ASPECTS OF THE BIOLOGY AND POPULATION DYNAMICS OF THE DEEP-WATER COMMERCIALLY EXPLOITED CRABS OFF SOUTH WEST AFRICA/NAMIBIA

by

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Frontispiece: Crab traps being hauled off Namibia. One trap is being emptied of its red-crab catch, while another is being dispatched to the stern for resetting. Fishermen (obscured by the tarpaulin) are 'sectioning' crabs and packing the raw product into the blue baskets (at the far right of the picture) for cooking

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ABSTRACT

Two crab species have been exploited on the South West African/ Namibian continental slope since 1973. The deep-sea red crab *Geryon maritae* forms >99 per cent of the catch made by traps, the balance being a by-catch of stone crab *Lithodes tropicalis*. Historical information dating back to the late 1970's has been examined, but most of the data analysed in this study have been collected since 1980. Most of the research has been conducted on red crab. Four aspects of its biology have been examined in some detail, namely its reproduction, growth, movements and causes of its specific depth zonation off Namibia. These (particularly the first two) aspects have been used, together with information from commercial sampling and catch statistics, to examine possible changes in the yield-per-recruit should the age at first capture be increased, or fishing effort reduced. On the basis of these results, some management options are presented. Several techniques (photography, trawling, effective fishing area and tag-recapture) have been used to examine the abundance and density of red crab off Namibia, and are critically compared. Research on the stone crab has been largely restricted to an analysis of commercial catch data, though an unusual symbiotic relationship with a liparid fish has been identified and discussed.

INTRODUCTION

INTRODUCTION

There is very little information dealing with the early years of the Namibian crab fishery. According to Japanese sources (Kaiyo-maru Gyogyo Company Ltd., 498-2 Minatomachi, Kesennuma-shi, Miyagi-Ken, Japan, pers. comm.), vessels from that country first started fishing for red crab off the Namibian coast during 1973 and have been present in fluctuating numbers ever since that time. More details in terms of foreign and local participation in the fishery are given later (see Paper 10).

South African interests became briefly involved in the crab fishery during 1976 and again in 1978 to early 1980. It was during this latter period of involvement that a 'crab programme' was initiated by the Sea Fisheries Research Institute. The programme was aimed at collecting and analysing data which could ultimately be used to provide stock management proposals.

There are two commercially important species of crab occuring off the Namibian coast, namely *Geryon maritae* (Manning and Holthuis, 1981) commonly known as the deep-sea red crab (Fig. 1) and *Lithodes tropicalis* (A. Milne Edwards, 1884) the stone crab (Fig. 2). The red crab accounts for more than 99 per cent of the present commercial catch and research has therefore been directed almost entirely at that species.

Fig. 1: The deep-sea red crab *Geryon maritae* (male, taken in a commercial trap catch made at 20°05,7'S 11°45,8'E, 548 m, July, 1987).

Fig. 2: The stone crab *Lithodes tropicalis* (male, taken in a commercial trap catch made at 21°01,1'S 12°28,8'E, 455 m, November, 1985).

The two species of crab that are caught commercially off Namibia have very different evolutionary histories. Red crabs belong to the infra-order Brachyura, or true crabs as they are commonly known. Stone crabs on the other hand, are members of the Anomura, a more primitive infra-order of crab-like crustaceans which includes hermit and mole crabs. Perhaps the most obvious characteristic of stone crabs is that their last pair of walking legs is reduced and is tucked under the posterior margin of the carapace, thereby giving them the appearance of only having three pairs of walking legs (Fig. 2) instead of four (Fig. 1).

Red crab of the genus *Geryon* are well represented in the oceans of the world and in particular in the Atlantic where there are at least 11 species recognized. Members of the genus are characteristically deep-water crabs, generally occuring on continental slopes. Many of the species are distinguished by subtle differences and this has resulted in numerous misidentifications in the literature. *G. maritae* has not escaped this confusion and was misidentified as *G. quinquedens* (Smith) by numerous authors (*inter alia* Le Loeuf et al. 1974, Cayré and Bouchereau 1977, Cayré et al. 1979 and Beyers and Wilke 1980) prior to being described by Manning and Holthuis (1981).

Red crab meat is a highly esteemed product and fetches high prices, particularly in the East. Based on product marketing prices (quoted by the Taiyo Fishing Company, 1-1-2 Ootemachi

Chiyoda, Tokyo, Japan, pers. comm.), the 1986 Namibian crab catch for all ships on the grounds, was worth in excess of 1 125 million yen (ca. R16 million). By comparison, the 1986 free on board (including processed product) values of the Namibian pelagic and rock lobster fisheries was R65 and R40 million respectively (unpub. statistics, Department of Economic Affairs South West Africa/Namibia, Sea Fisheries Branch, Windhoek, South West Africa).

As with the red crab above, the stone crab, *Lithodes tropicalis*, has also been misidentified in reports pertaining to the species off the Namibian coast. Numerous authors (Kensley 1980, Melville-Smith 1982, MacPherson 1983) have confused *L. tropicalis* with *L. murrayi* (Henderson). This confusion is not surprising, because the two crabs are remarkably similar and furthermore, *L. tropicalis* had hitherto been considered an extremely rare species. Prior to the realization that *L. tropicalis* is abundant off the Namibian coast, the only other record of the species was based on a single male specimen taken off the Saharan coast in 860 m (E. Dawson, D.S.I.R., Wellington, New Zealand, pers. comm.). *L murrayi* by comparison, is a well known and relatively common species (Yaldwyn and Dawson 1970, Campodónico and Guzmán 1972, Arnaud and Do-Chi 1977, Arnaud and Miguel 1985).

As has been mentioned, research on the commercial crab species off Namibia started in 1978. These first surveys, which are described by Beyers and Wilke (1980), made use of a standard otter trawl to catch the crabs. Useful data was collected on size frequency, stock density, biology and morphometric characteristics of *G. maritae*. All subsequent fisheries related work on red crabs off the Namibian coast is covered in this thesis.

The aim of the red crab research programme was to determine whether a management policy was necessary to protect the stock and if so, to make proposals as to what form it should take. In attempting to achieve this aim, research has followed two directions

(i) the biology of the species has been examined (Papers 1 to 5) and

(ii) some possible methods of estimating red crab density on the grounds have been described and discussed (Papers 6 to 9) and critically compared in Paper 9. These two themes have been drawn together in Paper 10. In this latter paper, red crab size frequency and catch trends over the last decade have been examined and these data, together with much of the information presented in the earlier papers, have been used to set out some proposals which should be considered if the stock is to be scientifically managed in the future. Paper 11 deals with product to whole mass conversion factors for red crab used in Paper 10.

The stone crab has (with the exception of a short period between

1979/1980 (Paper 12) never been considered more than a relatively unimportant by-catch of the red crab fishery. As a result of its secondary importance to the industry, it has not received a great deal of scientific attention. The aim of the work on this species (which is presented in Papers 12 to 14), was to show its distribution off Namibia, its relative abundance in these waters and to document its contribution to the Namibian deep-sea crab fishery.

The brief stone crab fishery off Luderitz (1979/80) is described in detail in Paper 12 and catches since then are discussed in Paper 14. Paper 13 deals with an interesting symbiotic relationship which has been shown to exist between the stone crab and a caraproctid fish. It has been included, because apart from its interest value, there is some speculation as to the effect that commercial fishing may have had on the observed quantity of crabs carrying fish eggs. Aside from this thesis and the few references mentioned above, the only other work of any significance that has dealt with either of the two commercial crab species off Namibia, is a report by Abelló and MacPherson (1986). Their work described the distribution, abundance, length frequency composition and sex ratio of *L. tropicalis* off southern Namibia.

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PAPER 1:

The reproductive biology of *Geryon maritae* (Decapoda, Brachyura) off South West Africa/Namibia

Crustaceana 53 (3) 1987, E. J. Brill, Leiden

THE REPRODUCTIVE BIOLOGY OF *GERYON MARITAE* (DECAPODA, BRACHYURA) OFF SOUTH WEST AFRICA/NAMIBIA

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ZUSAMMENFASSUNG

Die Fortpflanzungsbiologie der roten Tiefseekrabbe *Geryon maritae* wurde an Hand anatomischer und histologischer Studien untersucht. Proben wurden im Zeitraum August 1982 bis November 1984 in regelmäßigen Abständen aus Schleppnetz- und Reusenfängen namibischer Krabbenbestände aus Tiefen zwischen 400 und 900 m entnommen. Keinerlei Jahreszyklen wurden wahrgenommen, was auf ein gleichbleibendes Tiefenmilieu (Ausbleiben von Reproduktionsstimuli) zurückzuführen sein mag. Männliche Krabben erreichen die Geschlechtsreife bei einer Carapaxbreite von etwa 80 mm. Es wird ein Verfahren zur Bestimmung außerer Geschlechtsmerkmale am Merus des ersten Beinpaares erörtert. Dieses tritt nach der Häutung ein. Weibliche Krabben erreichen die Geschlechtsreife bei einer Carapaxbreite zwischen 70 und 100 mm.

Eizählungen bei 28 Krabben (74 bis 110 mm breit) ergaben Eizahlen zwischen 107000 und 350000 pro Tier. Eine Regressionsanalyse zur Beschreibung der Verhältnisses von Carapaxbreite zur Anzahl der getragenen Eier wird durchgeführt. Der Formwechsel der Vulvae zur Zeit der Reifehäutung wird beschrieben; ebenso Merkmale, die durch Reibung der Pleopoden des begattenden Männchens nahe der Vulvae der Weibchen hinterlassen werden. Die Geschlechtsöffnungen einiger Weibchen enthielten wachsartige Pfropfen, die wohl die Spermatophore nach der Paarung zurückhalten.

INTRODUCTION

The red crab *Geryon maritae* Manning & Holthuis, 1981, occurs in commercially exploitable quantities along several regions of the West African continental shelf and shelf break. The stock has been fished since 1973 off SWA/Namibia (Beyers & Wilke, 1980), yet published information dealing with the reproductive biology of the species has remained scant.

Several authors have provided data describing the sex ratio variability of *G. maritae* with depth off various areas of the West African coast. These studies include inter alia, Dias & Seita Machado, 1973 (Angola), Le Loeuff et al., 1978 (Ivory Coast and Congo) and Beyers & Wilke, 1980 (Namibia). Some of these studies have also suggested a size at maturity and possible reproductive seasons, but in general, work dealing with *G. maritae* reproductive biology has been superficial. The only detailed work of any relevance to this report, is a study conducted by Haefner (1977) on the female reproductive biology of *Geryon quinquedens* Smith, 1879, a species found off the east coast of the United States of America.

This research paper forms part of an ongoing project aimed at examining in detail those aspects of the biology of the red crab relevant to formulating a management strategy for that stock. A thorough knowledge of the reproductive biology of *G. maritae* is regarded as an important step in that direction.

METHODS

The red crabs used in this study were sampled over the period August, 1982 to November, 1984. The majority were obtained from commercial trap fishing catches while the balance were from research trap and trawl fishing catches. The crabs were caught in depths of between 400 and 900 m between latitudes 17°30′S and 21°00′S.

During the first year (August, 1982 to September, 1983), samples were taken at bimonthly intervals. In each of the months sampled, approximately 150 to 200 crabs of as wide a size range as possible were dissected and the gonads examined. Samples of the testis and vas deferens in the male and ovary and seminal receptacle in the female were taken for later histological examination, while at the same time notes were made on the size and colouration of those organs.

Externally visible physical features which were considered relevant for assessing size at maturity, for example, shell state, size of the vulvae, etc., were recorded on a routine basis during all research and commercial crab catch sampling.

All the gonad tissue retained for histological work was fixed in Bouin's solution for 24 to 48 hours and then transferred to 70% alcohol for storage. The tissues were processed using standard histological techniques and were embedded in paraffin wax. Sections were cut 8 to 10 μm thick and were stained using Delefield's hematoxylin and counterstained in Eosin.

Spermatophores and sperm were examined using a Cambridge S200 scanning electron microscope. A portion of the anterior vas deferens of a mature crab was maceratead in 25 ml of filtered sea water. The resulting solution containing seminal fluid in suspension was filtered through 3 μm pore filter paper assisted by a low vacuum filter pump. The filtrate (still attached to the filter paper) was fixed using the sequential mixed fixative method described by Eisenman & Alfert (1982). Further procedures prior to viewing, i.e. dehydration, critical point drying, mounting and coating, all followed standard scanning electron microscope techniques.

The fecundity of *G. maritae* was calculated by counting the eggs of 28 crabs incorporating as wide a size range as possible. It is not known what quantity of eggs is lost during their incubation and to avoid this possible source of error, only crabs carrying early stage eggs were used for fecundity purpose. The eggs of a gravid crab were counted by removing the pleopods from the crab and immersing each one in a separate concentrated solution of sodium hydroxide.

The eggs became free after three to six hours. The sample of eggs from each pleopod was then filtered through 300 μm plankton net and the eggs were spread out as evenly as possible over the netting. Excess liquid was removed by blotting the undersurface of the net with absorbant paper towel.

Two small (approximately 0.2 g) subsamples of eggs were removed from the net filter and accurately weighed and counted. Using these results, the mass of a single egg from each of the two samples was calculated and compared. If the two weights failed to be within 95% of each other, a third and if necessary a fourth sample was weighed and counted. When two results agreed to within 95% of each other, the mean mass of that result was used to calculate the number of eggs in the total pleopod sample. Similar calculations were done for each pleopod (there are eight pleopods per crab) and a total number of eggs for that crab was calculated from those results.

RESULTS AND DISCUSSION

Reproductive seasonality

Though a large number of visual and histological samples of red crab were examined at bimonthly intervals throughout the course of a full year (August, 1982, to September, 1983) and subsequently at less frequent intervals, no seasonal fluctuation in the reproductive cycle of *G. maritae* has been observed. This is contrary to most other brachyuran reproductive studies in the literature, inter alia Marukawa (1933), Broekhuysen (1941, 1955), Swartz (1978) and Sapëlkin & Fedoseev (1980), where clear reproductive seasons have been determined.

The difference in the reproductive pattern of *G. maritae* and most other brachyuran species is possibly the fact that the red crab is a relatively deep-water species. Seasonal reproductive cycles are usually triggered by environmental changes such as day length and temperature. The deep sea, by virtue of its unchanging environmental conditions, could be regarded as seasonless and consequently none of the usual reproductive trigger stimuli can operate. Rokop (1974, 1977) has examined the reproductive patterns of a variety of deep sea benthic invertebrates and has concluded that the common mode of reproduction in this environment is year-round. *G. maritae* generally occurs in depths of between 400 and 900 m off the Namibian coast (Beyers & Wilke, 1980; Melville-Smith, 1985) and therefore appears to fit the typical year-round deep-sea reproductive pattern.

Sex ratios

G. maritae exhibits partial segregation of the sexes by depth. This phenomenon has been extensively documented by inter alia Dias & Seita

Machado (1973), Intes & Le Loeuff (1976), Cayre et al. (1979) and Beyers & Wilke (1980). The latter authors showed that female crabs were numerically equal to males up to 400 m in depth off the Namibian coast, but that in deeper water they became scarcer and at depths greater than 800 m formed only 2,5 per cent of the catch.

Gonad development in the male

Anatomy of the reproductive organs. — The male reproductive organs are of standard decapod pattern. The paired testes when mature are white convoluted tubes which lie sandwiched between the digestive gland and hyperdermis of the carapace. Each testis is contained within a double wall of connective tissue and is made up of tight convoluted lobes. The seminiferous duct runs the length of the testis in amongst the lobes. Within each lobule there are various numbers of cysts each with reproductive cells at various stages of development. When mature the spermatozoa are released into the seminiferous duct and proceed to the vas deferens where they are stored.

The reproductive organs of male crabs ranging in size from 66 to 143 mm cw. (carapace width) were examined histologically. Crabs as small as 65 mm cw. were found to have prominent white vasa deferentia although in these small crabs the testes were thin and inconspicuous. Histology of the testes revealed that the only difference between large male crabs ($>$110 mm cw.) and small male crabs with developed vasa deferentia (i.e., 65-70 mm cw.), is that the testes of the smaller animals appear to have more developing germinal cells than the larger individuals.

