. R., & I. F. SOMERS. 1995. A maximum likelihood approach for estimating growth from tag-recapture data. *Can. J. Fish. Aquat. Sci.* **52:** 252-259.

ZAR, J. H. 1996. *Biostatistical Analysis*. 3d Edition. Prentice Hall, New Jersey. 662pp.

ZHENG, J., MURPHY, M. C., & G. H. KRUSE. 1995. A length-based population model and stock-recruitment relationships for red king crab, *Paralithodes camtchaticus*, in Bristol Bay, Alaska. *Can. J. Fish. Aquat. Sci.* **52:** 1229-1246.

Appendix A

Growth increment of all tagged crabs returned:

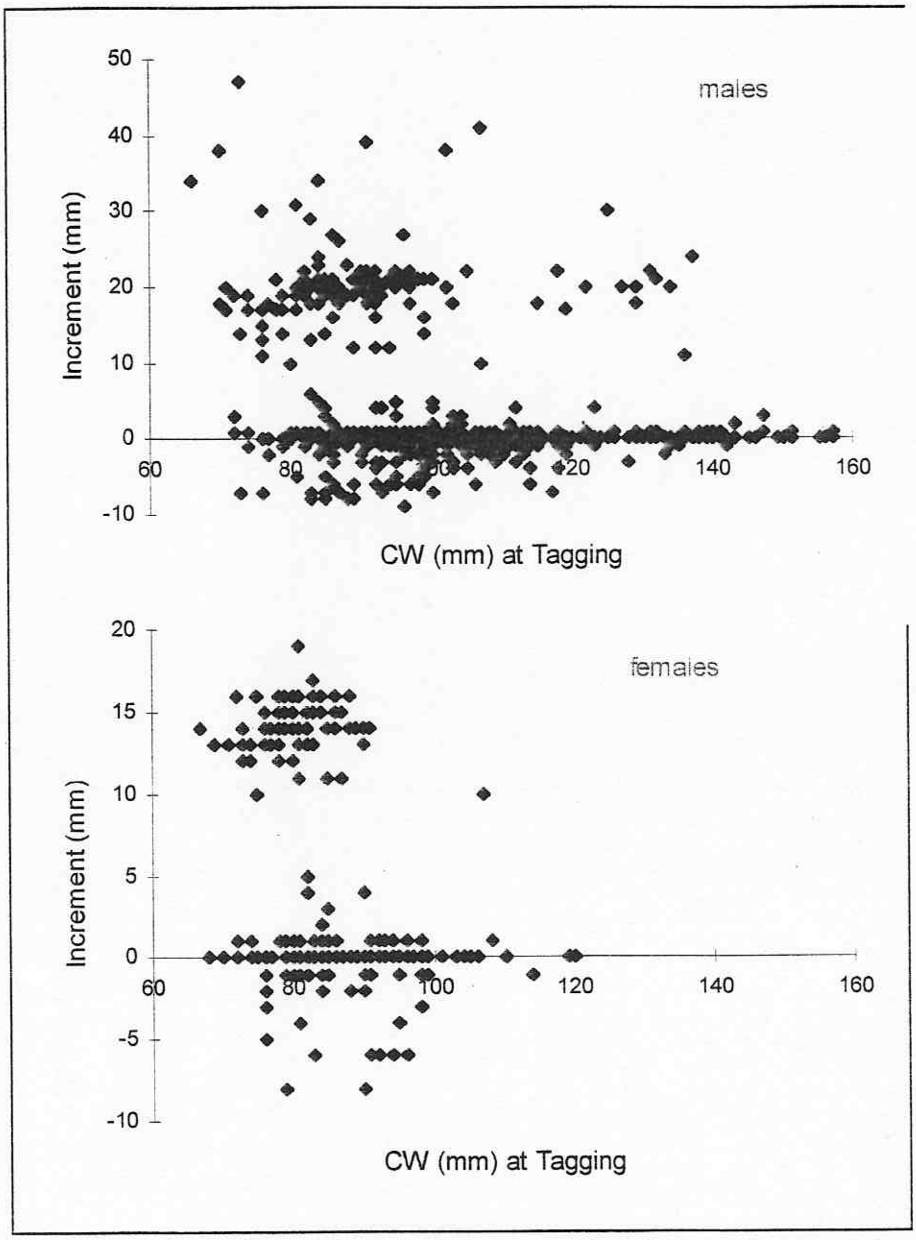


Figure A1: Plots of growth increment of male and female *C. maritae* as calculated from tag return data.

Appendix A

Table A1: Statistics of various growth regressions.

Regression	r^2	n	P
%growth factor (males)	0.281	114	1.26E-09
%growth factor (females)	0.231	77	9.8E-06
ln(%growth factor) (males)	0.311	114	1.18E-10
ln(%growth factor) (females)	0.270	77	1.26E-06
Hiatt growth diagram (males ≤ 88mm CW)	0.600	59	6.13E-13
Hiatt growth diagram (males > 88mm CW)	0.918	55	1.26E-30
Hiatt growth diagram (all males)	0.931	114	6.84E-67
Hiatt growth diagram (females)	0.917	77	2.67E-42
Intermoult period (males)	0.388	42	1.06E-05
ln(Intermoult period) (males)	0.313	42	1.16E-04
Intermoult period (females)	0.071	19	0.270

Appendix A

Residual plots of various growth functions:

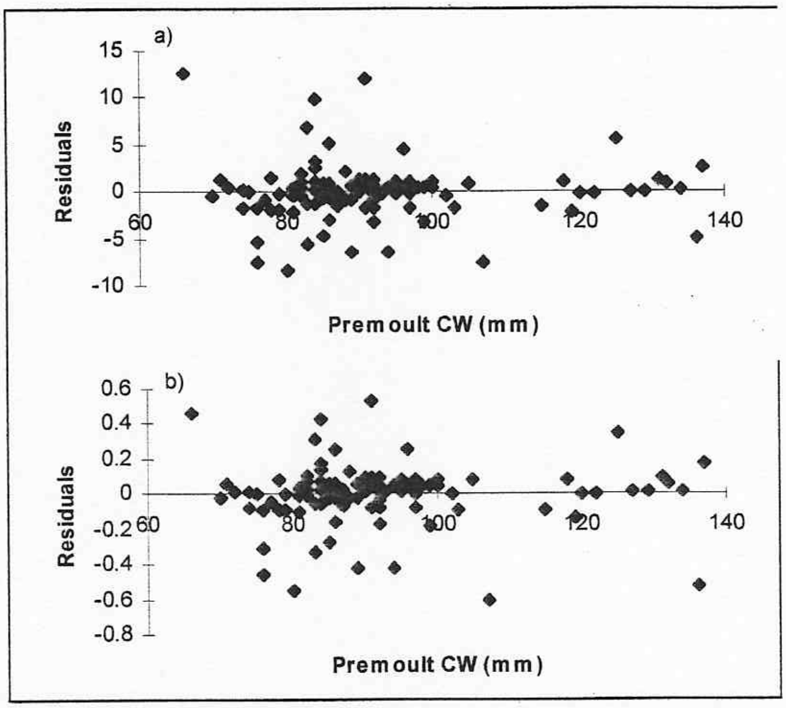


Figure A2: Residual plots for the regressions of %growth factor and ln(%growth factor) against premoult CW for male *C. maritae*. (a) linear regression, (b) log/linear regression.

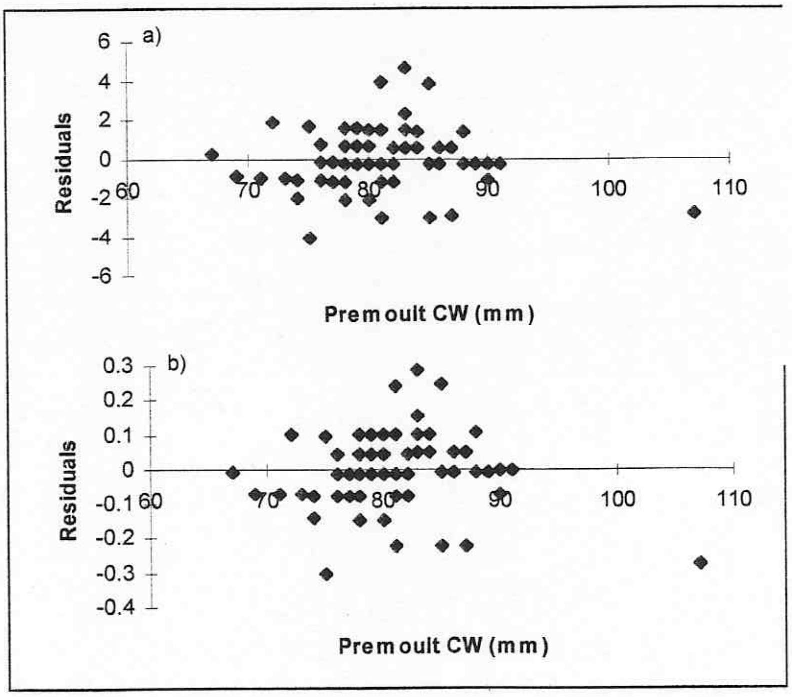


Figure A3: Residual plots for the regressions of %growth factor and ln(%growth factor) against premoult CW for female *C. maritae*. (a) linear regression, (b) log/linear regression.