Serial sections from different areas of the testes reveal that regardless of size, the sex cells from the distal portion of the testes are generally less well developed than those from the proximal area. It therefore appears that development takes place as the sex cells are transported towards the vas deferens.

Spermatogonia occupy the whole testis of small animals. In maturing and mature crabs they tend to be situated near the wall or lobes of the testis in generally small numbers compared to other maturing sex cells. They have comparitively large nuclei varying in size from 13.5 to 16.0 μm in diameter (measured by taking a mean for the measured diameter of the long and short axes).

Primary and secondary spermatocytes differ from spermatogonia in that their nuclei are smaller (9.5 to 10.5 μm in diameter). It is usual to find that all the cells within a lobe are at the same stage of development.

Each secondary spermatocyte gives rise to two spermatids by meiotic division and each spermatid gives rise to a single spermatozoon. It was extremely difficult to distinguish between the mature sex cells as both spermatids and spermatozoa were found to exhibit similar characteristics, the most obvious of which was the affinity with which their large nuclei took up the eosin stain.

Mature sperm were found to be slightly oval in shape with a diameter of ∿4.5 µm. Spermatophores, which are common in a portion of the vas deferens, vary considerably in size but are generally 20 to 70 µm in diameter.

Vas deferens. — The vasa deferentia are long, paired, tubular organs extending from the proximal portion of the testes through the thoracic cavity on either side of the digestive tract to where they finally exit at openings on the coxa of the 5th pereiopod. The vas deferens can be divided into two regions which differ in size, shape and function.

The anterior vas deferens is white in colour and is tightly coiled and thin. The sex cells present are of an advanced stage of development, and this portion of the vas deferens is the only region where spermatophores are found. Also present in the fluid surrounding the spermatophores are large quantities of eosinophilic granules.

The posterior vas deferens is the widest region of the duct. The walls are extremely thick and the epithelium lining the lumen is composed of columnar cells. The contents of the lumen in sectioned material is somewhat featureless, since it contains neither the spermatophores or eosinophilic granules observed in the anterior region.

Male sexual maturity

From histological evidence, all male crabs examined larger than 80 mm cw. had spermatophores in the vas deferens and must therefore be considered as being sexually mature and capable of mating. These data have been substantiated by what appears to be a reliable means of visually determining whether a male red crab has mated since his last moult.

As with many other decapod species, the two sexes pair prior to mating. During this time the male carries the female, using his first pair of walking legs to draw her against his thoracic sternum. This act results in certain areas of the shell of the male being damaged by the female chafing against it. Damage to the shell results in blackened areas in those regions and, consequently, a portion of the merus of the first walking leg of male crabs which have 'coupled' with one or more females since their last moult is usually distinctly blackened (fig. 1). In very large male crabs (>120 mm cw.), the merus does not chafe against the female and under these circumstances the technique does not apply. The smallest male crab which has been observed to have a blackend merus had a carapace width of 76 mm.

Le Loeuff et al., 1978, estimated the size at sexual maturity for male red crab off the Ivory Coast using morphometric means. Their data suggested that sexual maturity in the male was probably at sizes between 105 and 115 mm cw., though they did emphasize that this means of determining sexual maturity was very subjective.

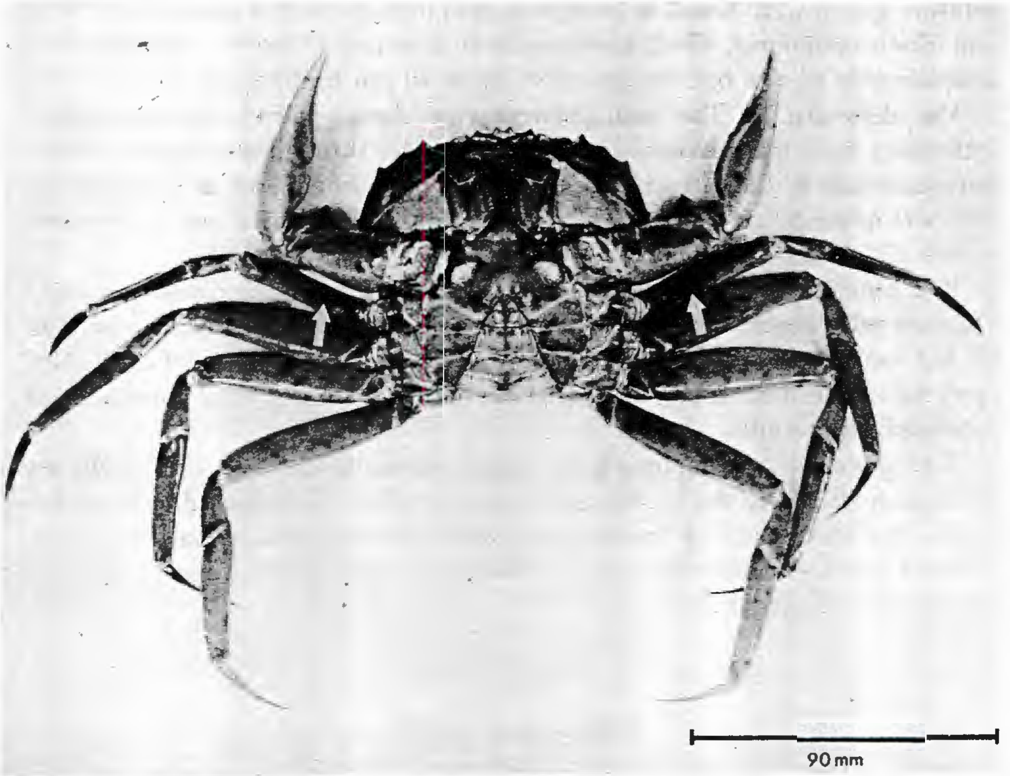

Fig. 1. Ventral surface of male crab showing blackened areas on merus of first pair of walking legs (arrows) caused by chafing during pairing.

Gonad development in the female

Anatomy of the reproductive organs. — The reproductive biology of female *Geryon quinquedens* has been documented in detail by Haefner (1977). The ecology and morphology of *G. quinquedens* appears to match closely that of *G. maritae* and consequently much of what Haefner (1977) has documented in his report is applicable to *G. maritae* in this study.

The ovaries of the red crab lie in very much the same position as has been described for the testes in the male. In the anterior region they extend laterally as two horns. These horns unite behind the foregut and then proceed posteriorly, close to each other, separated by the digestive tract. The ovaries descend ventrally in the area lying underneath the heart. They form a short oviduct before opening to the exterior at the vulvae, which are located on the sternite of the sixth thoracic segment.

The seminal receptacles or spermathecae are bordered by the external sternites of the gill chamber on one side and the ovary and the digestive tract on the other. At their posterior base they join up with the oviducts on their respective sides.

The ovary development. — The colour variation and descriptive stages of ovarian development described by Haefner (1977) for *G. quinquedens* have been found to be similar for *G. maritae* and have been broadly followed in this report. In addition to the above, Haefner (1977) described horn width range, ovary volume and gonad index for each descriptive stage. These measurements were not within the scope of this study and it is therefore not known whether they are similar for *G. maritae*. Briefly the stages can be be described as follows:

Very early development. — The ovary is thin, flat, colourless and extremely difficult to locate macroscopically. The central lumen and the germinal strand are prominent and the ovary is largely composed of fibrous connective tissue. The diameter of ova varies considerably up to a maximum size of about 50 μm.

Early development. — Ovaries in this stage are visible macroscopically and vary in colour from white or ivory to grey. At this stage the ovary has a well developed lumen and germinal strand and much of the fibrous connective tissue so dominant in the previous stage is replaced by developing oocytes varying in size up to 130 μm in diameter.

Intermediate stage. — Ovary colouring may be ivory, white, light yellow, yellow, yellowish orange or light brownish orange. Ova are not conspicuous in the ovary when viewed macroscopically. Oocytes vary in size from 100 to 300 μm. This stage has the widest definition of the ovary stages recognised in this report and incorporates crabs in both a mature and immature condition (see size at maturity).

Mature. — In this stage the ovary occupies a large volume of the carapace. The ovary colouration is generally darker than in the intermediate stage, varying from dark orange to brownish orange. Bulges caused by the large ova can clearly be seen macroscopically and when measured are between 300 and 450 μm diameter. By comparison extruded eggs varied from 550 to 680 μm in diameter. The ova in the mature stage contain large quantities of yolk granules and are difficult to section. The germinal strand is no longer visible, because the ovary is packed to capacity with the large yolk-filled ova. All crabs recorded in this stage were mature (see size at maturity below).

Redeveloping ovaries. — Ovaries of ovigerous female crabs are similar in size and colour to those described for animals in the intermediate stage (see above). Their histology differs, however, in that they are less compact than in the intermediate and mature animals and, particularly towards the outer edges, there tends to be a large amount of loose tissue. Ova are small in size and no atretic oocytes were noted, even from sections taken close to the oviduct.

Bimonthly visual staging of the ovaries revealed no seasonal reproductive cycle trends. The reproductive course of development appears to relate to size rather than season and the combined bimonthly visual reproductive staging data (September, 1982, to December, 1983) resulted in the histogram shown in fig. 2.

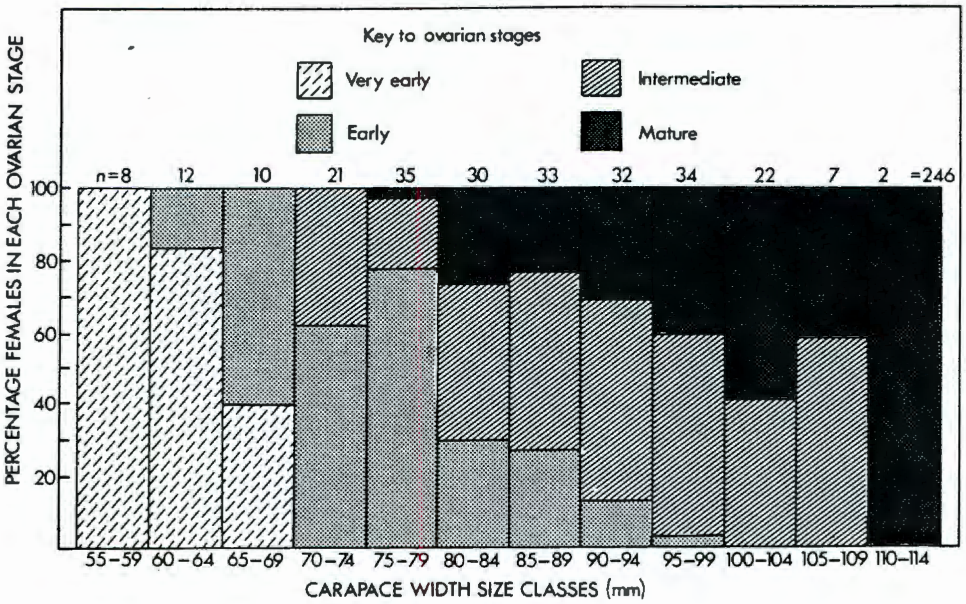

Fig. 2. Histogram showing female histological stages visually categorised during commercial sampling 1982/83. It was attempted to obtain five crabs in each size class per bimonthly sample, though in certain size classes this was not always possible.

It can be generalised from fig. 2 that crabs in the 60-64 mm cw. size class and smaller fall into the 'very early' stage of ovary development. Between the 65 to 69 and 75 to 79 mm cw. size classes the gonads become more visible and enter the 'early' stage of development in preparation for the maturity moult. Crabs classified as mature (see size at maturity) were all either in an intermediate or mature stage of ovary development.

It should be noted that the 'redeveloping ovary' stage has not been included in fig. 2, because it is not possible to recognise a gonad in this stage macroscopically (unless of course the animal is ovigerous). Any crabs in this stage would probably have been categorised as being in the 'intermediate stage'.

The seminal receptacle. — The seminal receptacles of a number of crabs were macroscopically and histologically examined. The organ was found to vary in size and turgidity, apparently influenced by the state of maturity and the moult cycle. Crabs in a shell condition close to, or immediately after, their pubertal moult were all observed to have large turgid seminal receptacles in apparent readiness for the storage of the male reproductive products at copulation. Animals in other shell states generally had small flaccid seminal receptacles.

Crabs in a late premoult condition were found to have a clear fluid in the enlarged seminal receptable, whereas those in an early postmoult stage had a white wax-like substance occupying this same space. Several crabs with seminal receptacles containing this waxy material were histologically examined and were found to have sperm present.

Ryan (1966a, b) reported a similar substance in *Portunus sanguinolentus* (Herbst, 1783) and was able to experimentally prove that this wax-like material was a sperm plug. He postulated that the fluid present in that crab's seminal receptacle prior to moulting may cause the male products to harden, thereby forming this plug. All available evidence from the seminal receptacles that were histologically examined would suggest that the formation and the function of the waxy substance in the seminal receptacles of *G. maritae* are similar to those described for *P. sanguinolentus*.

Unlike the sperm plugs found in many other brachyuran species, the plugs in *G. maritae* only occupy space in the seminal receptacles and are not visible externally at the mouth of the vulvae. As is the case with *P. sanguinolentus* (cf. Ryan, 1966b) and *Neopanope sayi* (Smith) (cf. Swartz, 1978), the sperm plug disappears after some time, probably by disintegration. Its function is thought to be retaining of spermatophores during early post copulation (Ryan, 1966b; Hartnoll, 1969; Swartz, 1978).

Size at maturity

Because the female crab is capable of storing sperm until ovulation occurs, their maturity cannot be determined by the condition of the gonads (Hartnoll, 1969). Maturity is therefore generally accepted as being that stage when the maturity or pubertal moult has been attained. The above criterion is particularly easy to apply to *G. maritae* females, because the vulvae undergo a drastic change of shape after that moult.

Haefner (1977) described six forms in the development of the vulvae of *G. quinquedens*. Staging based on those forms has been used in this study, but for ease of sampling the six forms have been reduced to three stages.

Stage 1. — The vulvae take the form of a closed slit (fig. 3). Crabs in this stage are virgin females and no crabs smaller than 70 mm cw. were recorded in either of the next two stages.

Stage 2. — The vulvae remain slit-shaped but are now partially open. This stage was recorded infrequently and histological samples of the ovary and seminal receptacle taken from animals being in this stage revealed them to be virgins, generally in a more developed stage of maturity than those recorded as stage 1.

Stage 3. — The vulvae appear as fully opened holes (fig. 4), often blackened at the periphery or in the area immediately posterior to their opening. The discolouration around the vulvae is caused by the abrasive action of the male pleopods during copulation (see copulatory behavior: p. 272). All crabs in this

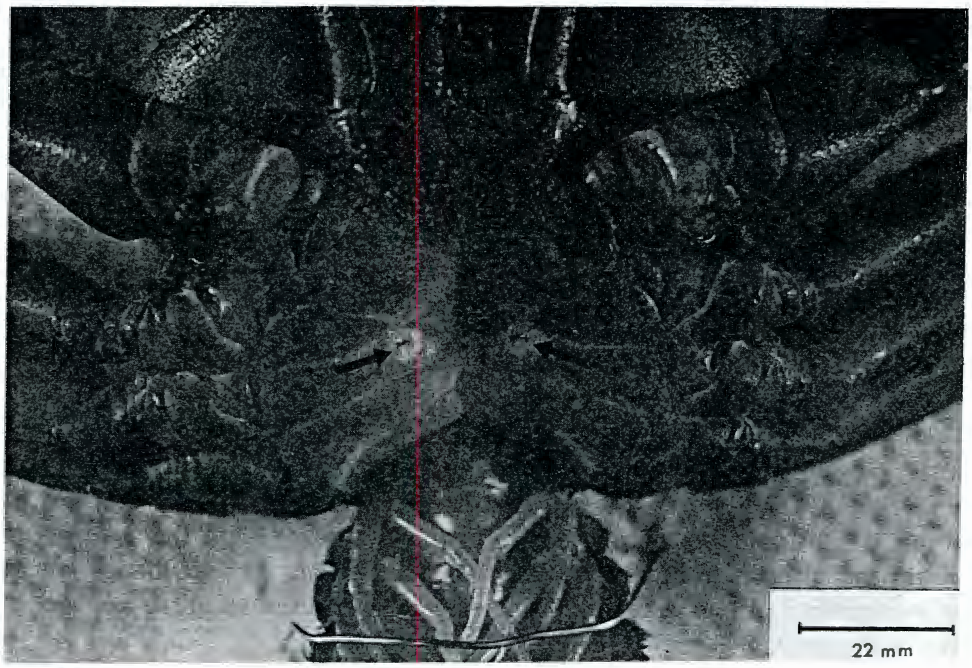

Fig. 3. Ventral surface of immature female crab. Arrows indicate closed slit-shaped vulvae.

Fig. 4. Ventral surface of mature female crab showing open vulvae of mated crab. Note blackened periphery of vulvae, as well as markings (arrows) caused by abrasive action of male pleopods.

stage were found to have ovaries that, although not necessarily mature, were always well developed and clearly visible.

The maturity stages of female crabs have been recorded during the course of commercial sampling, using the criteria described above. Two methods have been applied to this data in order to establish the size at maturity of females.

In the first and most common method used in crustacean studies (inter alia Berry, 1973; Pollock & Augustyn, 1982; Watson, 1970), the percentage ratios of mature to immature females in different size classes were compared. The results presented in fig. 5 were compiled from all the female crabs sampled in commercial catches during 1983. They show that the size at 50% maturity is about 84 mm cw.

Somerton (1981) has criticized this method of establishing size at maturity for two reasons. Firstly, because it reflects the relative abundance of adults and

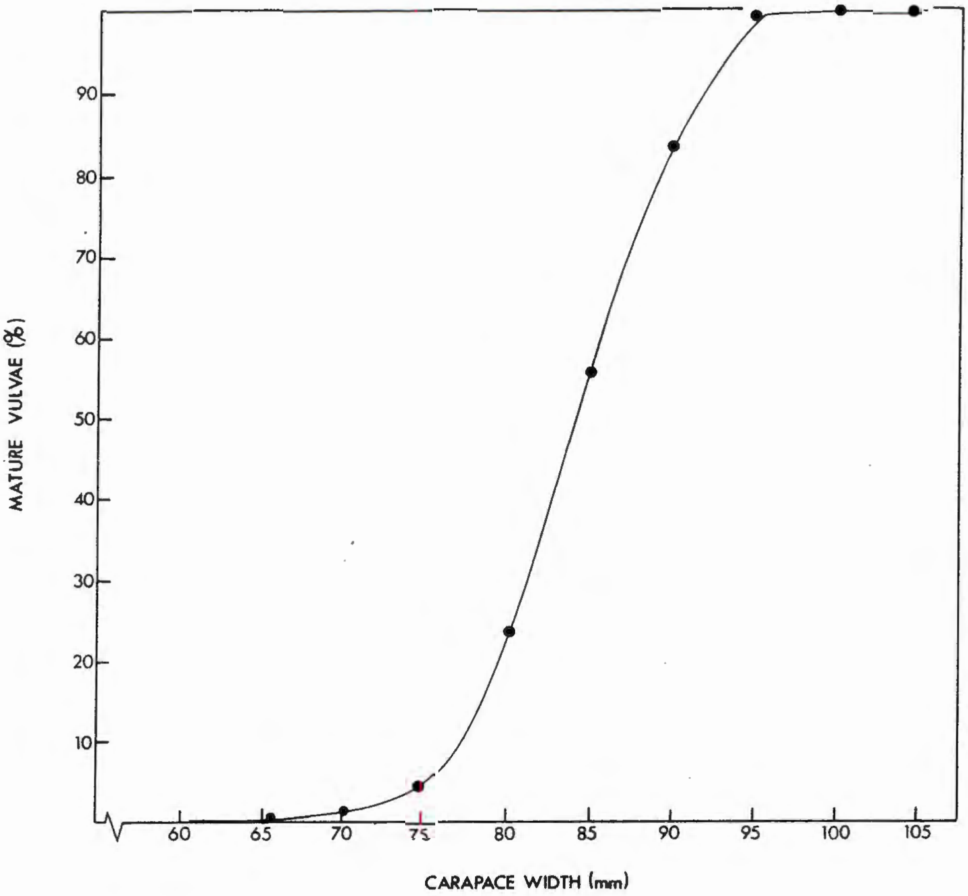

Fig. 5. Percentage of females with mature vulvae per five millimetre size class (n = 3,077).

juveniles; the size at 50% maturity may be distorted by the variability of year-class strenghts. Secondly and of more relevance to the results obtained from fig. 5, the size at 50% maturity can be affected by mortality, in particular the size selective mortality induced by fishing gear.

Virtually the entire red crab catch irrespective of sex is utilised by the commercial fishery. Though data are incomplete, present approximate indications are that 50% gear selectivity stands at 71 mm cw. and 100% at 75 mm cw. (Melville-Smith, unpublished data). It is therefore obvious that the removal by the fishery of the larger mature animals could have led to a deceptive abundance of immature crabs and a consequent lowering of the size at 50% maturity reflected by fig. 5.

There is strong evidence from research sampling and from tagging programme return results (Melville-Smith, unpublished data) that, once female crabs have successfully copulated, they do not moult again in their life time. Similar findings have been reported for seveal other crab species inter alia *Chionoecetes opilio* (O. Fabricius, 1788) (cf. Watson, 1970), *Chionoecetes bairdi* Rathbun, 1924 (cf. Somerton, 1980) and *Callinectes sapidus* Rathbun, 1896 (cf. Olmi, 1984). Should this be the case, it would be more accurate to assess the size at female maturity by establishing the mean size of adult female as proposed by Somerton (1981). Applying the above method to the data used in compiling fig. 5, the size at maturity of female red crabs is 96 mm cw., but again this answer is biased by the selective mortality effect of the fishery.

In an attempt to overcome these effects, the above method was applied to a small sample of mature female crabs (N = 120) taken from an area which has seen very little commercial exploitation (21°15′S 12°27′E). The mean size of the crabs in this sample was 100 mm cw. and it is therefore presumed that this would be the size at maturity of female red crabs in an unexploited stock.

TABLE I

Fecundity of red crabs per size class

Size class mm CW	No. of	Mean no. of eggs per female	SD*	Std.**
70-74	1	106,600		
75-79	nil			
80-84	5	155,900	14,800	6,600
85-89	5	159,500	27,500	12,300
90-94	9	201,700	24,200	8,100
95-99	1	201,800		
100-104	4	260,700	49,000	24,500
105-109	1	349,700		
110-114	2	296,600	36,400	25,700

* SD: standard deviation. ** Std.: standard error of the mean.

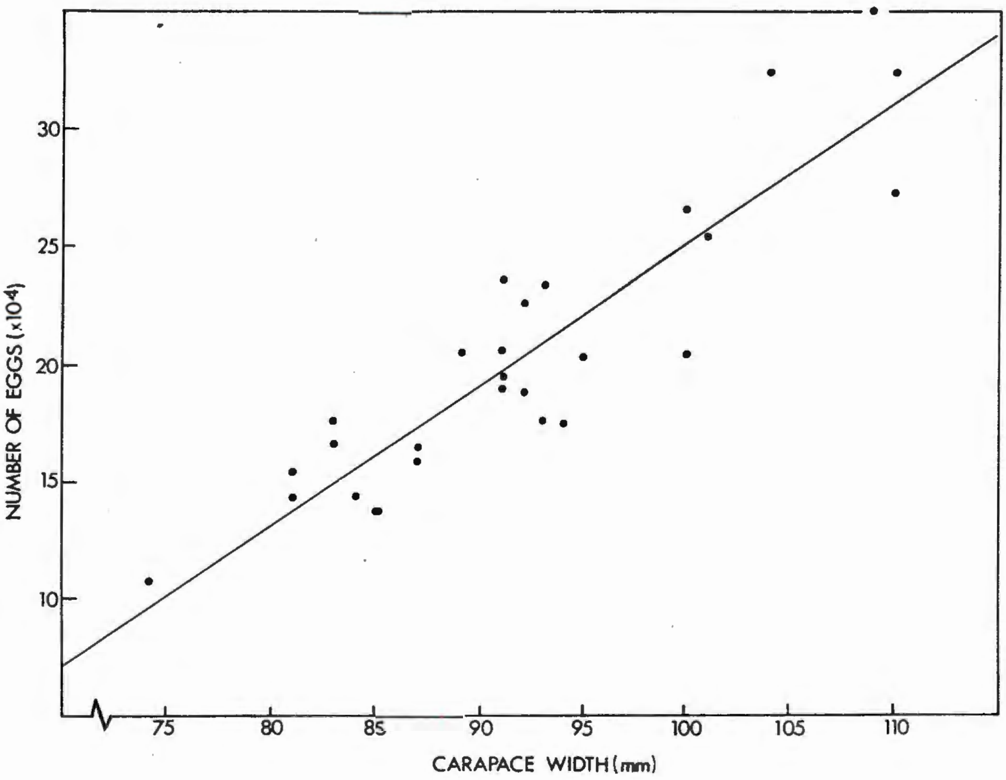

Fig. 6. Relationship between carapace width and number of eggs carried by *Geryon maritae* Manning & Holthuis.

Other workers (Le Loeuff et al., 1978), have suggested that female *G. maritae* attain maturity between 80 and 90 mm cw. off the Ivory Coast. Findings presented by Beyers & Wilke (1980), suggesting that sexual maturity is attained at a size smaller than 62 mm cw. are undoubtedly incorrect.

Egg bearing females

Although a large number of crabs were in a 'mature' reproductive stage (fig. 2), there was an inexplicable paucity of gravid crabs in research and commercial catch samples.

In the course of sampling commercial catches between 1982 and 1984, over 6,890 female crabs (mature and immature animals combined) were measured and examined. Of this total only 7 or 0.1 percent were recorded as being ovigerous. Other researchers working on *G. maritae* have obtained similar disproportionate numbers of gravid females in experimental trap fishing catches (Le Loeuff et al., 1978; Cayre et al., 1979; Dias, personal communication). Le Loeuff et al. (1978) have suggested that gravid crabs may modify their behaviour. They considered that the crabs probably eat sparsely while ovigerous, but conceded that there could be other explanations, such as the crabs being less mobile and therefore unable to climb up the mouth of the traps or their remaining hidden to escape predation.

Bearing in mind the above suggested explanations for the scarcity of gravid crabs, trawling surveys would be a more effective method of capturing egg-bearing crabs. This Institute has conducted a total of five trawling surveys between 1978 and 1982. A wide range of depths covering large areas of the red crab grounds were trawled at different months of the year (April, June, August and September (X2)). Records show that of the 2,403 female crabs caught, only 5 or 0.2 percent were ovigerous. This is a substantially higher proportion than from trap catches, but is nevertheless an extremely low proportion of the population and does nothing to substantiate the theories postulated by Le Loeuff et al. (1978).

Red crabs have been recorded as occurring off Namibia in depths of between 270 m (Macpherson, 1983) to 900 m (Melville-Smith, 1985). As has been mentioned, the sexes show an affinity for different depths, with females tending to be most common in the shallow depths of the species' distribution. The majority of the gravid red crabs which have been sampled to date (∿50) have been caught in shallow 400 to 500 m depths and none have been recorded in this study deeper than 610 m.

Haefner (1978) showed that gravid *G. quinquedens* tended to predominate in the shallower depths of the distribution of that species. He found this distribution to be especially marked for crabs carrying eggs in a late stage of development and suggested that there may be a sound ecological explanation for this distribution. He suggested that crabs with late stage eggs may migrate into shallower, warmer water, thereby enhancing egg development. The same proposal would appear to apply to the female *G. maritae* sampled in this study. Detailed data (Stander, 1964) have shown the temperature at 400 m over the region of the Namibian crab grounds to be about 8°C, compared with temperatures at 600 m of 4,3° to 6,6°C.

It is unlikely that ovigerous red crabs occur in any number shallower than 350 m, as these depths are regularly trawled for hake and no record of such crabs being caught in quantity exists.

In conclusion therefore, the possibility of gravid crabs being scarce because of their migrating either east/west or north/south seems remote. Whether the low numbers are normal for the stock or due to incorrect sampling techniques is not known.

Le Loeuff et al. (1978) and Cayre et al. (1979), have suggested a reproductive season extending from March to July for *G. maritae* caught off Zaire and the Ivory Coast. As has been mentioned, the same trend was not found off the Namibian grounds. Gravid crabs have been recorded in all but four months of the year (December, February, March and May). Likewise, moulting, which appears from observations to be a prelude to fertilisation in maturing *G. maritae* females, has no seasonal pattern (Melville-Smith, unpublished data), thus providing further evidence for a year-round reproductive cycle.

Copulatory behaviour

On numerous occasions two crabs of opposite sex have been observed paired. In all cases the female has been in a soft-old intermoult shell state (i.e. about to moult) and has been carried underneath the male as described earlier under male sexual maturity. Copulation has only been observed on one occasion. The female was newly moulted and was carried around with only the pleopods of the male in the vulvae of the female keeping the two animals together. The pair were observed in a copulatory position for more than four hours, though it is not known for how long before this observation they had been in that position. No post-copulatory pairing has been noted for *G. maritae*.

Fecundity

Egg counts were made on 28 specimens and carapace size and fecundity data were regressed (fig. 6). The number of eggs per female increases with increasing carapace width (table I, fig. 6) and can be described by the relationship

$$y = 5993.0\,x - 348253.9$$

where y = fecundity and x = carapace width (mm). The correlation coefficient (r) was 0.9000.

Based on commercial sampling length frequency data obtained during 1983, the mean size of mature female crabs was 96 mm cw. From the relationship above, a crab of this size would be expected to carry approximately 227,000 eggs.

No comparative fecundity data exists for *G. maritae* in other areas; however, egg counts have been made on *G. quiquedens* (Hines, 1982). Using the data for *G. quinquedens* presented by Hines (1982), it can be calculated that his sample of 17 animals had egg counts ranging from 126,000 to 191,000, similar to the range (107,000 to 350,000) found for *G. maritae* in this study.

The logical extension of fecundity data is to estimate the relative fecundity of different sized female crabs, taking into account the number of eggs per brood, the time interval between broods and the number of broods that a crab is capable of producing in her lifetime. As noted earlier, there is an inexplicable infrequency of berried crabs in the samples and this has prevented the latter two issues from being resolved.

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PAPER 2:

A growth model for the deep-sea red crab (*Geryon maritae*) off South West Africa/Namibia

Crustaceana: in press

A GROWTH MODEL FOR THE DEEP-SEA RED CRAB (*GERYON MARITAE*) OFF SOUTH WEST AFRICA/NAMIBIA

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ZUSAMMENFASSUNG

Von 1979 bis 1986 wurden etwa 1660 markierte *Geryon maritae* aus kommerziellen Fängen vor Namibia wiedergewonnen. Von diesen Tieren zeigten 518 Hinweise darauf, daß sie seit der Markierung gewachsen waren und sich gehäutet hatten. Die prozentualen Wachstumsraten weiblicher Exemplare waren signifikant niedriger als die von Männchen ($P<0{,}01$). Für beide Geschlechter ist eine Abnahme der Wachstumsraten in Abhängigkeit von der Körpergröße zu verzeichnen. Die errechneten Zwischenhäutungsperioden stehen in direktem Verhältnis zur Körpergröße zu verzeichnen. Die errechneten Zwischenhäutungsperioden stehen in direktem Verhältnis zur Körpergröße. Männchen neigen bis zur ersten Geschlechtsreife zu längeren Zwischenhäutungsperioden als Weibchen. Danach scheinen sich die Weibchen seltener zu häuten. Ein hypothetisches Wachstumsmodell zeigt, daß die Männchen etwa ab dem siebten Lebensjahr kommerziell genutzt werden können. Vollständig rekrutierende Jahrgänge treten aber erst mit Eintritt der Geschlechtsreife ab dem neunten Lebensjahr auf. Ein Vergleich mit Literaturangaben über das Wachstum dreier Flachwasser-Krabbenarten zeigt, daß *Geryon maritae* verhältnismäßig langsam wächst.

INTRODUCTION

It is essential to have an understanding of growth and age/size relationships, if one is to apply equilibrium yield models to the management of a fishery. In crustaceans, growth is discontinuous and each species can therefore be simplistically described by a model incorporating (i) the length of time between moult intervals and (ii) the increase in carapace size between moults. The model is also generally dependent on the animal's sex and the stage of its life cycle (whether larval, juvenile or adult), as well as changes in environmental conditions and the availability of food.