Appendix A

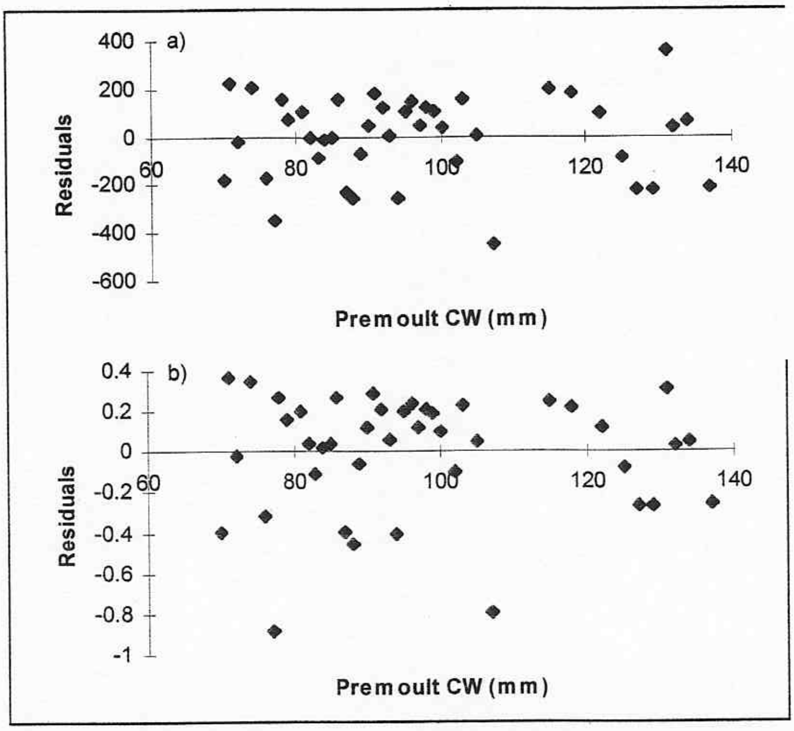


Figure A4: Residual plots of the regressions for intermoult period and ln(intermoult period) against premoult CW for male *C. maritae*. (a) linear regression, (b) log/linear regression

Appendix A

Table A2: Statistics related to t-tests.

Values for the slopes and intercepts found by Melville-Smith (1989b) are denoted by β_0 and α_0, respectively. Values for the slopes and intercepts found in this study are denoted by b and a respectively. For the comparison of Hiatt growth diagrams in this study, b_1 denotes the slope of the regression for males $\leq L^*$, and b_2 denotes that of males $> L^*$.

Regression **Melville-Smith (1989b):**	β_0	**b**	**df**	**t**	**P**	α_0	**a**	**df**	**t**	**P**
%growth factor (males)	-0.117	-0.126	112	0.507	0.613	31.75	29.59	112	1.215	0.227
%growth factor (females)	-0.202	-0.142	75	2.016	0.047	32.99	26.47	75	2.701	0.0085
Hiatt growth diagram (males $\leq L^*$)	1.164	1.044	57	1.063	0.292	4.793	15.96	57	1.213	0.230
Hiatt growth diagram (males $> L^*$)	1.014	1.013	53	0.049	0.961	----	----	----	----	----
Hiatt growth diagram (females)	1.025	1.002	75	0.661	0.511	11.44	14.11	75	0.949	0.346
This study:	b_1	b_2	**df**	**t**	**P**					
Hiatt growth diagrams (males) as found by Sommerton's method	1.044	1.013	110	0.461	0.646					

Appendix A

Residuals plots from the analysis of sexual segregation:

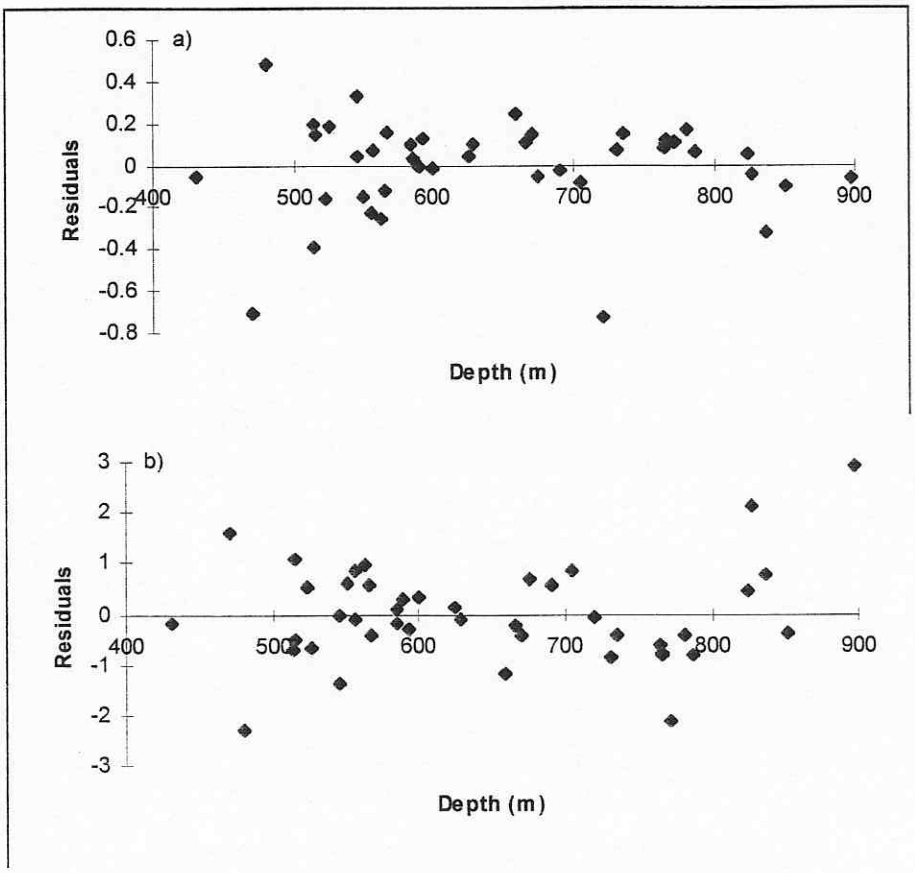


Figure A5: Residuals of two curves fitted to sex ratio data of *C. maritae* from 1994 to 1996. (a) arcsine transformed data, (b) logistic curve.

Appendix A

Length frequencies from 1980 to 1995 (males):