Growth models of varying refinement exist for a number of decapod species, inter alia *Cancer magister* Dana, 1852 (Butler, 1961), *Cancer pagurus* L., 1758 (Hancock & Edwards, 1967), *Paralithodes camtschatica* (Tilesius, 1815) (McCaughran & Powell, 1977), *Homarus gammarus* (L., 1758) (Conan & Gundersen, 1979) and *Chionoecetes bairdi* Rathbun, 1924 (Donaldson et al., 1981). In this paper, a similar model is attempted for the deep-sea red crab, *Geryon maritae* Manning & Holthuis, 1981, which is commercially fished on the continental slope off the Namibian coast from west of Cape Cross (~21° 50′S) to the Angolan border (17°15′S).

In addition to its prime objective, which was its application to the management of the Namibian red crab stock, this study provided a rare opportunity to examine in situ growth of a relatively deep-water crustacean. Because of logistical problems associated with deep-water work, there exists far more speculation than information on this topic (see Roer et al., 1985).

METHODS

Tagging. — During the period September 1979 to February 1984, a total of 10 246 crabs was tagged on the Namibian red crab grounds, in depths ranging from 400 to 900 m. Floy FT2 dart tags were inserted through the epimeral suture with the toggle lodged in the branchial cavity, permitting the crab to moult without losing the tag.

For each crab that was tagged, a record was made of its position and depth at release, tag number, carapace width (CW), sex, shell state, whether appendages were missing and, in the case of females, their state of maturity based on the shape of the vulvae (Melville-Smith 1987). The animals were released at the same depth and near the position at which they were captured, using a cage specially designed and constructed for this purpose.

The grounds on which the crabs were released were fished year-round by five Japanese crab vessels. Tagged crabs caught in the traps set by these vessels were retained and returned together with details regarding their position, depth and date at recapture.

Data analysis. — Standard techniques were used to describe the average growth increment and intermoult period for crabs of varying carapace width. This study relied on tagged crabs returned by the commercial fishery and, because the gear was biased against catching small crabs, there is a gap in growth data for crabs smaller than 60 mm CW. This has necessitated extrapolation into the smaller size classes.

Although crabs were tagged in several areas of the Namibian red crab grounds, there were insufficient data to permit an analysis of possible differences in growth rate by area.

Growth increments. — The growth factor or percentage growth increment between successive moults was calculated by plotting the percentage CW increment against premoult CW. Using this method, those crabs that had moulted more than once while at large could be identified and separated from those moulting once for further growth-per-moult analysis.

The relationship between pre and post moult carapace width (Hyatt growth curve) was established separately for males and females as described by Somerton (1980). The slope of the Hyatt growth curve changed near the size at which sexual maturity is attained by male crabs. The point at intersection of the resulting two linear regression lines (for juvenile and adult males) was found using a technique described by Somerton (1980), whereby a premoult size is found, which minimises the residual sum of squares pooled for both lines.

Intermoult period. — Intermoult periods have been graphically presented for males in 5 mm CW size increments, based on the length of time that crabs in the various size intervals were at large before moulting. A theoretical method (whereby the number of moults per days at large was regressed against size) has been used to calculate an equation describing the relationship between intermoult period and carapace width, and the resulting regression line has been compared with the observed data.

Less emphasis has been placed on female intermoult period data, for reasons which are dealt with under results. A table showing maximum lengths of time immature female crabs were at large without moulting has been used as a very generalised means of comparing differences in intermoult period between the sexes.

RESULTS

Growth increments. — Growth factors for all the male crabs that had grown are presented in fig. 1a and those for females in fig. 1b. From fig. 1a, it is clear that the points lying between growth increments of 35 to 60 per cent are for male crabs that had moulted twice while at large. Double moult increments were not recorded for any female. Male crabs showing double growth increments were excluded from the data and predicted relationships between growth increment and size then fitted for male and female animals (fig. 1a, b). The equations for the fitted regressions (fig. 1a, b) are:

$y = -0{,}1167x + 31{,}75$ for males and

$y = -0{,}2016x + 32{,}99$ for females,

where y = the growth factor or percentage moult increment between pre and post moult carapace widths and x = the premoult carapace width in mm. The r values for the equations above were 0,60 and 0,50 for males and females respectively.

The regressions in fig. 1a and b were compared statistically with a view to combining the male and female data. Male crabs had, however, larger growth increments than females and the difference between the regressions for the sexes was significant ($P<0{,}01$). Male and female data were therefore kept separate in all further analyses.

A Hyatt growth diagram for male red crab is presented in fig. 2a and described in table I. The two regression equations for male growth in table I have their point of intersection, as calculated by Somerton's (1981) method, at 93 mm premoult CW. This point of intersection where growth changes, is generally considered to be the point at which sexual maturity is attained. In the case of *G. maritae*, all males larger than 80 mm CW have been found to be mature (Melville-Smith, 1987). The difference, therefore, between the theoretical and observed estimates of the size at male maturity was approximately one moult.

A Hyatt growth curve for female crabs is presented in fig. 2b. In contrast with that for males, the female growth curve is best described by a single linear relationship throughout the life of the crab (table I). The reason for this is that very few females have been shown to moult after attaining maturity (which generally occurs from about 84 mm CW and larger (Melville-Smith 1987)) and consequently insufficient data exist as to whether their growth increments change once maturity is attained.

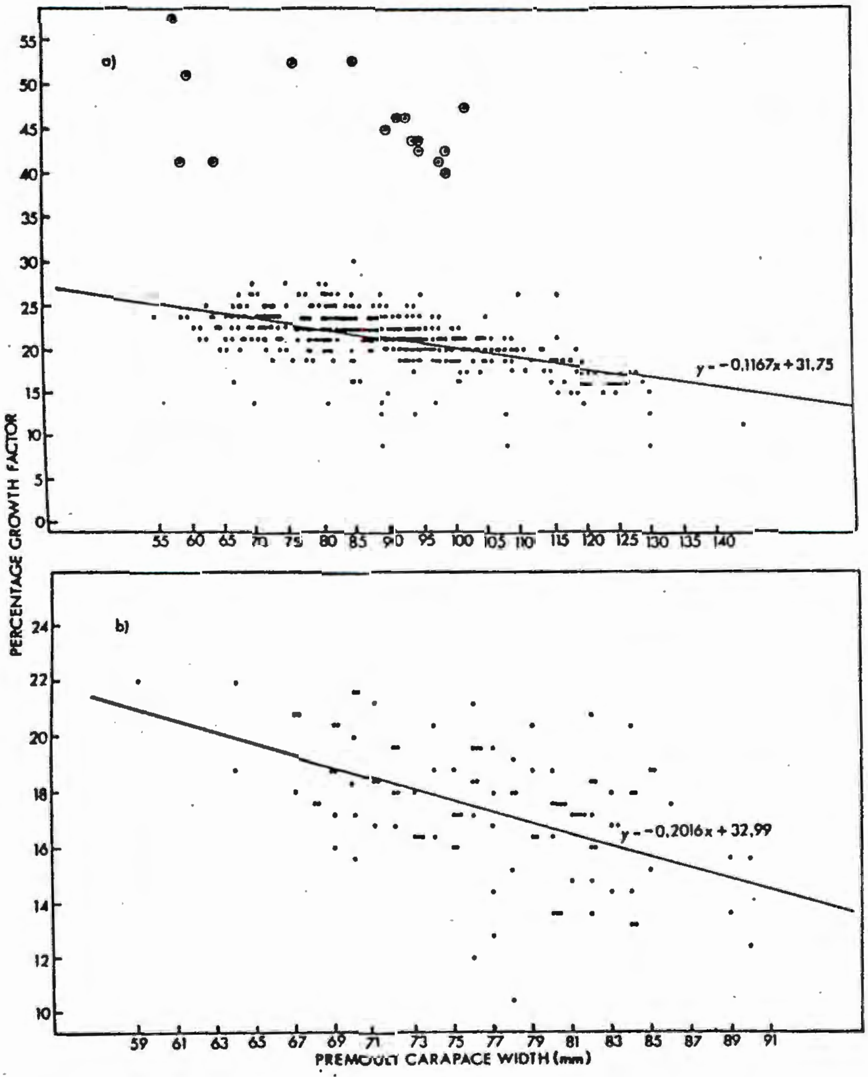

Fig. 1. Growth factors (percentage moult increment) for (a) males and (b) females of different premoult lengths. Circled observations in (a) are believed to be double moults and have been excluded from the regression.

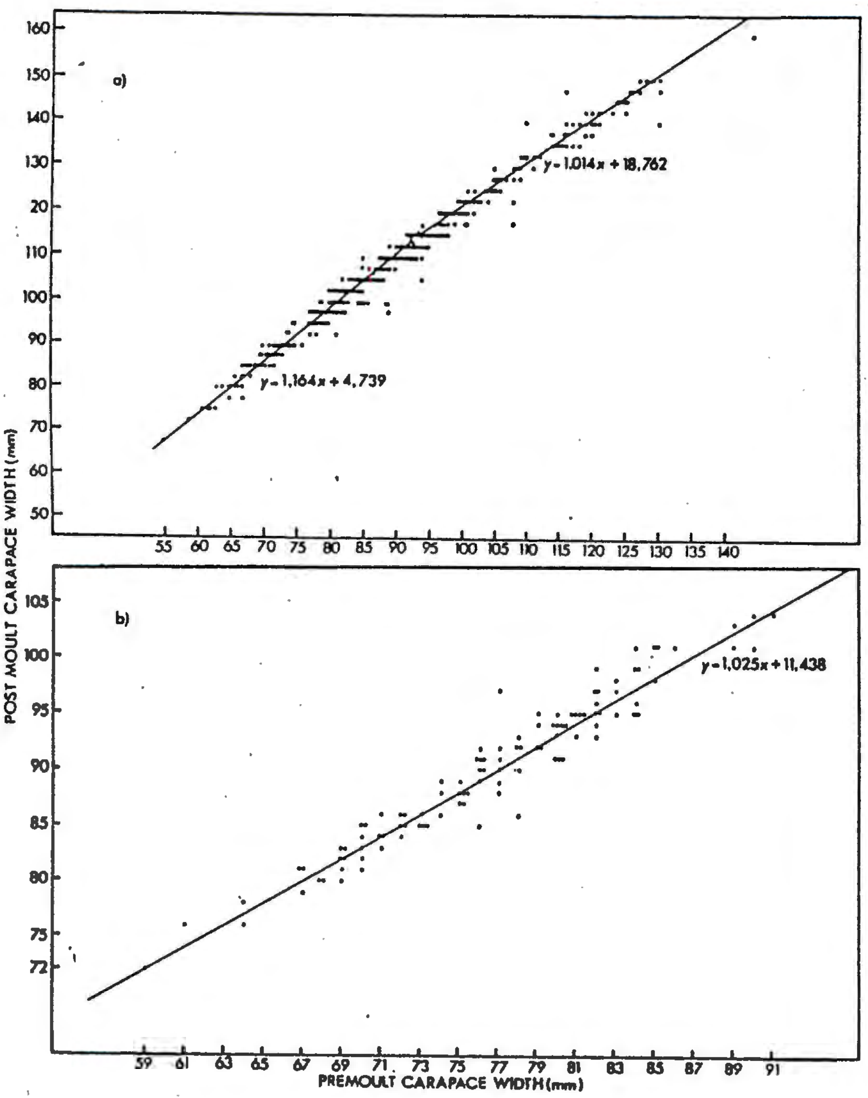

Fig. 2. Hyatt growth diagrams for (a) males and (b) females.

TABLE I

Regression equations describing the Hyatt growth curve for *Geryon maritae*

Sex	Size class (mm)	Regression	r value
Male	55 to 93	$y = 1,164x + 4,739$	0,96
	>93	$y = 1,014x + 18,762$	0,98
Female	>59	$y = 1,025x + 11,438$	0,97

Intermoult periods. — Though data on intermoult periods for females were obtained for *G. maritae*, they have not been diagrammatically presented in this report because (i) they only cover a limited size range (between 59 and 91 mm premoult CW) and (ii) from a fisheries management point of view, they are of less importance than the males, because their contribution to the total crab catch is small both in terms of numbers and mass caught (Melville-Smith, unpubl. data). Instead, a detailed analysis has been made of the more comprehensive male data (figs. 3 and 4) and comparisons have been drawn in the

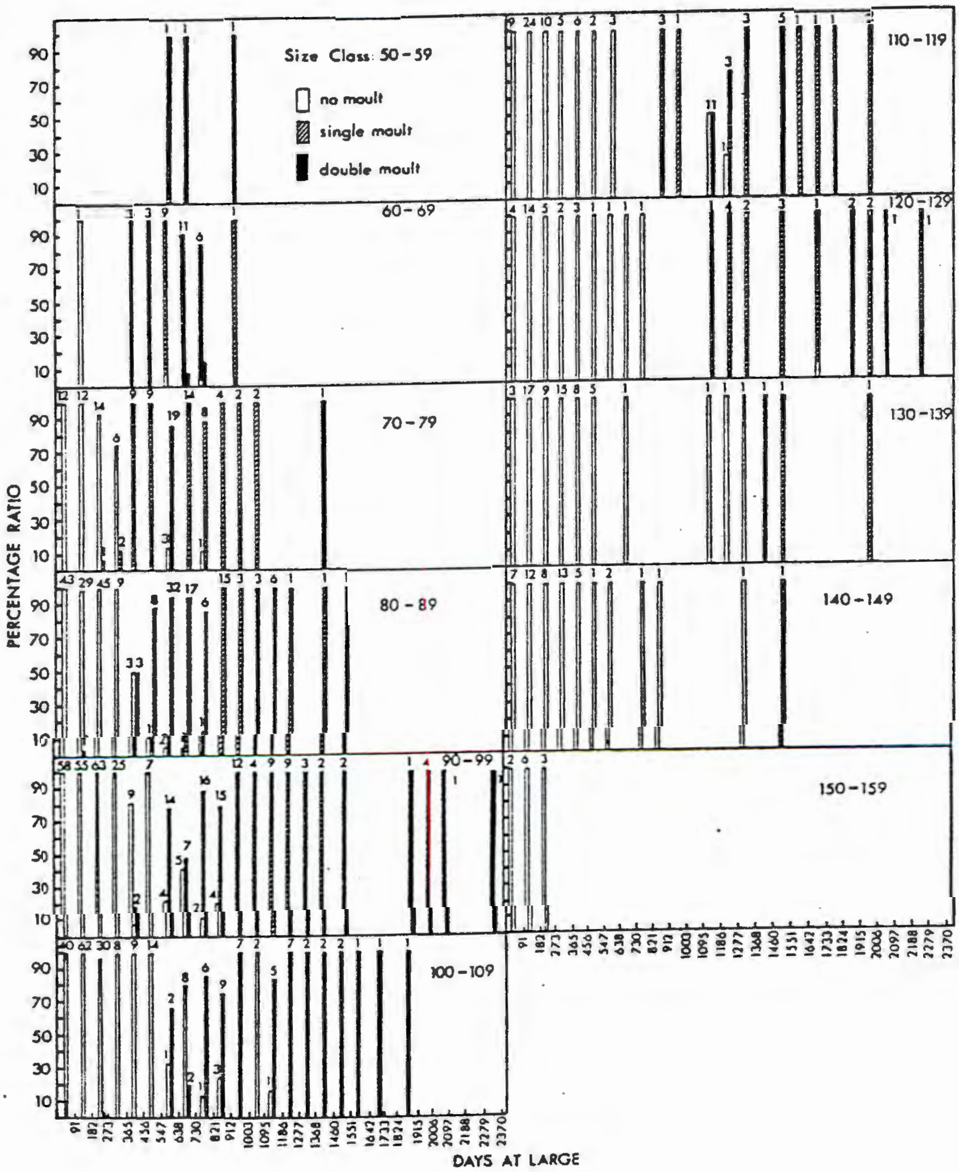

Fig. 3. Percentage moulted : unmoulted ratio of male crabs plotted against time for 10 mm carapace width size classes. Numbers of recaptured crabs appear above each bar.

discussion between these results and those observed for the females.