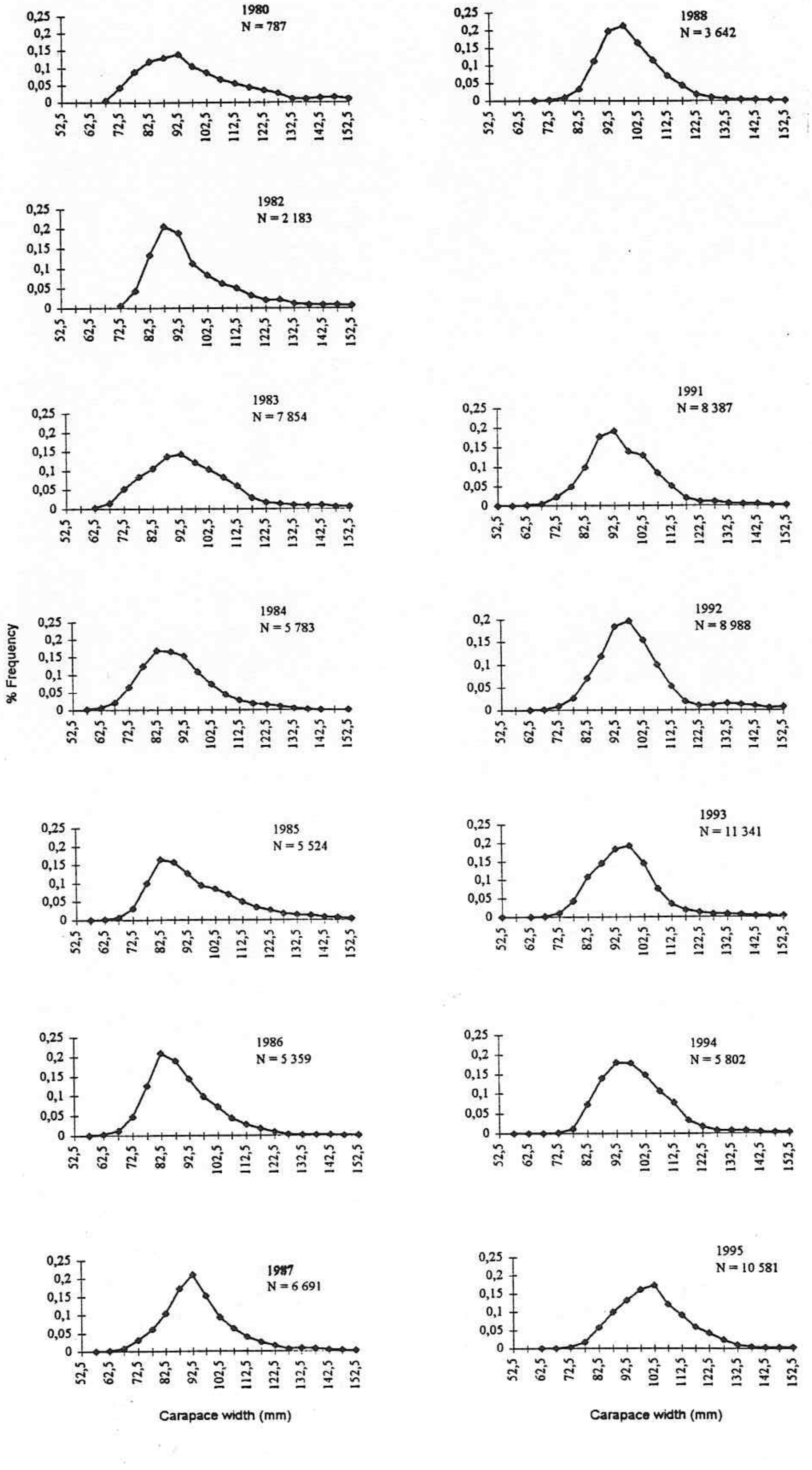


Figure A6: Length frequencies of male *C. maritae* as from samples of the commercial catch.

Appendix A

Length frequencies from 1980 to 1995 (females):

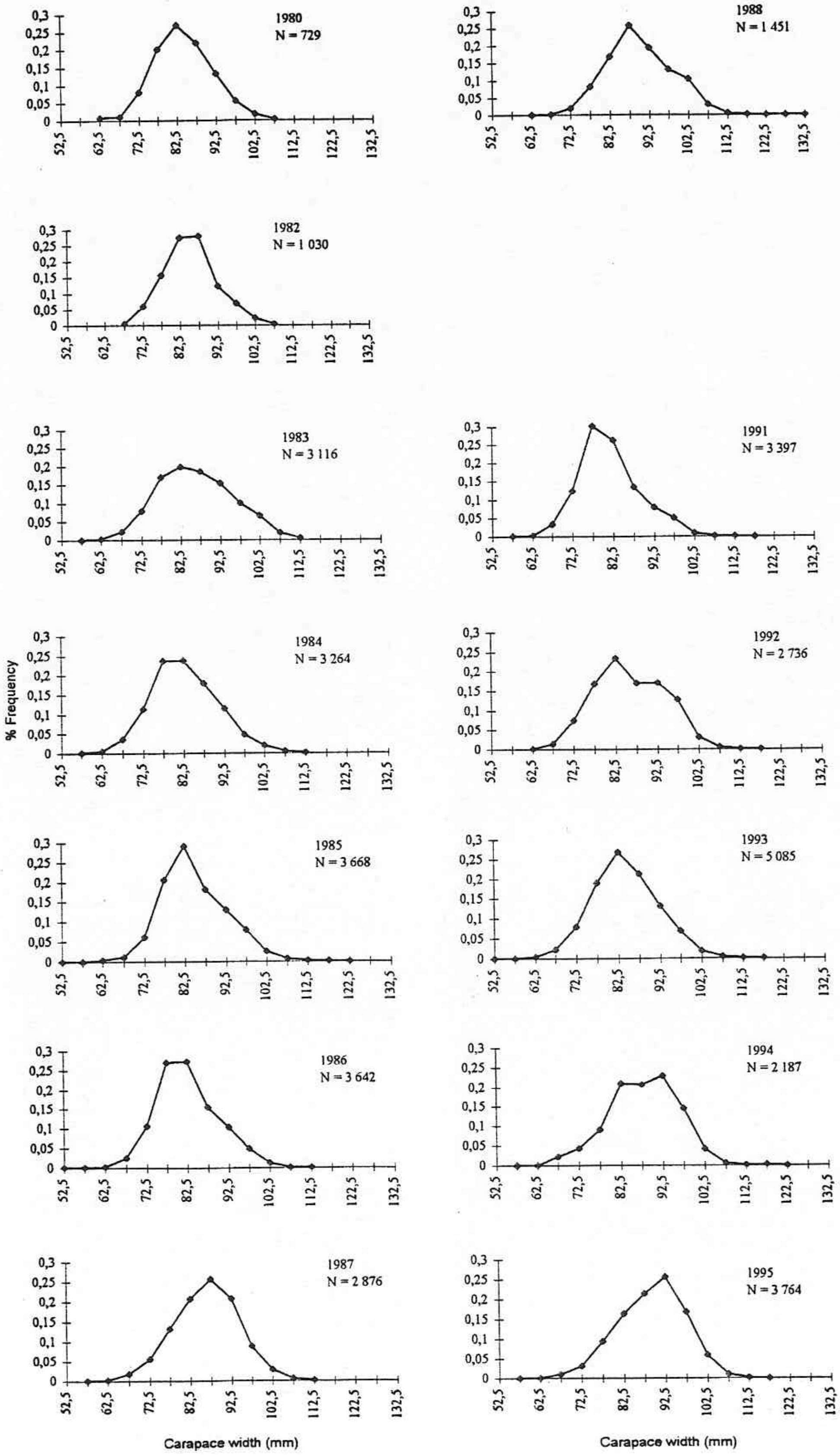


Figure A7: Length frequencies of female *C. maritae* from samples of the commercial catch.

Appendix A

Plots of Ft against mean N from cohort analysis:

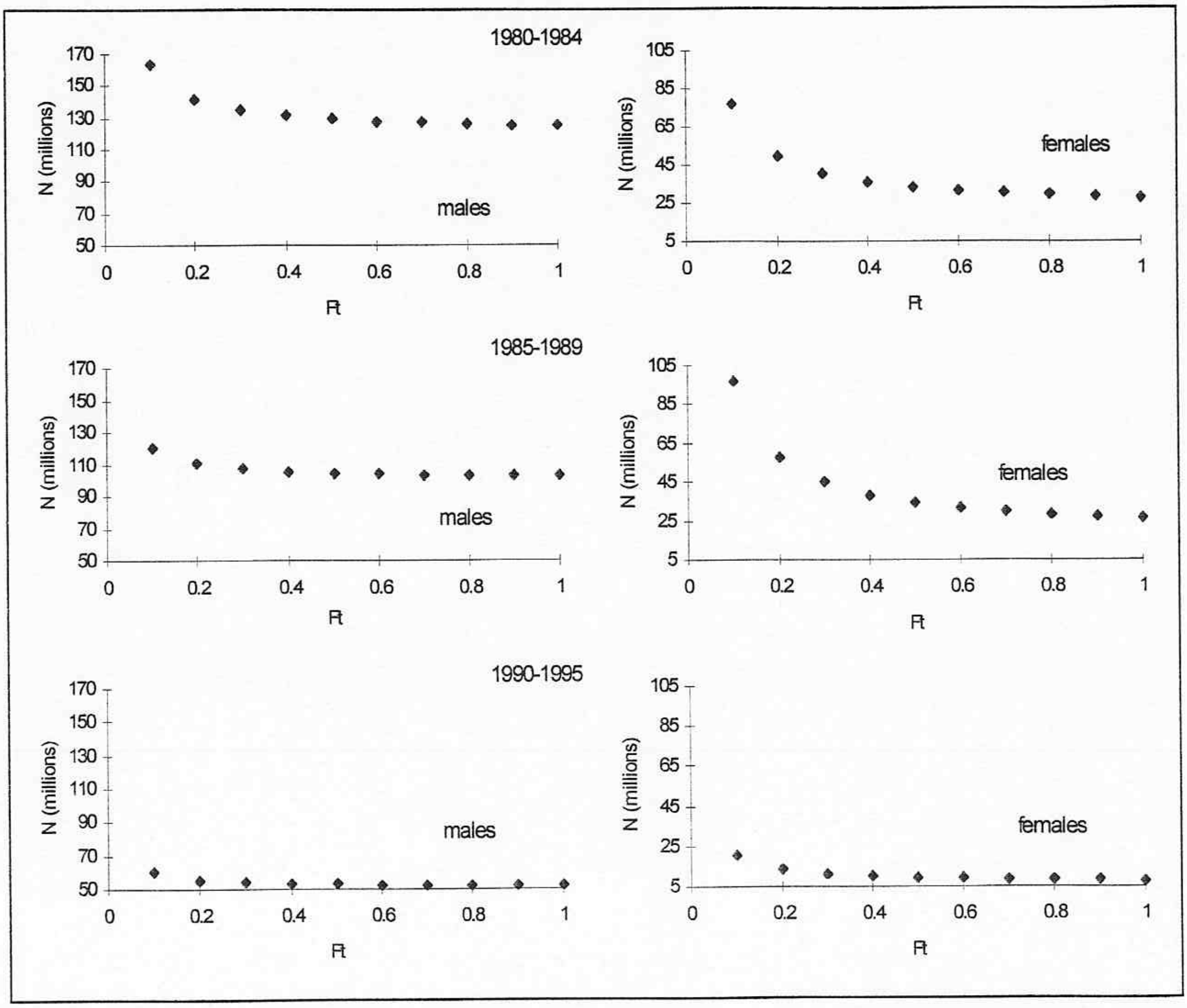


Figure A8: Plots of mean population number (N) against a range of F_t values in length based cohort analysis of male and female *C. maritae* for three periods.