Crab returns for males are presented in fig. 3. From this figure two points are obvious, (i) the intermoult period increased as the size of the crabs increased, and (ii) after tagging relatively long periods passed before the first moulted crabs were recovered.

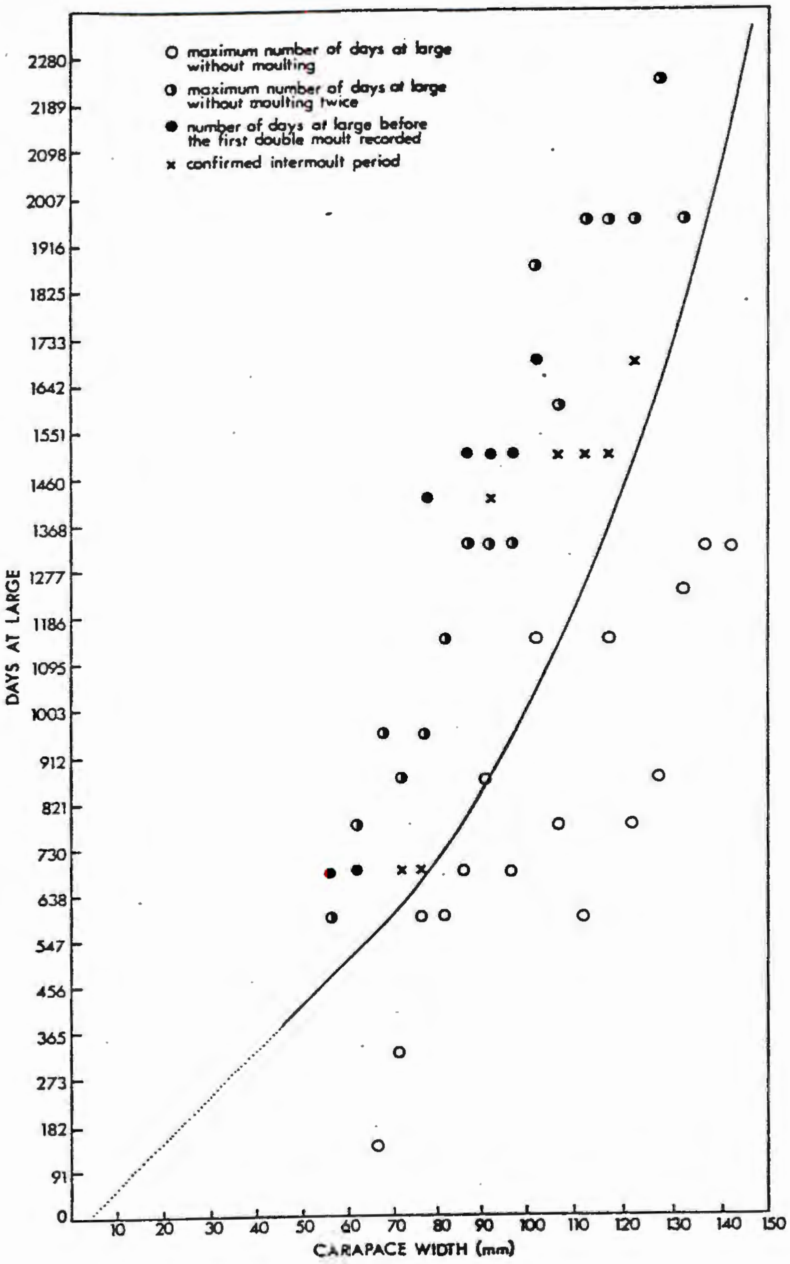

Fig. 4. Estimated intermoult periods for males of different sizes. The dotted section has been fitted by eye.

The comprehensive data for crabs over 60 mm CW in fig. 3 have been separated into 5 mm size classes and condensed into a more manageable format in fig. 4. This figure has been used to calculate the predicted intermoult period for crabs of varying sizes by assuming that any relationship between premoult size and days between moults should (i) not be less than the recorded maximum number of days at large without moulting and (ii) not be more than the number of days at large before the first double moult was recorded.

The above data points (presented in fig. 4) give no clear indication as to which curve would best describe the relationship between premoult size and intermoult period. Data from a variety of shrimp, crab and lobster species were used by Mauchline (1977), to show that this relationship is usually a linear one, but it is not possible to draw a straight line through the points plotted in fig. 4, without violating the two maxims in the previous paragraph.

A theoretical method has been employed to examine the relationship between intermoult period and carapace size, by regressing moults per days at large against carapace width (in practice only one moult can be used, because as the animal increases in size, so too does the intermoult period). The relationship (for crabs over 50 mm CW) can be described by the equation $y = 0{,}006\ e^{-0.018x}$ where y is 1/days at large, x is carapace width in mm and the r value is 0,68.

The above regression has been plotted in fig. 4 and shows a good fit with the observed data, by only passing outside of one point-indicating a crab that had been returned without having moulted and by not passing inside of any points representing crabs that recorded double moults.

Since some crabs completed double moults, one can obtain an indication of the accuracy of the regression line (fig. 4), by plotting the minimum number of days taken by those crabs to complete the first of their two moults. The carapace size at the first of a double set of moults can be estimated for each size class using the Hyatt curve (fig. 2a). These points, as plotted in fig. 4, represent known intermoult periods i.e. periods during which a crab had undergone a full moult cycle prior to recapture. It can be seen that the above points all fall inside of and reasonably close to the regression line (these points obviously also include an indeterminable number of days prior to the first moult and prior to capture after the second moult).

Growth model. — The ultimate aim of this study was to construct a growth model that could be used to predict various growth parameters important for management of the stock. As has been noted, good data exist for crabs of a size which appear in the commercial catch but not for smaller animals. In these smaller sizes it has been necessary to make use of juvenile growth data for crabs <20 mm CW, which exist for the closely related species *Geryon quinquedens* Smith, 1879, and to extrapolate the data in this study for *G. maritae*, to include crabs of 20 to 55 mm CW.

The size at which *G. maritae* metamorphoses into juvenile crabs is unknown, but is probably close to that documented for the west Atlantic species (*G. quinquedens*). The two species resemble each other so closely, that they were confused with each other up until 1981 (see Manning & Holthuis, 1981). Furthermore, they reach approximately the same sizes, live at about the same depths and show similar behavioural characteristics (table II), all factors that justify comparisons in growth between the species.

Kelley et al. (1982) have estimated that *G. quinquedens* requires between 23 and 125 days from hatching until the megalopa settles, depending on water temperature. From fig. 1 in Van Heukelem et al. (1983), it appears that the species settles out from its larval stages at 4 mm CW and moults five times before reaching 22 mm CW. Although growth factors are apparently high (~50 per cent) for three of the five moults, the factors for the last two moults are about 30 per cent, which agrees with the predicted growth factor for *G. maritae* of that size from the relationship in fig. 1a.

A growth model for *G. maritae* has been predicted in table III, by assuming that moult increments and intermoult periods for *G. quinquedens* and *G. maritae* are similar for animals <20 mm CW in both species. Growth increments in the larger size classes have been calculated from the relationships presented for figs. 1a and 2a. It was necessary to extrapolate the intermoult period data for juvenile crabs in the size range 5 to 50 mm CW by eye (fig. 4), because, owing to the lack of data for these size classes, the predicted relationship for crabs >50 mm CW did not fit in the smaller size ranges.

DISCUSSION

Based on the theoretical growth model in table III and mesh selectivity of commercial fishing gear (Melville-Smith, 1986), red crab first become available to the fishery in their sixth year. The crabs are theoretically fully recruited to the fishery in their ninth year and, based on size at maturity data (Melville-Smith, 1987), most would attain sexual maturity in that same year (12th post-larval instar). The largest crab measured to date was 165 mm CW, which would suggest that it was over 25 years old and probably in its 15th or 16th post-larval instar.

The predicted model presented in table III and discussed above, is based on increments and intermoult periods recorded for male crabs. As explained under results, the recaptured female crabs that showed growth fell into a relatively narrow size range. To have used these data to construct a separate growth model for females, would have entailed extrapolating over almost half of the total possible length for that sex. An extrapolation of that magnitude was considered unacceptable.

TABLE II

Comparisons of some morphological and behavioural characteristics of *Geryon quinquedens* (off north-eastern U.S.A.) and *Geryon maritae* (off Namibia)

Parameters	*Geryon quinquedens* observations	Source of information	*Geryon maritae* observations	Source of information
Depths of high red crab concentrations	320-640 m	Wigley et al., 1975	400-900 m	Melville-Smith, 1985
Temperatures at above depths	5-8°C	Wigley et al., 1975	4-8°C	Stander, 1964
Maximum density estimate	382 crabs ha^{-1}	Wigley et al., 1975	350 crabs ha^{-1}	Melville-Smith, 1985
Depths at which females predominate	320-503 m	Wigley et al., 1975	<400 m	Beyers & Wilke, 1980
Maximum size male and female sampled	142; 121 mm CW	Wigley et al., 1975	165; 120 mm CW	Melville-Smith, 1987
Size at which most females mature	80-91 mm CW	Haefner, 1977	84-100 mm CW	Melville-Smith, in press

TABLE III

An estimated age at size/mass relationship for male *Geryon maritae*. Reliable mass figures are not available for animals in the small size ranges

Instar no.	Carapace width (mm)	Approximate mass (g)	Predicted age (yrs)
1	4		
2	6		0,05
3	9		0,22
4	13		0,46
5	17		0,82
6	22		1,39
7	28		2,01
8	36	13,6	2,83
9	46	29,5	3,87
10	58	61,4	5,17
11	72	121,5	6,83
12	89	237,1	9,10
13	108	436,7	12,29
14	128	746,6	16,86
15	149	1205,8	23,53
16	170	1828,2	33,27

Nevertheless, one generalisation that can be made from the data recorded for females is that the mean growth increments were smaller than those for males of the same size. These differences in increments may be related to the fact that the majority of females recaptured after moulting in this study had moulted to maturity, and this possibly resulted in some energy being channeled away from growth into reproduction. A similar decrease in the rate of growth after the attainment of maturity, was noted for *Paralithodes camtschatica* by McCaughran & Powell (1977).

TABLE IV

Maximum number of days at large after tagging without having moulted as recorded for immature females in different size classes

Size class (mm)	Days at large	Number returned unmoulted
60-69	441	4
70-79	364	34
80-89	456	45
90-99	241	10

Another interesting difference in growth between the sexes was that intermoult periods for immature females tended to be shorter than for males (compare data for females in table IV with those for males in fig. 4). The reason for this may be that the sex ratio of the population is strongly influenced by depth. Beyers & Wilke (1980) showed that off the Namibian coast *G. maritae* females dominate water less than 400 m, while males tend to be found in deeper water down to 900 m. The temperatures over these depth intervals differ by ~4°C (from ~8°C at 400 m to ~4°C at 900 m (Stander, 1964)) and, since temperature is the most important extrinsic factor affecting intermoult period (Hartnoll, 1982), one would expect growth to be faster for the animals in the shallower water.

Melville-Smith (1987), has recently speculated as to whether female red crabs moult once they have attained maturity and successfully mated. This study has shown that a small number of recaptured females (three or 1,6 per cent) did moult after being tagged as mature animals. It therefore appears that mature females are capable of moulting more than once, but that there is probably a lengthy interval between moults. The longest period over which a mature female remained unmoulted was 1217 days (3,3 years). The fact that few females reach 110 mm CW, suggests that it is unlikely that they moult more than twice after maturity.

A comparison of male and female growth might therefore be expected to show that females grow slightly faster than males up to the point that they attain maturity, but that thereafter their growth is extremely slow.

Growth, particularly intermoult periods of juvenile red crab, is likely to remain a difficult problem to solve. A considerable quantity of juveniles larger than 13 mm CW was sampled from the gut contents of a predatory fish *Ebinania costaecanariae* (Cervigón, 1961) during the course of this study, but because of the asynchrynous spawning pattern of the adults no distinct year-classes were discernible. The numbers of juveniles sampled were insufficient to descrimate modes for successive instars from a size frequency histogram.

There is little information about growth rates and longevity of deep-water crustaceans in the literature. General impressions, based on Mauchline (1972, 1980), Omari (1974) and Childress & Price (1978), are that the longevity of these animals is considerably greater than for shallow-water species. The results from this study tend to confirm these opinions. Present data have shown the Namibian red crab to have an estimated age-at-maturity and longevity close to double similar estimates for some shallower-water species, such as the Alaskan king crab *P. camtschatica* (see McCaughran & Powell, 1977), the Pacific edible crab *Cancer magister* (see Butler, 1961) and tanner crab *Chionoecetes bairdi* (see Donaldson et al., 1981). The above comparisons do not, however, take into account that the latter crabs all live at mean temperatures warmer than those measured on the Namibian red crab grounds, a factor which might well account for at least some of the observed growth difference.

As stated under methods, *G. maritae* has an aseasonal moult cycle. Of interest in this regard is that trap and trawl catches made over different periods throughout the year have regularly sampled moulting females but, by contrast, have seldom caught males in a moulting condition. The fact that there is no moulting pattern for females is in line with the aseasonal reproductive cycle discussed in Melville-Smith (1987) and is therefore not unexpected. Why only females in a moulting condition should appear in catches is not clear, but it may be associated with the mating behaviour of the red crab. In *G. maritae*, copulation takes place immediately after the female has moulted and, for several days prior to mating, the male carries the premoult female under his thorax as described by Melville-Smith (1987). It is therefore possible that many moulting females obtained from trap catches were carried into the traps by males.

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PAPER 3:

Tagging study reveals interesting red crab (*Geryon maritae*) movements off Namibia (South West Africa)

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Short Note

Tagging study reveals interesting red crab (*Geryon maritae*) movements off Namibia (South West Africa)

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During the period 1979 to 1984, a total of 10246 red crabs were tagged and released in three areas on the Namibian commercial red crab grounds (which fall roughly between latitudes 17°12′S and 22°00′S and depths of 400 and 900 m). This short note reports some interesting and unexpected movements revealed by recaptures. *Geryon maritae* movement and its relevance to the Namibian fishery is discussed more fully elsewhere (Melville-Smith, 1987).

Chi-square contingency tests on a portion of the data showed that large male crabs (≥105-mm carapace width) moved significantly farther than small males do $P < 0{\cdot}01$), but considering that the distances ranged by males of all sizes were relatively limited (only about 10 % moved more than about 36 km), the data were not separated by size.

The movements of males were compared with those of immature females (the maturity of the females was established according to the method described by Melville-Smith (in press)), but no significant difference was found between these two groups ($P > 0{\cdot}50$), and they were therefore combined and tested against the distances moved by mature female crabs. This latter group was found to move significantly farther ($P < 0{\cdot}001$) than the rest of the population and, in line with this finding, they were treated separately in further analyses.

All usable recapture data collected over a six-year period are presented in Figure 1. In addition to showing the extent of the distances covered by mature females (approximately 32 % moved more than 100 km, compared with only 3 % of the males and immature females), the figure also shows that both sexes tended to move northwards and then generally dispersed farther from their point of release than those that went southwards. Though numerous tests were performed on the data, no correlation was found between season and extent or direction of movement.

The above trends, together with other data, suggest that mature female *Geryon maritae* may be more active foragers and as a result cover greater distances than males and immature females. It is further postulated that the northern Namibian crab grounds are environmentally more suited to red crab (as is evident from higher catch per unit effort figures in the north than the south (Melville-Smith, unpub. data)) and that crabs moving northwards are therefore more likely to remain or even wander farther north than those moving southwards. The maximum recorded distance covered by a crab during this study was 380 km for a mature female crab which moved northwards.

The mean velocity of movement for the two categories of crabs discussed in this note is presented in Table 1. The mature females moved faster than the other crabs, in line with the greater distances that they covered while at large. For obvious reasons, the true velocity of movement when a crab is moving in a specific direction is likely to be much greater than the figures presented in Table 1. This can be illustrated by the fact that several mature females covered considerable distances (100 to 180 km) at mean velocities of up to 2 km per day.

It is worth noting that some of the movements revealed for *Geryon maritae* by this study are similar to those that have been inferred by Hepper (1971) to explain carapace width frequency distributions of male *Geryon tridens* trawled off the west Irish coast. He noted that the mean size increased over a 90-km band from west to east and suggested that the main population lay to the east and "that the older, and hence larger, individuals move out from this centre". This hypothesis fits the observation that large *Geryon maritae* males move significantly farther than small ones, but superficially it does not appear to fit the fact that males do not tend to move particularly far from their point of release.

However, two factors have to be borne in mind when evaluating the tagging results presented in Figure 1. First, the majority of recaptures were taken within the first year of their release, and secondly, *Geryon* crabs are slow growing (maximum intermoult periods recorded for adult males are in excess of six years for *Geryon quinquedens* (Lux *et al.*, 1982) and over three years

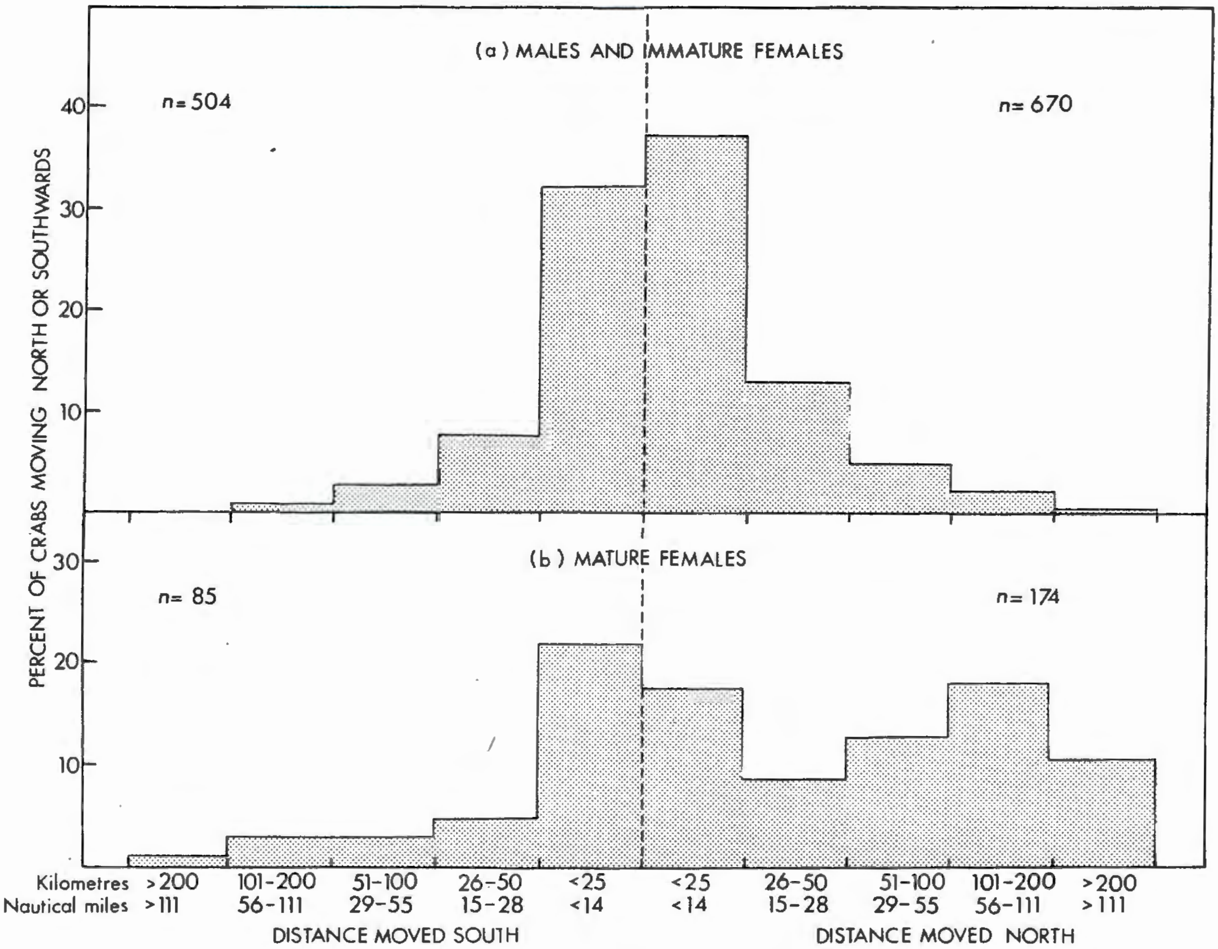

Figure 1. Distances moved between tagging and recapture by (a) males and immature females and (b) mature females.

for *Geryon maritae* (Melville-Smith, unpub. data). Over the long time intervals between moults, male crabs may cover substantial distances (for example, the mean distance moved by male *G. maritae* at large for longer than four years was 65 km). Bearing this in mind, trends in population size frequency such as were noted by Hepper (1971) are quite possible.

Table 1. Mean velocities in northward and southward directions, calculated from tag recoveries over a three-year period. Data taken from a tagging survey conducted during October 1982.

Males and immature females		Mature females	
Southwards (km day^{-1})	Northwards (km day^{-1})	Southwards (km day^{-1})	Northwards (km day^{-1})
0·05 (n = 284)	0·05 (n = 332)	0·11 (n = 52)	0·46 (n = 119)

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PAPER 4:

Movements of deep-sea red crab (*Geryon maritae*) off South West Africa/Namibia

S. Afr. J. Zool. 1987, 22(2)

Movements of deep-sea red crab (*Geryon maritae*) off South West Africa/Namibia

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Of 10 246 red crabs tagged between 1979 and 1984 on the continental slope of Namibia, a total of 1 604 were recaptured by commercial fishermen. Three tagging methods were tested. The most effective method was by inserting the tag through the epimeral suture. Though tagged crabs were released over a range of depths (from 400 to 900 m), the distances that they covered while at large were found to be unrelated to the depth at which they were released. No significant differences were found for distances moved by males compared to immature females, but differences ($P < 0{,}01$) did indicate that large males ($\geqslant$ 105 mm carapace width (CW)) move farther than small males. Mature females moved significantly farther ($P < 0{,}001$) than the other crabs and over 32% moved > 100 km. The farthest distance covered by a single crab was 380 km. No seasonal trends regarding distances or direction moved were noted for either sex or size groupings examined. Mature females did show a tendency, although unrelated to season, to move northwards. Movements of crabs by depth suggested that, although crabs of all sizes and sexes move freely between depths, small males (< 100 mm CW) do tend to favour deeper water than larger males and *vice versa*. Female crabs tend to favour shallow depths and, of those tagged at 800 and 900 m, over 60% were recaptured shallower than 700 m. Based on the results of this study, it is considered that the movement patterns of *G. maritae* could best be described as nomadic. A possible reason for the fact that mature females display different movement patterns compared to other crabs in the population is discussed, as are possible implications to the fishery of crab movements between Namibia and Angola.

Uit 'n totaal van 10 246 rooikrappe, tussen 1979 en 1984 op die vastelandse helling van Namibië gemerk, is altesaam 1 604 deur handelsvissers terugbesorg. Drie merkmetodes is beproef en een, waarvolgens die merk deur die epimere naat gesteek is, is heelwat doelmatiger as die ander twee bevind. Hoewel krappe op verskillende dieptes (van 400 tot 900 m) gemerk is, het die afstand deur hulle afgelê in die see nie verband gehou met hul diepte by vrylating nie. Daar is geen beduidende verskille gevind vir afstande afgelê deur mannetjies, vergeleke met onryp wyfies nie, maar verskille ($P < 0{,}01$) het daarop gedui dat groot mannetjies (rugdopwydte $\geqslant$ 105 m) verder as klein mannetjies beweeg. Geslagsryp wyfies het aansienlik verder ($P < 0{,}001$) as alle ander krappe in die bevolking beweeg, en van al die gemerkte geslagsryp wyfies wat teruggestuur is, het meer as 32% > 100 km beweeg. Die grootste afstand deur 'n enkele krap afgelê, was 380 km. Wat die afstand of rigting beweeg betref, is geen seisoenmatige tendense opgemerk vir enige van die geslags- of groottegroeperings wat ondersoek is nie, maar geslagsryp wyfies het 'n nie-seisoenmatige neiging getoon om noordwaarts te beweeg. Bewegings van krappe volgens diepte het daarop gedui dat, alhoewel krappe van alle groottes en geslagte vryelik tussen dieptes beweeg, klein mannetjies (rugdopwydte < 100 mm) wel geneig is om dieper water te verkies as groter mannetjies, en andersom. Wyfiekrappe gee meesal voorkeur aan vlakker water en, van dié wat by 800 en 900 m gemerk is, is oor die 60% weer vlakker as 700 m gevang. Op grond van die resultate van hierdie studie, kan gesê word dat *G. maritae* die beste by 'n nomadiese tipe van gedragspatroon inpas. 'n Moontlike rede vir die feit dat geslagsryp wyfies se bewegingspatrone verskil van dié van ander krappe in die bevolking, asook moontlike implikasies vir die vissery, van krapbewegings tussen Namibië en Angola, word bespreek.

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The deep-sea red crab, *Geryon maritae*, has a wide distribution ranging from Spanish Sahara to the Valdivia Bank off the Namibian coast (Manning & Holthuis 1981). Over large areas of this distribution it occurs in commercially exploitable quantities and this fact has contributed to the considerable amount of scientific attention which the species has received over recent years.

Despite a substantial amount of literature dealing with its general ecology and the potential for its exploitation off the African west coast [*inter alia* Dias & Seita Machado 1973 (Angola); Cayré & Bouchereau 1977 (Zaire); Le Loeuff, Cayré & Intés 1978 (Ivory Coast); Beyers & Wilke 1980 and Melville-Smith 1985 (Namibia); Gaertner, Le Hir & Sylla 1985 (Senegal)], there has been no published research on the extent of its movements, or whether any migration patterns exist. There consequently is no knowledge about the exclusivity of any part of the crab's distribution to particular territorial waters. Naturally this has important consequences with regard to stock assessments and the setting of catch quotas.

In order to obtain some understanding of the movements (and other biological information) of red crab off the Namibian coast, several tagging surveys were initiated during the period September 1979 to February 1984. In the course of these surveys, a wide size range of red crab was tagged in several areas of the Namibian crab grounds. In the analysis of the results, particular attention was paid to the possibility of differences existing in the magnitude and direction of movements undertaken by the different size classes and sexes.

Materials and Methods

Tagging has long been recognized as an important means of obtaining reliable data on growth and migration. The early tagging methods, such as those described by Cronin (1949), did not permit the animal to survive moulting and consequently valuable information on growth was lost. More recent tagging studies have employed techniques whereby the tag is inserted into an area of the crab's anatomy which allows the tag to be retained when the exoskeleton splits along the suture lines at moulting (Anon. 1955; Edwards 1979; Sullivan 1979).

In the first of the series of tagging surveys reported in this paper (September 1979), three tagging methods were attempted in order to assess the method most suited to the species. In all cases spaghetti-type FT-2 dart tags supplied by Floy Manufacturing Company were employed. The tagging methods used were as follows.

Method 1: The crab was tagged dorsally between the coxa and the basi-ischium of the fifth leg. The toggle of the tag was lodged in the musculature of the coxa region.
Method 2: The tag was inserted through the epimeral suture with the toggle lodged in the branchial cavity.
Method 3: The tag was inserted through the suture line on the merus of the cheliped with the toggle imbedded in the muscle.

The crabs used in this study were caught in baited beehive crab traps, except during August 1982 when they were caught by trawling. They were transferred from the traps into holding tanks supplied with circulating sea water and were tagged and released within hours of their capture.

The following record was kept for each tagged crab; tag number, size, shell state, whether ovigerous, whether any appendages were missing and state of maturity (based on the shape of the vulvae) (Melville-Smith, in press). During the first survey (September 1979), the state of maturity of the female crabs was not recorded.

The crabs were caught and released at depths between 400 and 900 m, using a cage specially constructed for this purpose. At the areas chosen for their release, the tagged crabs were lowered in the PVC cage to between 50 and 100 m off the bottom, whereupon a door on the undersurface of the cage was triggered to open by a messenger. The benefit of releasing the crabs in this manner, was that they had some protection from predation and furthermore their position at release could be accurately pinpointed. The release cage was not used during the September 1979 survey. During that survey all the crabs were released at the surface at an approximated position (20°50′S/12°10′E). It is likely that the estimated distances moved by crabs which were returned from this survey, would have been considerably less accurate than those which were calculated for crabs returned from the three later surveys.

During the entire six-year period of this tagging study, the red crab stock was consistently fished on a year-round basis (i.e. with no closed seasons) by five Japanese fishing vessels. The fishermen were asked to retain any tagged crabs caught in their traps and to record the date, position and depth of recapture. A token reward of R1,00 ($0,50) was paid for each crab returned to the Sea Fisheries Research Institute. The fishermen were generally very co-operative.

All relevant information on recaptured crabs i.e. the date, position, depth, size, sex, shell state and maturity at tagging and at recapture was computerized for analysis. The distances moved by the crabs between tagging and recapture were calculated by trigonometry, assuming that the crabs had moved in a straight line following the shortest possible route.

It should be noted that, even though the positions at tagging and at recapture were obtained by satellite navigation equipment, errors of up to 5 nautical miles (9 km) were possible for the reported positions at which tagged crabs were recaptured. These errors are due to possible cumulative effects of incorrect satellite navigation co-ordinates between fixes, coupled with the fact that fishermen reported the position of a tag return using co-ordinates at the beginning or end of a longline, most of which are 3 to 4 nautical miles (5 to 7 km) in extent, instead of reporting the precise point on the longline where the crab was caught. When the points of tagging and recapture were far apart, the shortest straight line between

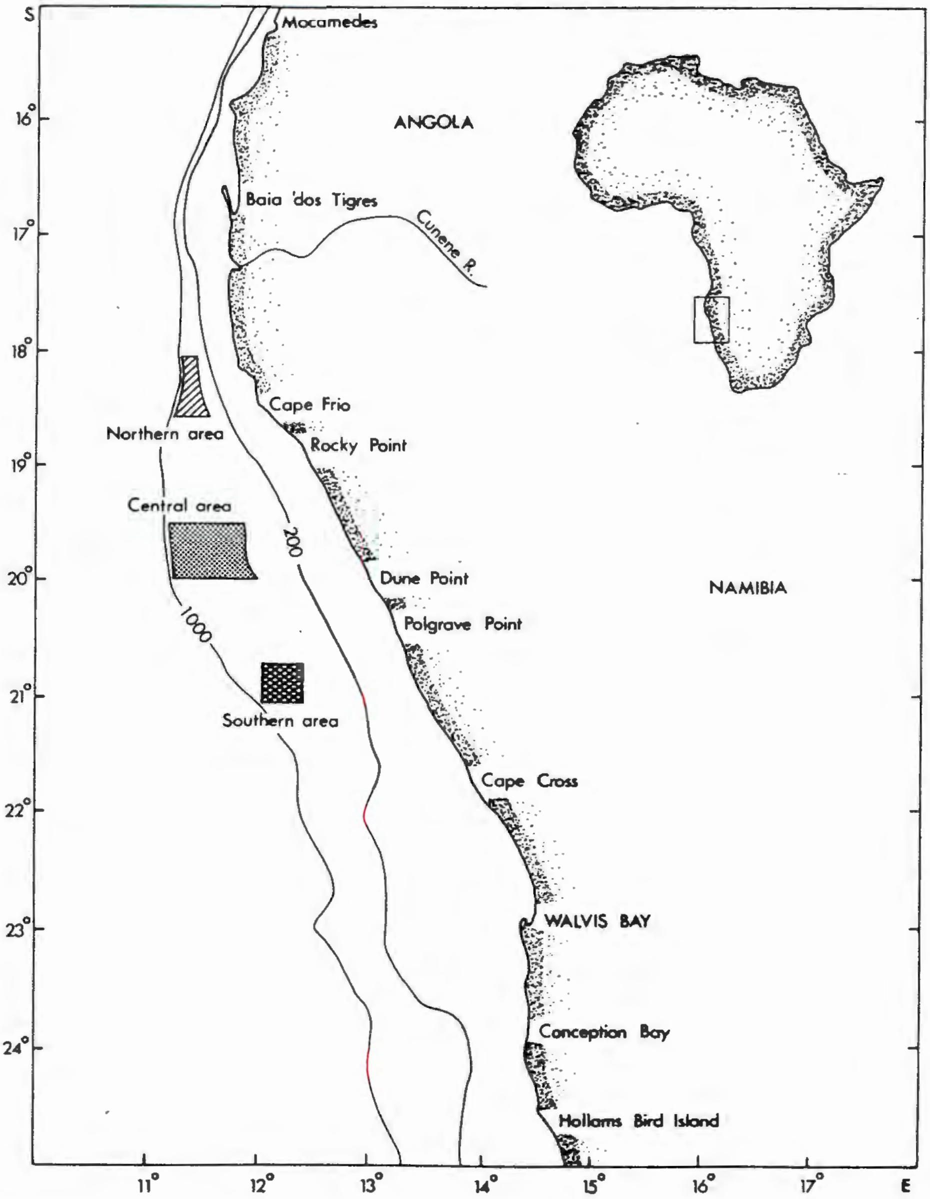

Figure 1 Areas where tagging took place. (a) Northern area: February 1984. (b) Central area: October 1982. (c) Southern area: September 1979.

the two points often crossed depths at which red crabs are not found. In these cases, the depths had obviously been detoured by the crabs, resulting in a greater distance covered than suggested by the result.