Appendix B

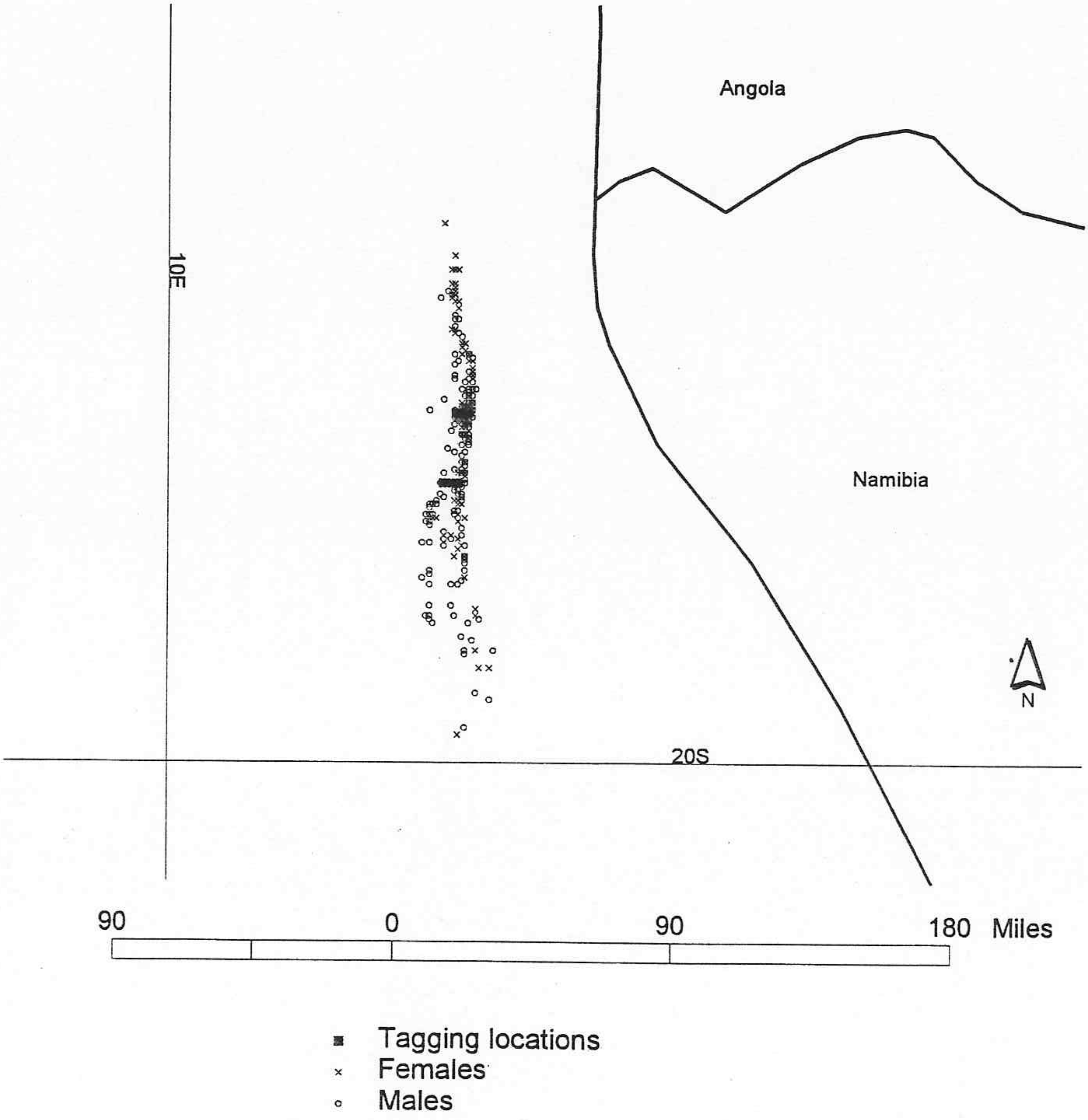


Figure B1: Movements of male and female *C. maritae* tagged in the area 18º-19ºS in 1991 within one year of tagging.

Appendix B

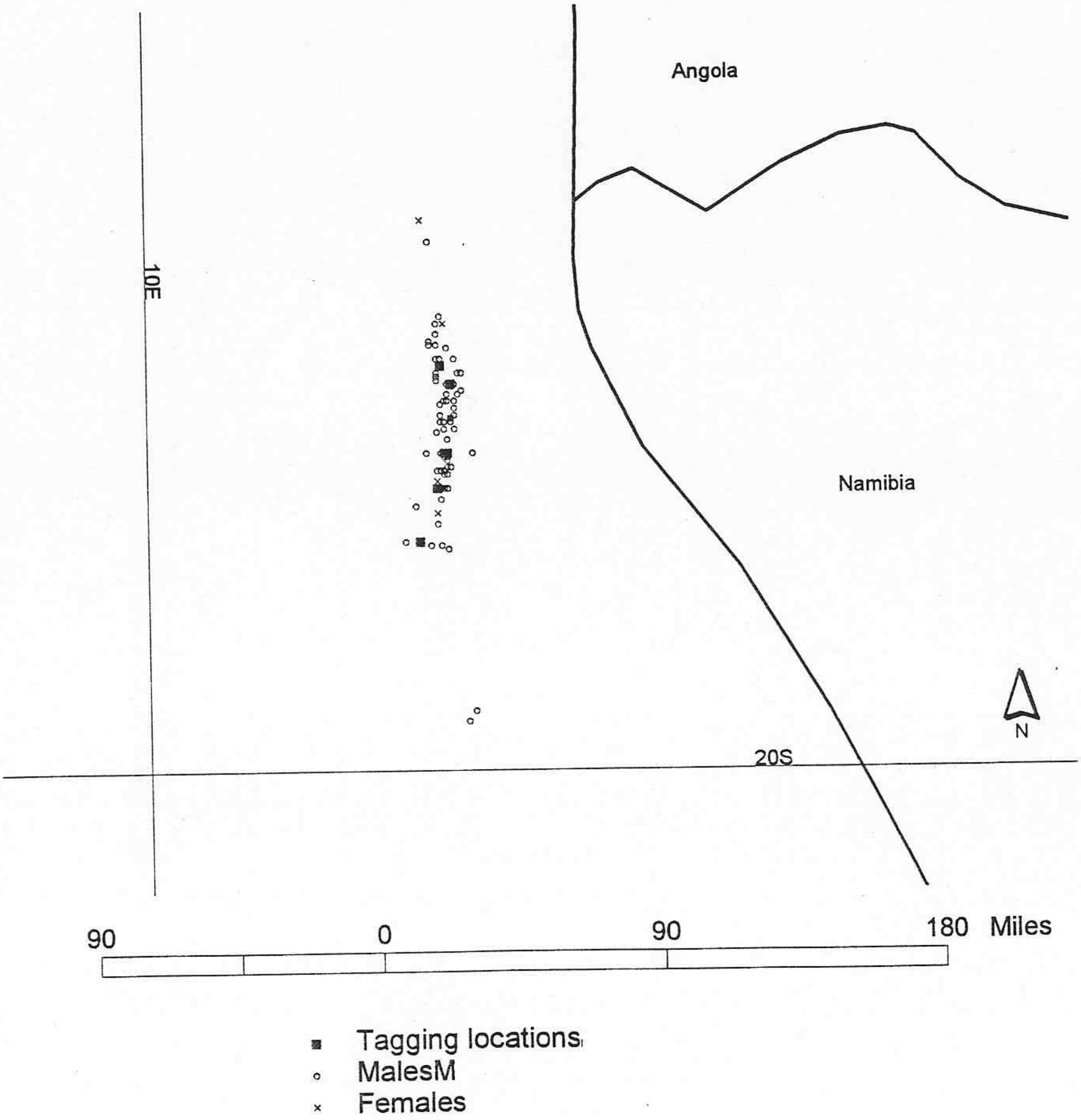


Figure B2: Movements of male and female *C. maritae* tagged in the area 18°-19°S in 1992 returned within one year of tagging.

Appendix B

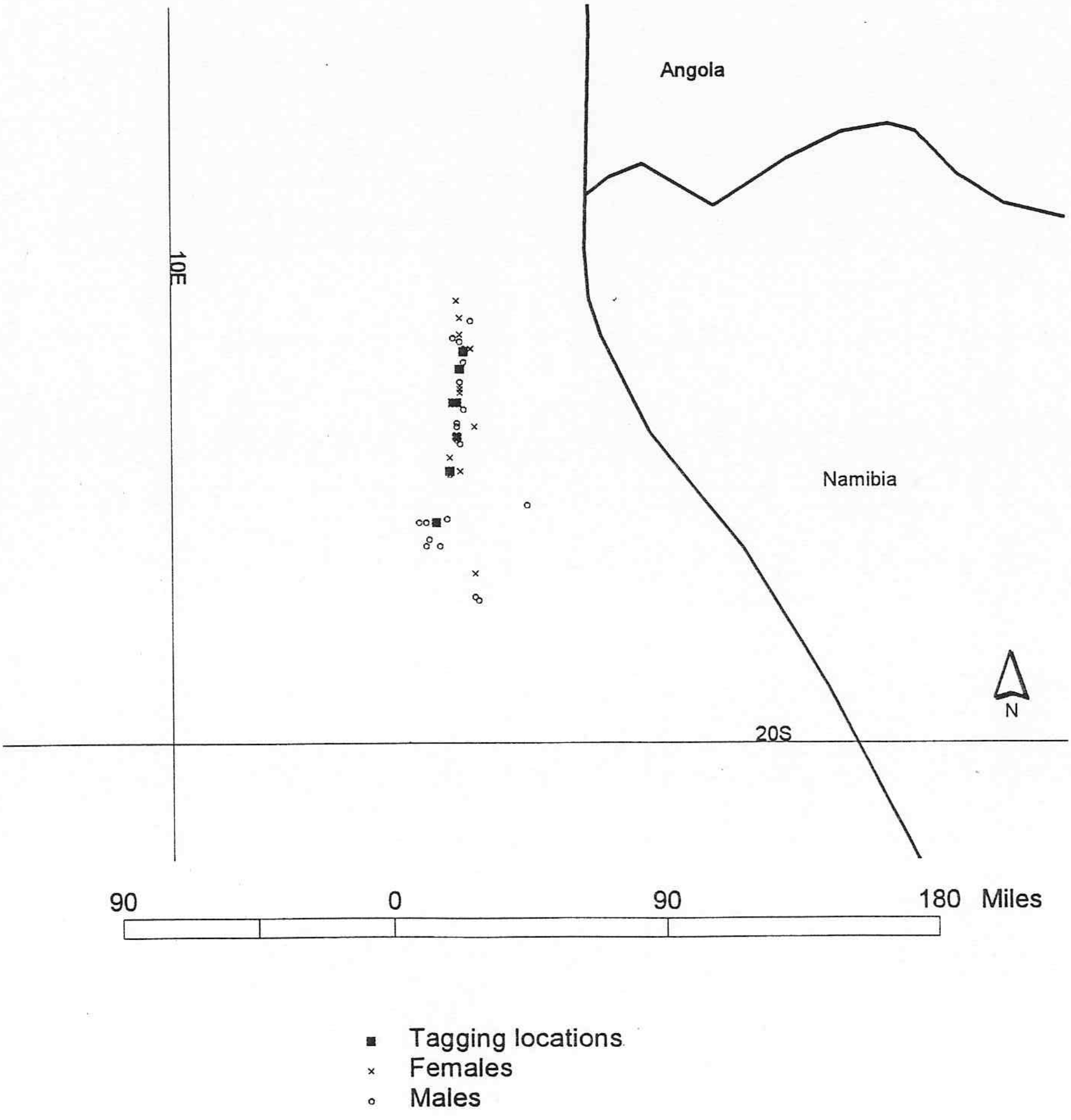
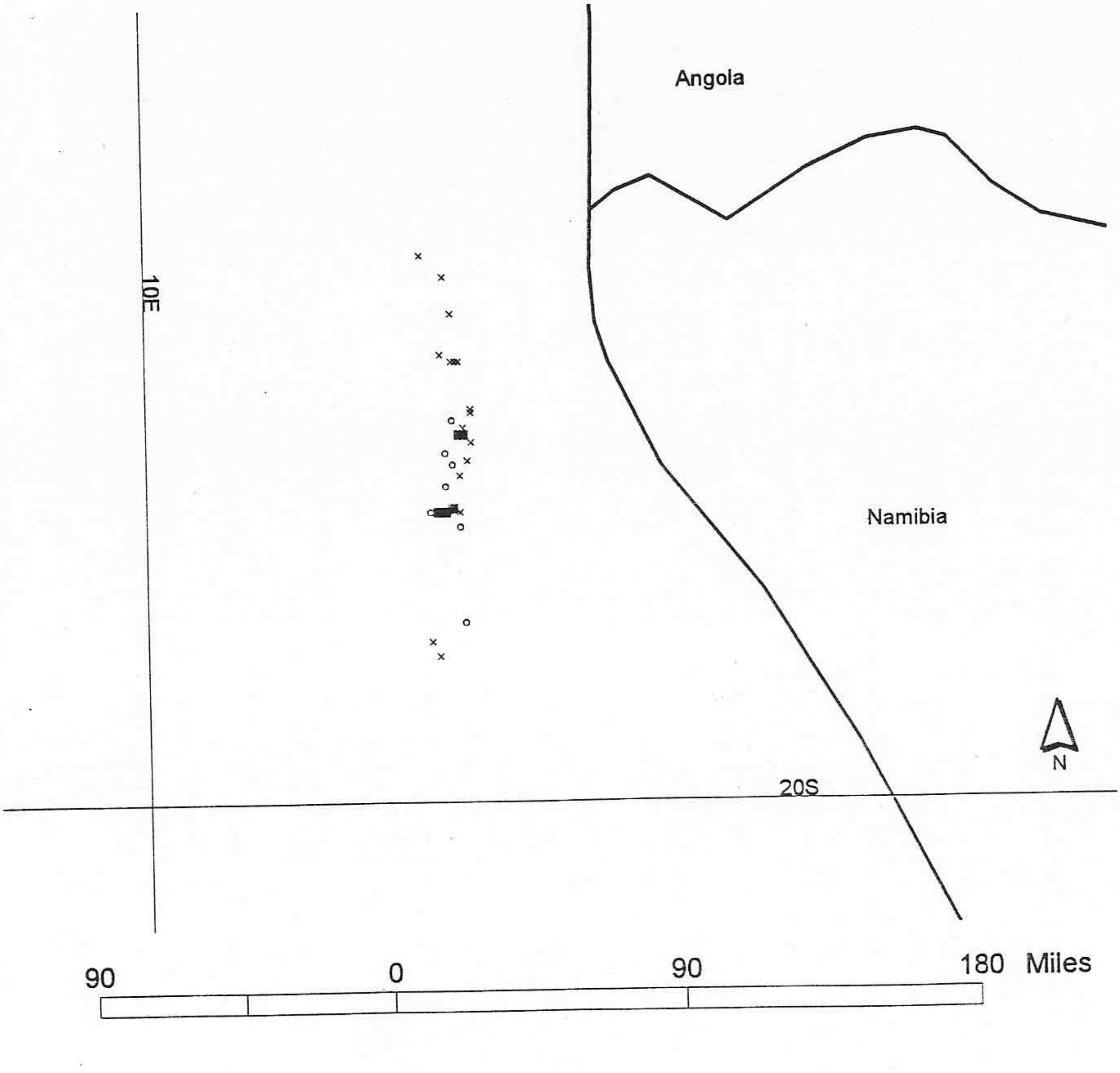


Figure B3: Movements of male and female *C. maritae* tagged in the area 18°-19°S in 1993 returned within one year of tagging.

Appendix B



- ■ Tagging locations
- ○ Males
- × Females

Figure B4: Movements of male and female *C. maritae* tagged in the area 18°-19°S in 1994 returned within one year of tagging.