The recognized techniques for analysing data on migrations, such as those described by Jones (1976) and used in other studies of this type (*inter alia* Saila & Flowers 1968; Campbell & Stasko 1985), were not used in this report because of the unusual distribution of the red crab population off Namibia. Red crabs in this region, are only found along a narrow bathymetric corridor running between 350 and 900 m. Within the boundaries of these depths, the crabs can only move in a north-westerly or south-easterly direction (these directions henceforth termed northwards or southwards for convenience) following the shape of the depth contours (Figure 1). Because the crabs are restricted to north – south movement patterns, the vector describing the mean direction of movement is obvious from simple proportional ratios (usually expressed

Table 1 The number of crabs tagged during this study, their position at release and the proportion recaptured as at January 1986. 'R' indicates the catch position when catch and release positions differed within an area

Survey dates	Catch and release position	Release depth (m)	No. tagged			No. recaptured			Percentage return
			Male	Female	Total	Male	Female	Total	
12.9.79 – 18.9.79	20°50'S/12°10'E (R)	400 – 650	4 875	579	5 454	266	8	274	5,0
12.8.82	18°06'S/11°18'E	900	103	16	119	28	3	31	26,1
14.8.82	17°30'S/11°21'E	400	0	56	56	0	17	17	30,4
14.8.82	17°29'S/11°15'E	580	4	14	18	1	1	2	11,1
15.8.82	18°26'S/11°21'E	710	40	19	59	7	6	13	22,0
15.8.82	18°26'S/11°21'E	800	9	4	13	4	0	4	30,8
16.8.82	18°32'S/11°23'E	590	50	33	83	12	6	18	21,7
16.8.82	18°29'S/11°24'E	500	10	11	21	1	2	3	14,3
16.8.82	18°27'S/11°26'E	400	8	8	16	1	0	1	6,0
16.8.82	18°58'S/11°22'E	503	7	41	48	0	7	7	14,6
18.8.82	18°56'S/11°18'E	600	36	44	80	18	7	25	31,3
18.8.82	18°56'S/11°16'E	700	39	21	60	11	5	16	26,7
18.8.82	18°56'S/11°14'E	780	11	3	14	5	0	5	35,7
19.8.82	19°55'S/11°40'E	498	6	2	8	2	0	2	25,0
19.8.82	19°55'S/11°36'E	600	14	5	19	4	0	4	21,0
20.8.82	20°55'S/12°17'E	596	4	3	7	1	0	1	14,3
20.8.82	20°55'S/12°17'E	596	9	8	17	1	3	4	23,5
			350	288	638	96	57	153	24,0
10.10.82	20°00'S/11°45'E (R)	500	85	43	128	29	15	44	34,4
10.10.82	20°00'S/11°39'E (R)	600	87	66	153	39	32	71	46,4
11.10.82	20°00'S/11°34'E (R)	700	62	23	85	26	8	34	40,0
11.10.82	20°01'S/11°29'E (R)	800	224	4	228	91	0	91	39,9
14.10.82	19°29'S/11°13'E (R)	900	772	35	807	262	17	279	34,6
15.10.82	19°30'S/11°16'E (R)	800	115	11	126	26	4	30	23,8
15.10.82	19°32'S/11°22'E (R)	700	158	43	201	66	15	81	40,3
17.10.82	19°33'S/11°33'E (R)	500	173	328	501	43	118	161	32,1
17.10.82	19°30'S/11°25'E (R)	600	72	49	121	24	14	38	31,4
18.10.82	21°01'S/12°21'E	600	40	8	48	16	4	20	41,7
			1 788	610	2 398	622	227	849	35,4
13.2.84	18°31'S/11°24'E (R)	500	47	24	71	12	7	19	26,8
13.2.84	18°29'S/11°22'E (R)	600	43	27	70	14	2	16	22,9
14.2.84	18°30'S/11°20'E (R)	700	28	37	65	9	6	15	23,1
14.2.84	18°30'S/11°18'E (R)	800	33	30	63	14	5	19	30,2
15.2.84	18°30'S/11°17'E (R)	900	149	11	160	32	2	34	21,3
16.2.84	18°03'S/11°20'E	800	81	33	114	17	4	21	18,4
16.2.84	18°02'S/11°19'E	900	2	2	4	0	0	0	0
17.2.84	18°02'S/11°22'E	600	86	34	120	20	6	26	21,7
17.2.84	18°02'S/11°20'E	700	113	12	125	15	3	18	14,4
18.2.84	18°10'S/11°27'E	400	53	142	195	3	13	16	8,2
18.2.84	18°01'S/11°26'E	500	41	77	118	5	11	16	13,6
19.2.84	18°17'S/11°28'E	400	56	103	159	11	25	36	22,6
19.2.84	18°12'S/11°23'E (R)	500	49	74	123	5	13	18	14,6
20.2.84	18°17'S/11°23'E	600	72	38	110	24	8	32	29,1
20.2.84	18°17'S/11°23'E (R)	700	37	37	74	11	10	21	28,4
21.2.84	18°12'S/11°21'E (R)	800	70	24	94	12	3	15	16,0
21.2.84	18°22'S/11°21'E	900	57	34	91	4	2	6	6,6
			1 017	739	1 756	208	120	328	18,7

as a percentage) of crabs moving in one direction or from one depth to another.

This study reports on the results obtained from four tagging surveys, the positions and dates of which are documented in Table 1. For various reasons dealt with in the discussion, there were discrepancies between the four surveys regarding the percentage of tagged crabs returned by the fishermen, and consequently direct comparisons between surveys are not possible.

Where trends of crab movement have been examined for different regions of the grounds, the four surveys have been grouped into a northern, central and southern area (Figure 1). As can be seen from Table 1 these areas have been largely based on the positions where tagging took place during three of the four surveys. Results from the August 1982 data have been used to supplement the data on the three areas where applicable (Table 1).

For much of the analysis of movement, the October 1982 data has been selected to illustrate the trends. The chief reason for this is that that survey was conducted in the central area of the crab grounds and was therefore probably most representative of the Namibian red crab fishery. Other reasons are that (a) it covered the total depth range of the crab, (b) all crabs caught were tagged (so that the ratios of crabs tagged corresponded with their densities at the various depths) and (c) it was the most successful tagging survey in terms of the condition of the crabs at release and, correspondingly, the number of crabs that were returned.

Results

Time at liberty

Of the 10 246 crabs tagged between 1979 and 1984, 1 604 have been recaptured (until January, 1986) with reliable information (Table 1). In all four of the surveys undertaken during the course of this study, the vast majority of tagged crabs (particularly those that had been tagged as mature females) were recaptured within the first year of their release. This trend is clearly illustrated by the comprehensive October 1982 survey data (Figure 2). Small numbers of crabs tagged in September 1979 continue to be recaptured. The last recaptured crab had been at large 2 236 days (over six years).

Tagging methods

Results of the three methods of tagging used during September 1979 are presented in Table 2. The H_0 that the likelihood of a crab retaining its tag through a moult would be equally probable with the three tagging methods was tested with a chi-square test. The calculated value of 37,9 permits rejection of the H_0 at $P < 0{,}01$. Suture tagging is clearly a better method than the others and was used in all subsequent crab tagging surveys.

Effects of distance between points of capture and release

Herrnkind, VanderWalker & Barr (1975), quoted by Herrnkind 1980, have shown that nomadism in lobsters may be induced by displacing them from their home range or a familiar region. When capturing, tagging and releasing crabs at the depths discussed in this report, it is unlikely that the tagged animals would have been released in their home range (assuming that they have such a range). However, by using the release apparatus described earlier, it could be assumed that they were probably released into an environmentally familiar region.

During the October 1982 and February 1984 surveys, approximately half of the crabs that were tagged, were released

Table 2 Returns from each tagging method used during September 1979

Crab number	Fifth leg	Suture	Claw
Tagged	1 815	1 821	1 818
Returned (unmoulted)	94	39	36
Returned (moulted)	12	68	17
Returned (total)	106	107	53
Percentage moulted	11,3	63,6	32,1

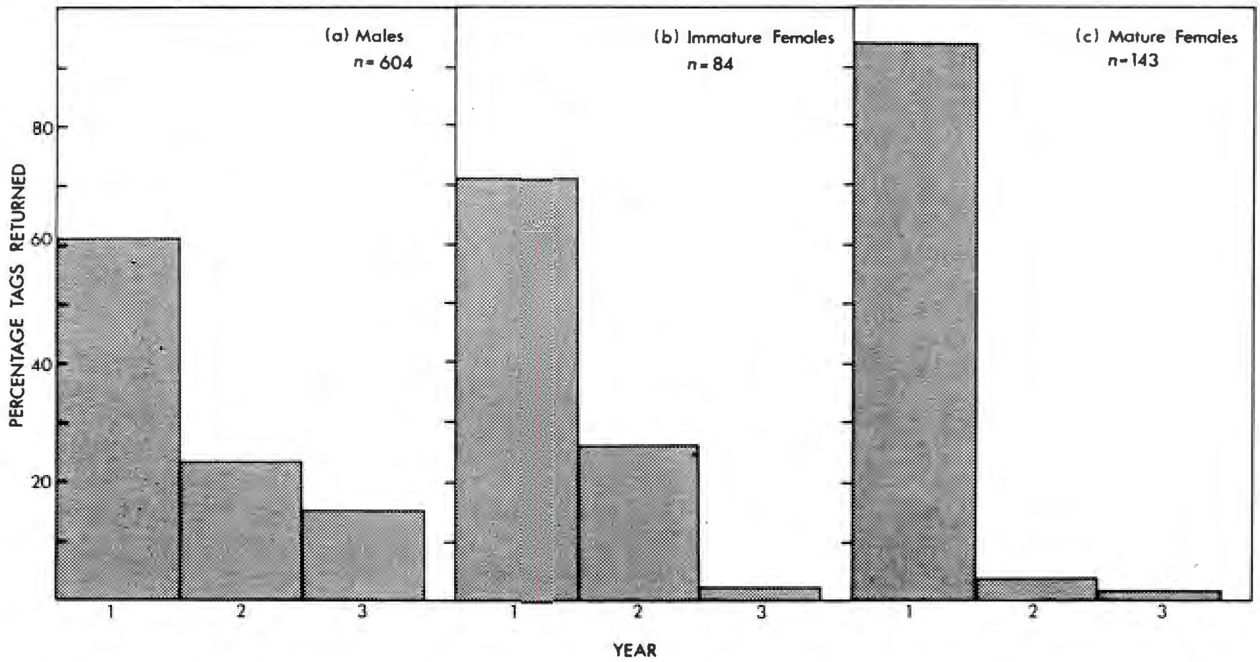

Figure 2 Tag returns for three succeeding years after tagging in October 1982; (a) males (b) immature females and (c) mature females. The sizes and maturity states are those recorded at release of the crabs.

at the position of their capture (Table 1), while the other half were released approximately 10 nautical miles away. An analysis of the distances moved by male crabs failed to show any significant difference ($P > 0,10$) between the distances moved by crabs released at their point of capture and those released farther away.

A comparison of movement by sex, size and maturity

Chi-square contingency tests were performed on a portion of the data in order to investigate whether the size, sex or maturity of the crabs played any part in the extent of their movements. In order to eliminate unnecessary variables which may have interfered with the results, only crabs tagged during October 1982 between latitudes 19°30'S and 20°00'S were used in the sample analysed.

The crabs used in this study were tagged and released at different depths. To test whether this variable could be disregarded, the distances moved by male crabs tagged deeper than 750 m and those tagged shallower than this depth were compared. This test was only performed on a male crab sample, because female crabs are not sufficiently abundant at depths greater than 600 m on which to perform a meaningful test. There was no significant difference in the distances covered by the two groups of males ($P > 0,10$), and depth was consequently ignored when testing distances moved by the sexes and different size or maturity stages.

A further analysis was performed on male crabs to establish whether the distance they moved was size related. Large males ($\geqslant 105$ mm CW) were found to move significantly farther than smaller individuals ($P < 0,01$) but, considering that the distances covered by males of all sizes were so limited (only about 10% of all the male crabs moved $\geqslant 36$ km), no further effort was made to analyse the data separately for different size classes.

The distances covered by all male crabs were tested against the movements of immature females to determine whether the distances that they moved were sex related. There was no significant difference ($P > 0,50$) between the two groups so they were combined and tested against the distances covered by mature females. The data showed a highly significant trend ($P < 0,001$) pointing to the fact that mature females move greater distances than the rest of the population. In all further analyses mature females were treated separately from the rest of the crabs.

Direction and distances moved

A detailed analysis of the data failed to reveal any seasonal trends associated with the distance and direction covered by the crabs between the point of tagging and recapture. Other trends, the significance of which is less apparent, have been noted in the data and are discussed below.

Data from all surveys showed that the crabs were relatively near to their point of release when recaught within the first 90 days after tagging. Thereafter they dispersed unpredictably as is evident from the fluctuating means and high standard deviation recorded in Table 3.

Both Table 3 and Figure 3 show that mature female crabs tagged in all areas were prone to extensive movement compared to other crabs in the population. Approximately 32% of the mature female crabs moved > 100 km compared with only 3% of the males and immature females. Only 33 crabs (2,3% of all returns) moved more than 200 km and all but four were mature females. The farthest distances covered were 380 km in a northerly direction and 344 km southwards. A few of the more spectacular rovings (in terms of distance covered) by crabs tagged in different areas are shown in Figure 4.