Appendix B

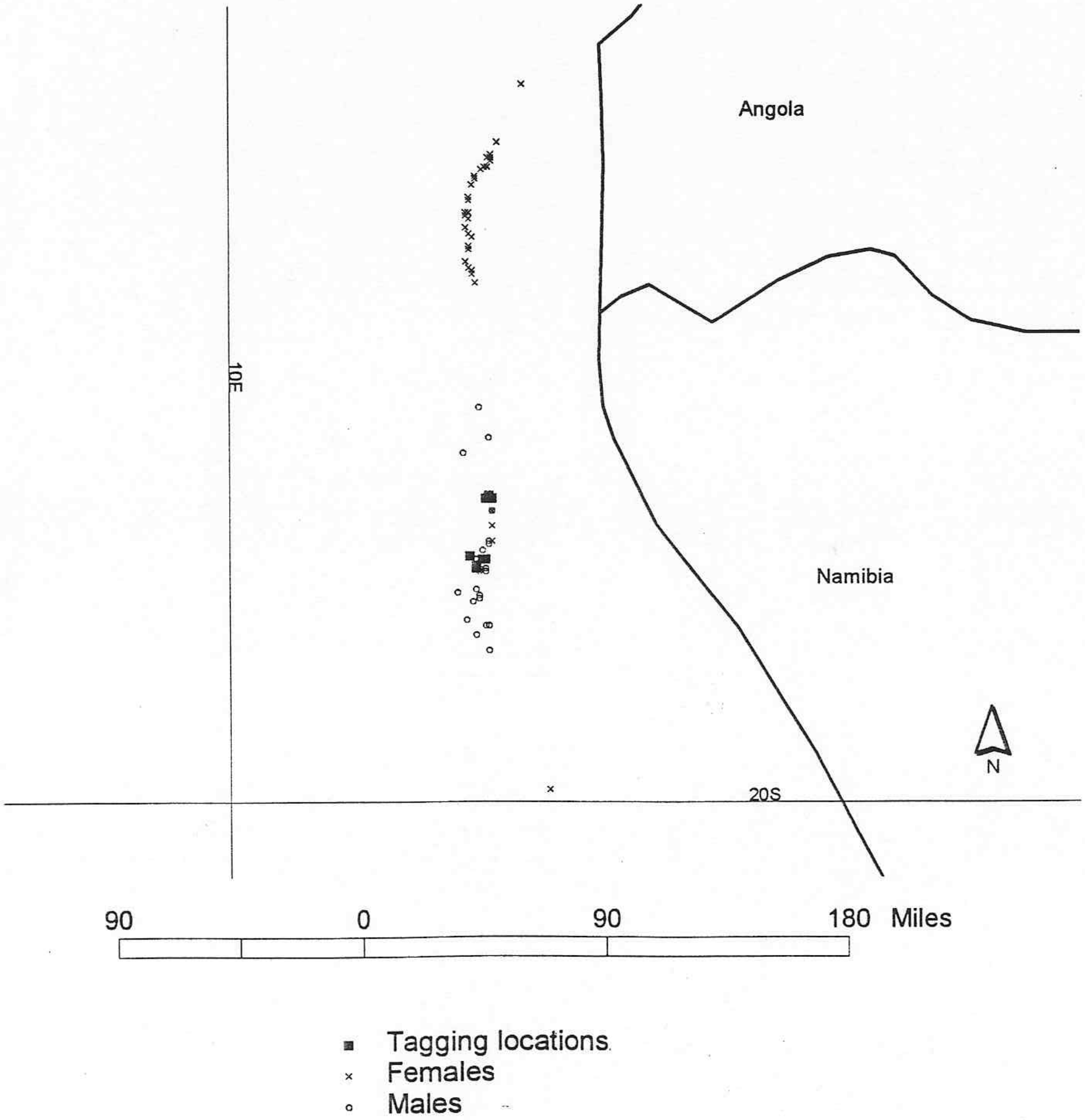


Figure B5: Movements of male and female *C. maritae* tagged in the area 18°-19°S in 1995 returned within one year of tagging.

Appendix B

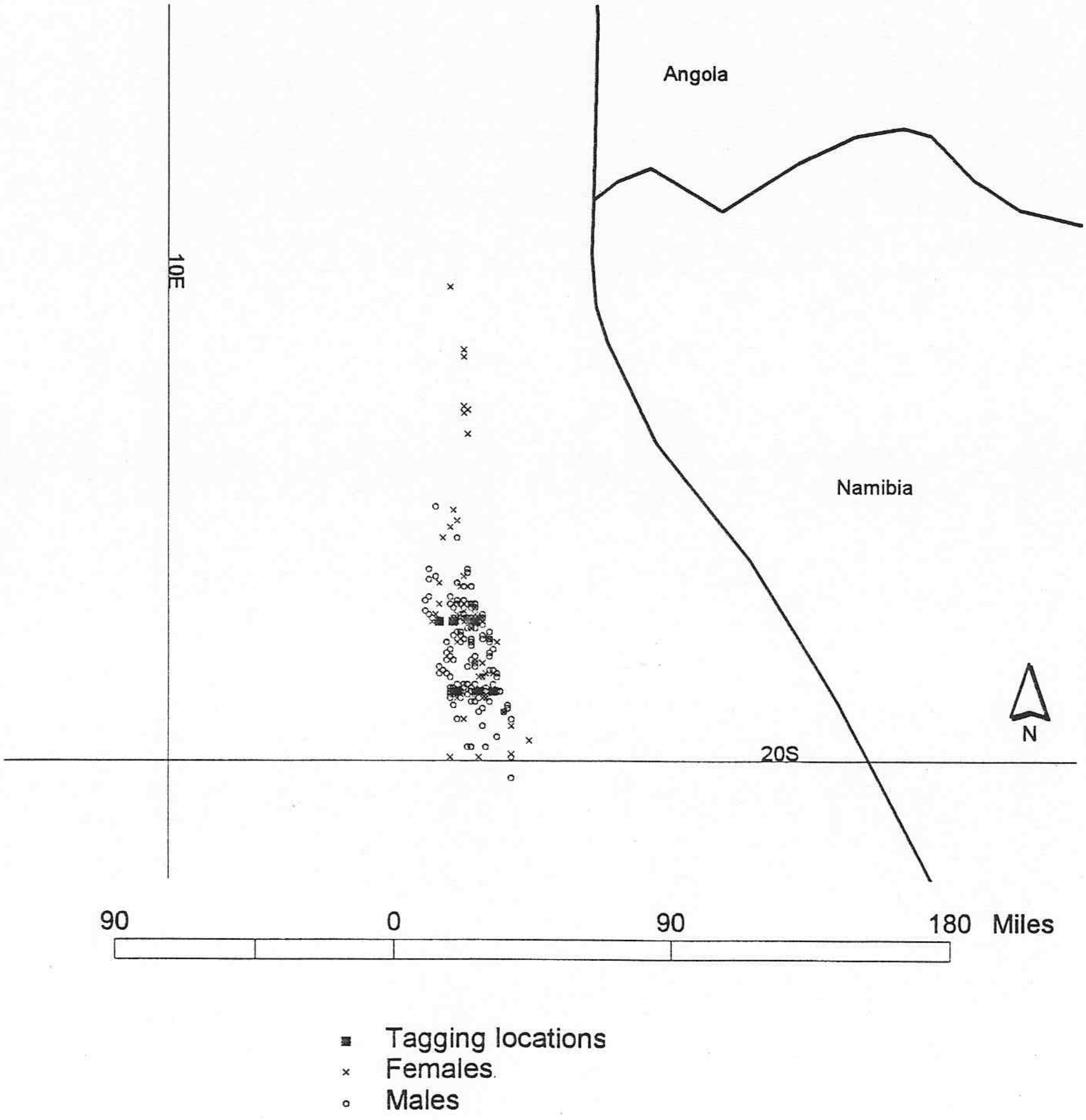


Figure B6: Movements of male and female *C. maritae* tagged in the area 19°-20°S in 1991 returned within one year of tagging.

Appendix B

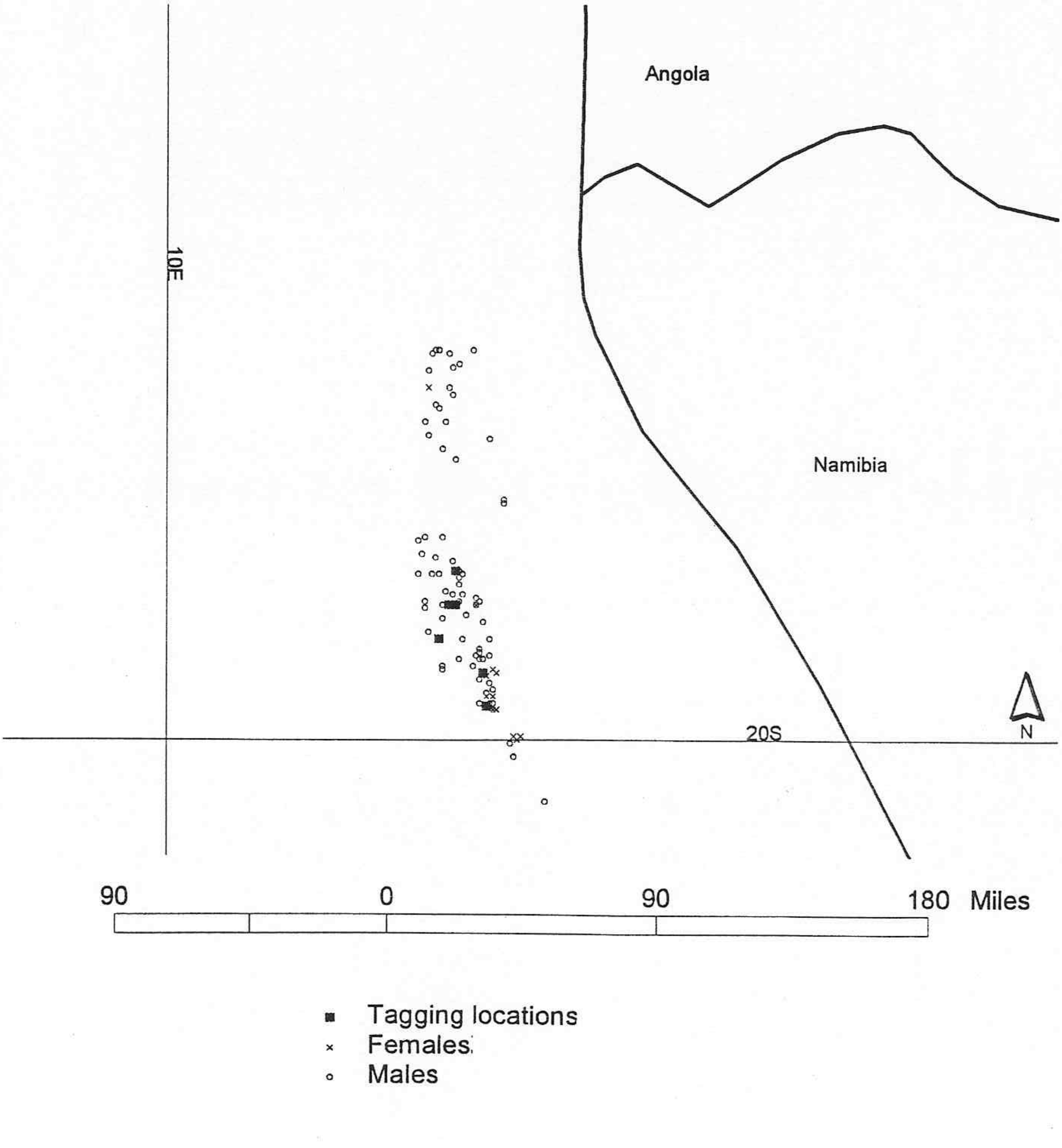


Figure B7: Movements of male and female *C. maritae* tagged in the area 19°-20°S in 1993 returned within one year of tagging.

Appendix B

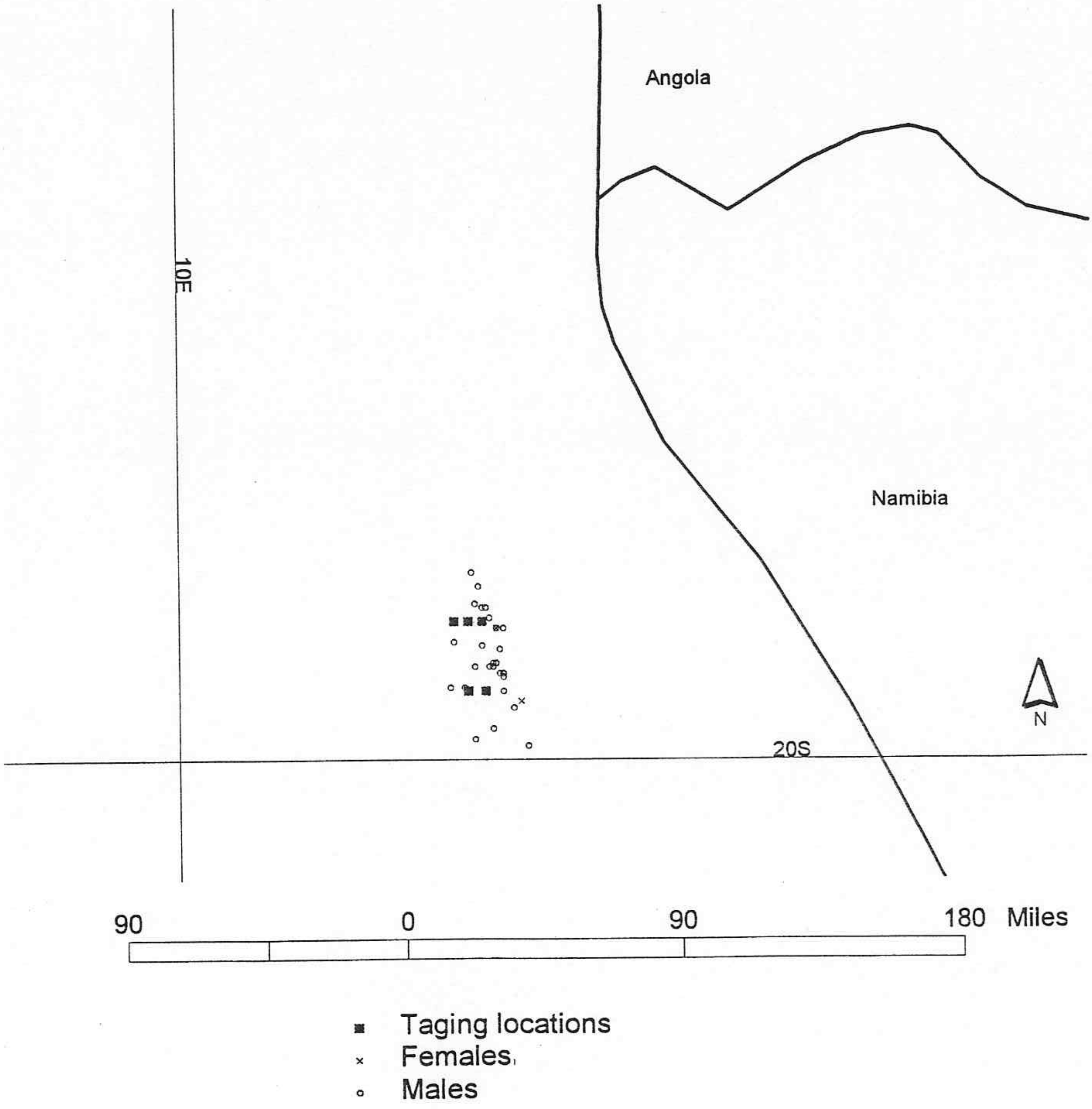


Figure B8: Movements of male and female *C. maritae* tagged in the area 19°-20°S in 1994 returned within one year of tagging.

Appendix B

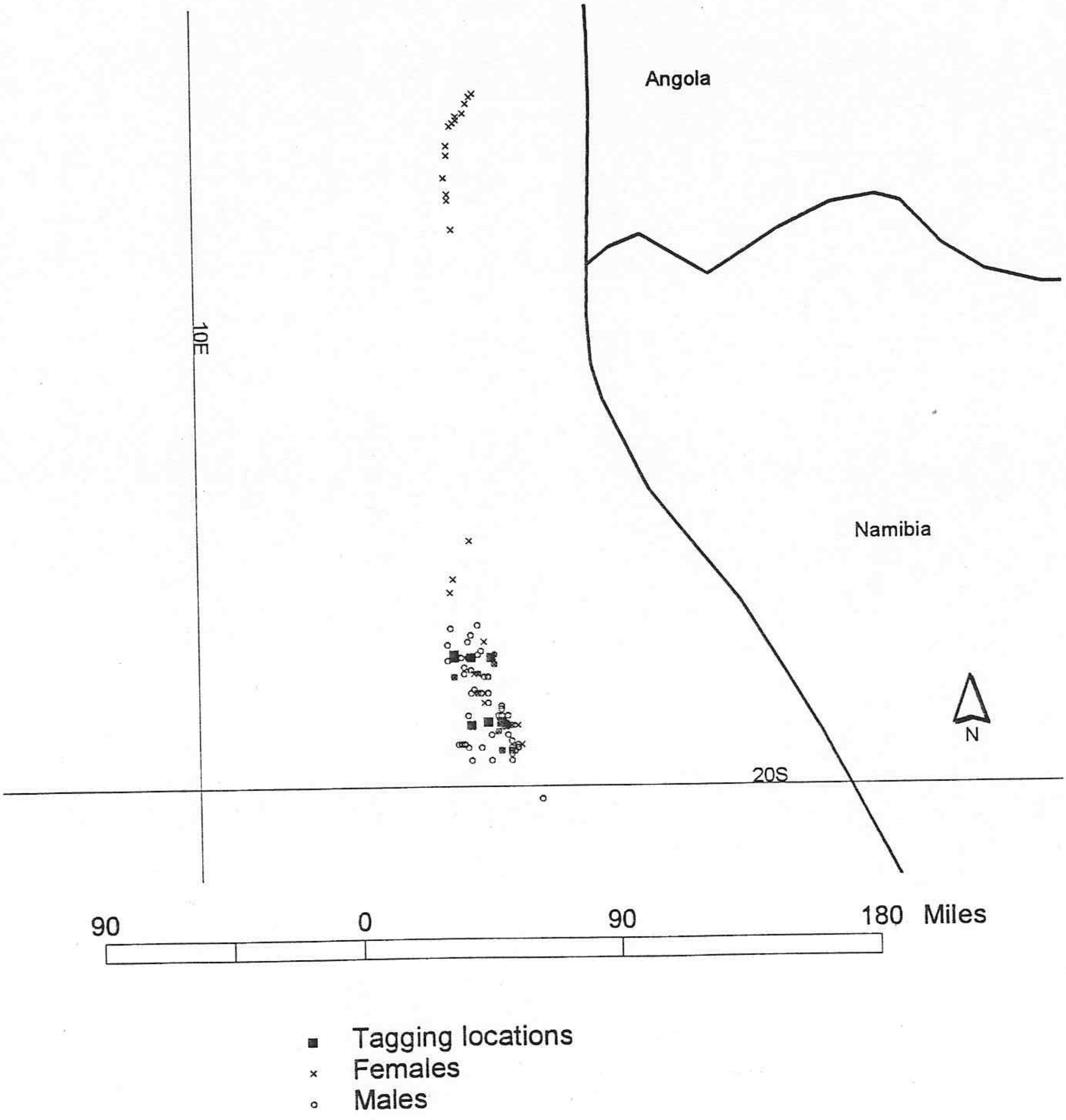


Figure B9: Movements of male and female *C. maritae* tagged in the area 19°-20°S in 1995 returned within one year of tagging.

Appendix B

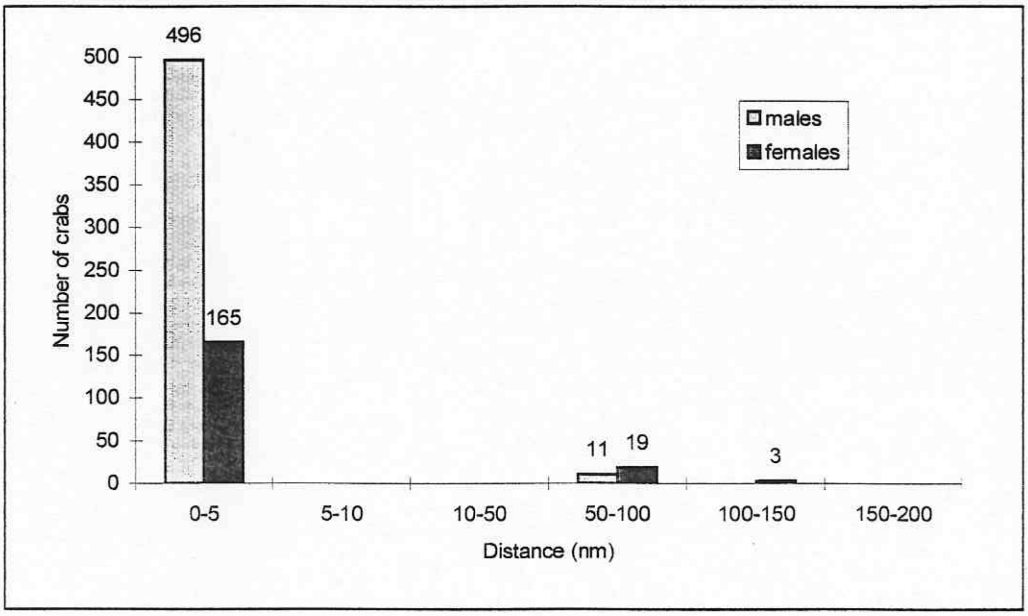


Figure B10: Distances (nautical miles) moved by male and female *C. maritae* tagged in 1991 within one year of recapture.

Appendix B

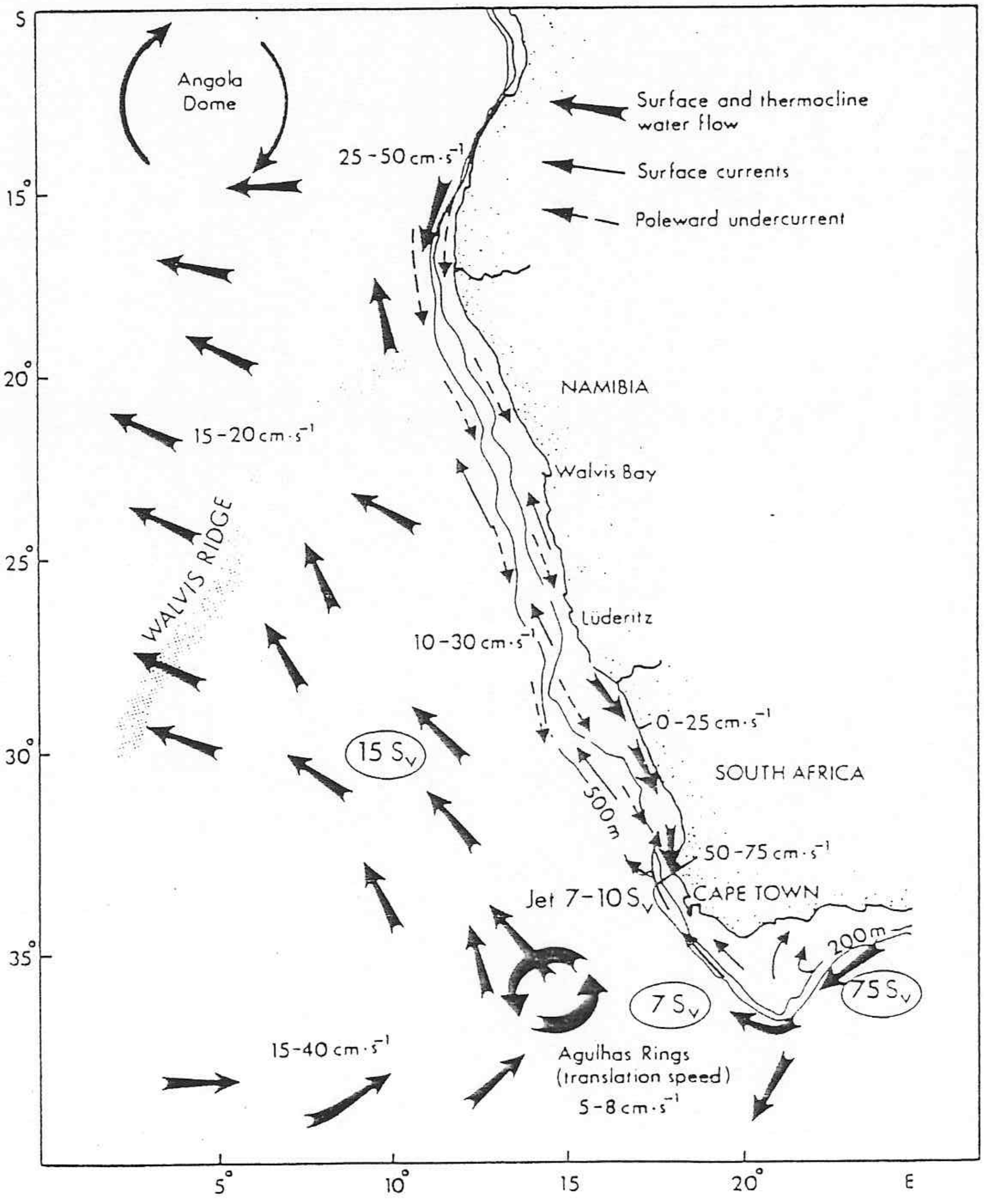


Figure B11: Schematic flow field of surface and thermocline water in the South-East Atlantic. Speeds refer to surface values. Transport values are for the upper 1 500m. (From O'Toole & Shannon 1997).

Appendix C

List of abbreviations used:

CPUE	catch per unit effort as kg per trap
CW	carapace width
$F_{0.1}$	optimum exploitation level = point at which the slope of the yield curve is 0.1 of its initial value
MSY	maximum sustainable yield
NATMIRC	National Marine Information and Research Centre, Swakopmund, Namibia
SFRI	Sea Fisheries Research Institute, Cape Town, South Africa
TAC	total allowable catch
Y/R	yield per recruit

List of symbols used:

a, b, d, and q	parameters of various equations
ϕ_A	latitude of location A
λ_A	longitude of location A
ϕ_B	latitude of location B
λ_B	longitude of location B
Δt_i	the time an animal spends in length class i
$\bar{B}$	Mean annual biomass
C	catch in numbers
D	depth in metres
D_{AB}	distance moved in nautical miles
dL	$(L_R - L_T)$ = difference in length from tagging to recapture
dt	number of days at large
$\hat{E}_m$	proportion of animals that has emigrated
F	Fishing mortality
F_{MAX}	maximum fishing mortality for all length classes
F_t	Terminal fishing mortality
L	carapace width in mm.
L^*	some specified value of premoult CW
$\bar{L}$	$(L_R + L_T)/2$ = mean carapace width (mm)
L50%	length at which 50% of animals are retained

L75%	length at which 75% of the animals are retained
L_i	Carapace width in mm at the beginning of the *i*th length class
L_R	postmoult carapace width or CW at recapture
L_T	premoult carapace width or CW at tagging
M	natural mortality
Mf	natural mortality for females
Mm	natural mortality for males
n	sample size
$\hat{N}$	population size estimate in numbers
$\bar{N}$	Mean annual population number
N_{Li}	Number of crabs attaining length L_i
p	proportion of males
p'	arcsine transformed value of p
R	number of tags returned
R_A	number of tag returns from Angola
R_N	number of tag returns from Namibia
R_T	total number of tag returns ($R_N + R_A$)
S	fraction of animals retained by gear currently in use
S1	parameter of the selection ogive
S2	parameter of the selection ogive
T	number of animals tagged
T_N	estimated number of tagged animals that have not emigrated to Angola
w	weight in grams
$\bar{W}$	mean weight in grams
X	F-factor or factor with which F is multiplied
y	dependent variable of various regressions
$\bar{Y}$	Mean annual yield
Z	total mortality $= F + M$