The proportions of tag returns north or south of their release positions respectively, were analysed separately for mature females, and for males together with immature females (Table 4). The results show a particularly strong tendency for the mature female crabs to have moved north rather than

Table 3 Means and standard deviations (in km) for distances moved northwards and southwards from each area for periods of up to six years

			Distance covered in km (mean and standard deviation)								
Area	Category	Direction	1st quarter	2nd quarter	3rd quarter	4th quarter	2nd year	3rd year	4th year	5th year	6th year
North	Males and immature females	North	11,9 ± 7,2 $n=53$	19,6 ± 16,4 $n=21$	30,4 ± 33,3 $n=15$	27,0 ± 17,5 $n=11$	15,3 ± 18,5 $n=34$				
		South	12,1 ± 8,1 $n=55$	28,1 ± 31,7 $n=29$	16,6 ± 13,1 $n=14$	37,3 ± 37,1 $n=9$	20,9 ± 13,0 $n=57$				
Central	Males and immature females	North	14,0 ± 14,9 $n=51$	20,9 ± 28,3 $n=74$	18,0 ± 19,1 $n=67$	16,6 ± 19,3 $n=20$	28,3 ± 38,7 $n=78$	23,2 ± 13,3 $n=42$			
		South	11,9 ± 11,5 $n=22$	16,4 ± 14,2 $n=59$	16,4 ± 15,8 $n=71$	15,1 ± 13,0 $n=24$	17,8 ± 13,0 $n=72$	25,0 ± 14,9 $n=36$			
South	Males	North	34,0 ± 5,6 $n=15$	39,2 ± 31,1 $n=57$	43,0 ± 45,5 $n=30$	52,7 ± 43,4 $n=27$	72,0 ± 69,3 $n=24$	41,9 ± 37,3 $n=13$	68,4 ± 42,7 $n=21$	52,0 ± 44,5 $n=7$	49,9 ± 27,9 $n=10$
		South	$n=0$	5,5 $n=1$	$n=0$	$n=0$	25,7 ± 19,3 $n=6$	31,0 ± 17,8 $n=20$	39,4 ± 7,9 $n=7$	63,2 ± 35,6 $n=15$	81,5 ± 52,9 $n=7$
North	Mature females	North	48,2 ± 70,2 $n=9$	119,0 ± 39,6 $n=15$	51,7 ± 33,3 $n=9$	88,7 ± 28,8 $n=3$	51,5 ± 26,3 $n=8$				
		South	24,5 ± 22,3 $n=8$	120,2 ± 76,7 $n=4$	13,7 ± 6,8 $n=5$	88,6 ± 129,6 $n=6$	90,0 ± 66,6 $n=8$				
Central	Mature females	North	39,4 ± 46,8 $n=20$	67,5 ± 62,3 $n=35$	155,2 ± 86,6 $n=29$	131,6 ± 81,2 $n=15$	99,7 ± 82,3 $n=16$	344,2 ± 44,1 $n=4$			
		South	12,1 ± 10,6 $n=23$	17,8 ± 23,8 $n=17$	9,5 ± 3,8 $n=4$	41,4 $n=1$	32,4 ± 16,4 $n=7$	$n=0$			
South	Females	North	86,4 $n=1$	49,1 ± 20,2 $n=3$	160,7 ± 58,1 $n=3$	142,2 ± 101,9 $n=3$	$n=0$	$n=0$	316,8 $n=1$	$n=0$	$n=0$
		South	$n=0$	$n=0$	$n=0$	10,8 $n=1$	102,6 $n=1$	$n=0$	$n=0$	$n=0$	$n=0$

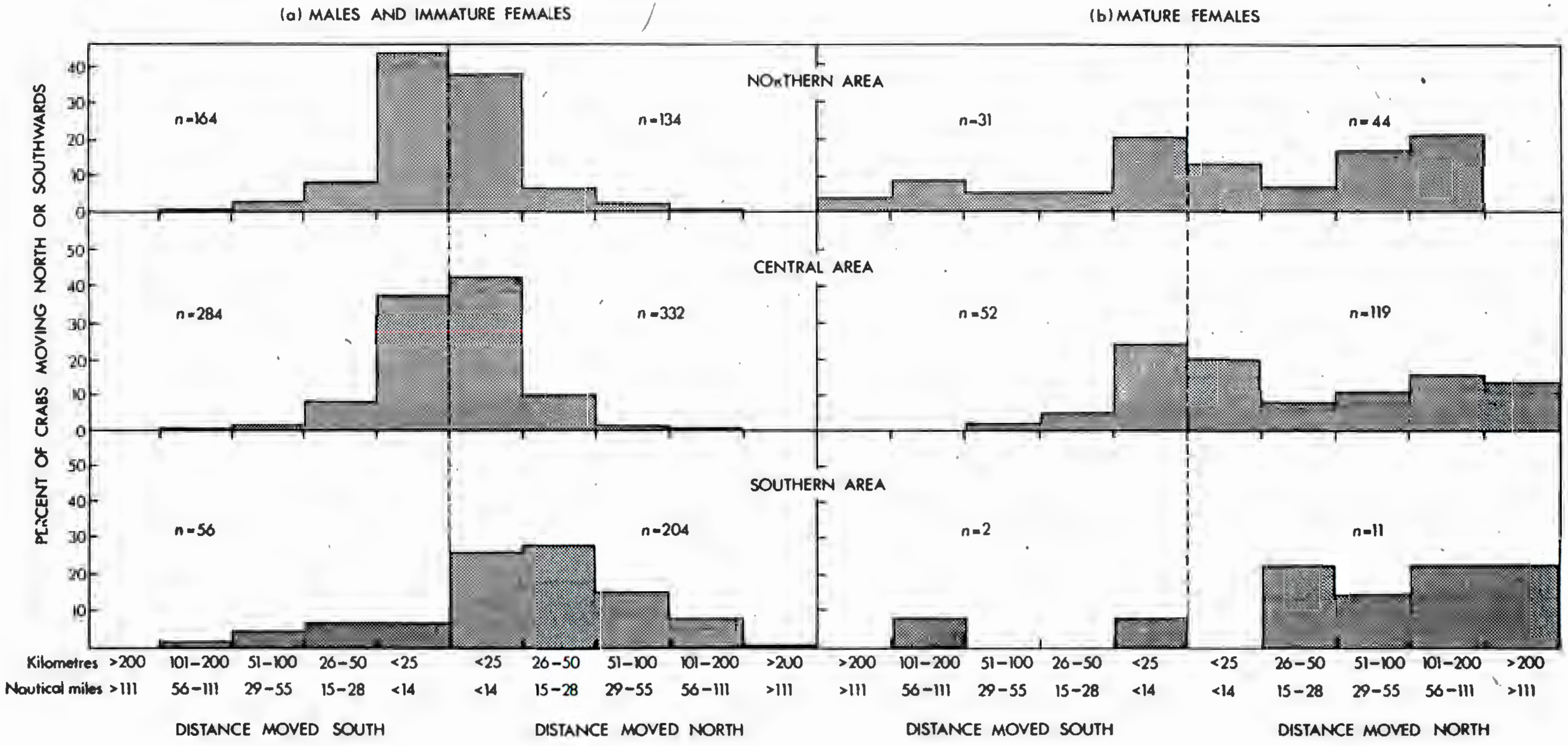

Figure 3 Distances moved northwards and southwards by red crabs tagged in three areas; (a) males and immature females, (b) mature females.

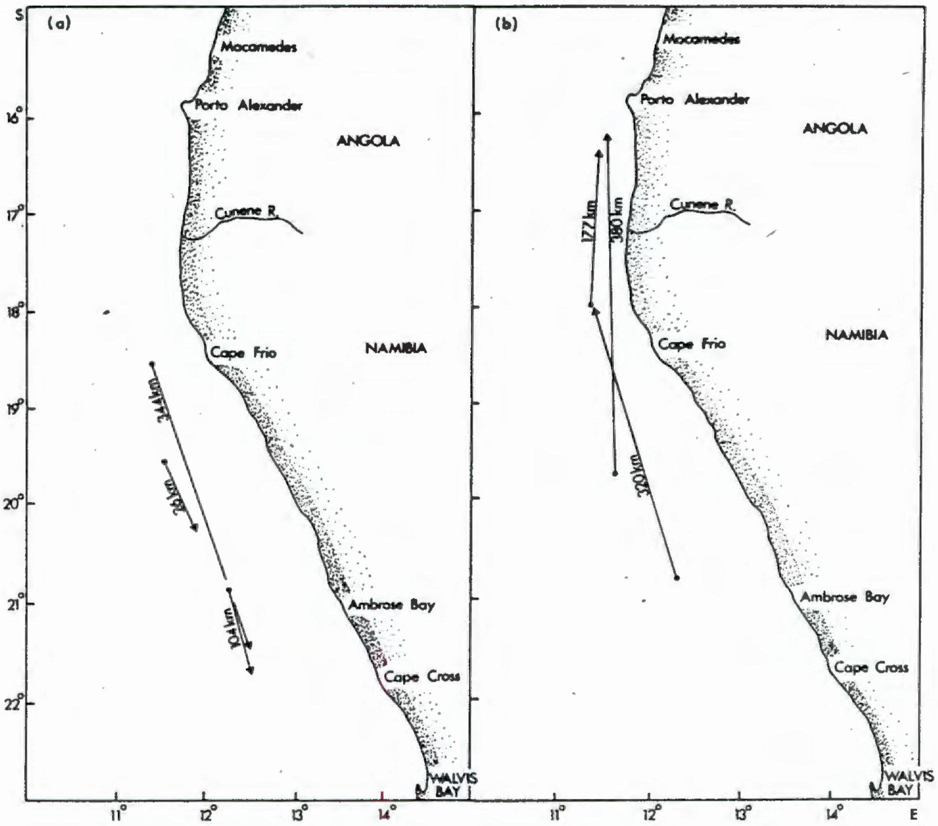

Figure 4 Farthest movement (a) southwards and (b) northwards by crabs released in each of the three tagging areas. In all cases the crabs were mature females.

Table 4 Ratio of tagged crabs recovered north to those recovered south of their release positions. Returns for the northern central and southern areas were recaptured over two-, three- and six-year periods respectively

	Males and immature females			Mature females		
	Southwards	Northwards		Southwards	Northwards	
Area	(Number)	Number	%	(Number)	Number	%
Northern	164	134	45,0	31	44	58,7
Central	284	332	53,9	52	119	69,6
Southern	56	204	78,5	2	11	84,6

Table 5 Mean velocities in northward and southward directions, calculated from tag recoveries over a three-year period for two crab categories tagged in the central area

Males and immature females		Mature females	
Southwards (km day^{-1})	Northwards (km day^{-1})	Southwards (km day^{-1})	Northwards (km day^{-1})
0,05 (n = 284)	0,05 (n = 332)	0,11 (n = 52)	0,46 (n = 119)

south. Furthermore, where mature female red crabs did move south, the distances that they covered were generally smaller than those of crabs that had gone north (Table 3 and Figure 3). Of the 83 mature female crabs that moved more than 100 km (Figure 3), 89% of them went northwards.

Speed of movement

The mean velocity of dispersion of crabs as deduced from tag returns is presented in Table 5. Mature females moved faster than males and immature females, reflecting the greater distances travelled by them while at large. Some crabs covered vast distances in a relatively short period and individual velocities for mature female crabs were as high as 2 km per day.

Depth

Despite careful analysis of the depth movements of crabs of different sizes, states of maturity and sex, no seasonal trends could be found in data from any of the tagging surveys. Data on male crabs from the October 1982 tagging survey were analysed (Tables 6 to 8) in order to examine whether any trends existed in the redistribution by depth of crabs subsequent to their tagging. As discussed earlier, only male crabs were used, because of the scarcity of females at deeper depths. Furthermore, the analysis was limited to returns from October 1982 because that survey provided the best depth coverage.

Examination by depth (Table 6), shows that crabs that were tagged deep (800 and 900 m) were generally recaptured shallower, while those tagged shallow (500 m) generally moved deeper. Crabs tagged between 600 and 700 m showed depth displacement values closest to a 50:50 ratio. Although the above observations are rather predictable, given that red crab are only found between certain well defined depth limits off the Namibian coast, they are nevertheless presented because of their bearing on Tables 7 and 8.

The mean depth at recapture for crabs released at five depths is shown in Table 7. The results show an obvious correlation between the depth at tagging and the depth at recapture, particularly for crabs that were returned prior to

Table 6 Numbers of males tagged in the central area which were recovered either deeper, shallower or at the same depth as at tagging

Tagging depth (m)	Depth movement (numbers of crabs)		
	Deeper	Shallower	Same
500	44	21	3
600	28	32	1
700	42	48	0
800	18	88	6
900	0	248	0

Table 7 Depth at tagging and corresponding depth at recapture for moulted and unmoulted males from the October 1982 survey

Tagging depth (m)	Mean depth at recapture (m)								
	Unmoulted	*n*	*sd*	Moulted	*n*	*sd*	Total	*n*	*sd*
500	554	55	106	610	13	99	565	68	106
600	588	48	101	647	13	107	601	61	104
700	661	52	119	692	38	113	674	90	117
800	690	65	111	702	47	103	694	112	107
900	721	201	119	702	47	125	717	248	120

Table 8 Recaptures deeper and shallower than 700 m, of two size categories of unmoulted males returned at 500 and 900 m respectively in October 1982

	< 100 mm CW	⩾ 100 mm CW
Releases at 500 m	$n = 25$	$n = 30$
Mean depth at recapture	575	537
% recaptured > 700 m	28	3
Releases at 900 m	$n = 129$	$n = 72$
Mean depth at recapture	757	656
% recaptured < 700 m	27	58

moulting. The fact that crabs recaptured subsequent to moulting showed less correlation could be ascribed to two causes; first, those crabs that had moulted before recapture had generally been at large longer than those that had not moulted and therefore would have had more time to redistribute themselves. The second and, in my view, more likely possibility, is that the depth of recapture is related to the size of the crab. To test this possibility, the male crabs tagged at 500 and 900 m during October 1982 were analysed in two size categories (Table 8). The table shows that the smaller crabs tagged and released at 500 m tended to move deeper than the larger crabs, though not by a significant amount ($P > 0{,}10$). Expressed as a percentage, however, the results show that 28% of the smaller crabs moved to depths > 700 m while only a single individual (3%) in the larger size class moved deeper than that. In contrast, for crabs tagged and released at 900 m, the larger size classes moved into shallower water than did the small crabs (240 m shallower for larger and only 140 m for the smaller crabs). This difference was significant ($P < 0{,}001$). In addition, the proportion of large-sized crabs moving into shallower water (i.e. < 700 m) was more than double that of small-sized animals (58 compared with only 27%).

The above observation suggests that, although red crabs move across a wide depth range, they do have preferential depths that may be related to size. These preferences have given rise to the characteristic trends documented by Beyers & Wilke (1980), namely that the mean size of male crabs decreases with depth. Likewise, of the 21 recaptured female crabs that were tagged at 800 and 900 m during the October 1982 survey (Table 1), 66% were taken < 700 m. This conforms to the observed pattern reported in the literature (*inter alia* Dias & Seito Machado 1973; Cayré & Bouchereau 1977; Beyers & Wilke 1980) of the sex ratio in shallower water being biased in favour of females.

Discussion

The great differences between the percentage of crabs recaptured during the various surveys can be ascribed to a number of reasons. Because of insufficient publicity, the 1979 survey elicited a poor response from the fishermen to return tagged crabs. The August 1982 survey utilized trawled crabs, which were obviously more stressed when tagged than trap-caught crabs, presumably decreasing their survival. During the October 1982 survey only 'lively' trapped animals were used and the apparent high recovery (Table 1) was not unexpected. The February 1984 survey was unfortunately conducted during an anomalous intrusion of particularly warm Angolan equatorial water into Namibia. The crabs suffered the effects of being brought up from deep water (< 8°C) and being kept in warm surface water (> 22°C) circulating in holding tanks prior to tagging and release. The temperature shock resulted in a high mortality of crabs in the holding tanks and probably adversely affected the survival of the tagged animals during the first few hours after their release.

The biases which may be introduced into analysis of movements recorded from tag recovery data supplied by commercial fishing vessels have been well documented by *inter alia* Bennett & Brown (1983), Campbell & Stasko (1985) and Diamond & Hankin (1985). These biases generally take two forms. First, a lack of co-operation on the part of the fishermen and, secondly, an unequal distribution of fishing effort during the course of the year or over the extent of the fishing grounds.

The most apparent bias which was experienced during this study, has been the general confinement to recognized Namibian commercial red crab fishing areas. Red crab have been recorded from 270 to 900 m off Namibia (Melville-Smith, in press), but because catch per unit effort is uneconomical on the fringes of these depths, fishing has been restricted to between ~380 and 850 m. For the same reason, commercial fishing seldom extends south of latitude 22°00'S, even though *G. maritae* has been recorded as far south as 27°03'S (MacPherson 1983).

The northern extent of the Namibian red crab ground is restricted by territorial limits rather than catch considerations. To date 17 tagged crabs have been returned from inside Angolan territorial waters (the farthest north being 16°12'S/ 11°31'E), but the amount of effort directed at red crab fishing in those waters has been minimal compared to that off the Namibian coast.

The result of these sampling biases is that the mean distances (Table 3) and numbers of crabs in the northern area recorded as moving northwards (Tables 3, 4 and Figure 3) were probably underestimates. Likewise, the same biases apply in Tables 3, 4 and Figure 3 for crabs moving southwards in the southern area. Owing to the fact that mature female red crabs have been shown to move greater distances than other red crabs in the population, it is probable that these results were more biased than those for males and immature females.

With regard to depth movements, the lack of commercial fishing effort deeper than 850 m would have led to underestimations in the numbers of crabs recorded as moving deeper than 900 m (Tables 6 to 8), as well as in their mean depth at recapture (Tables 7 and 8). Inshore roaming by crabs is less likely to have been underestimated because commercial fishing takes place in water shallower than the depths at which the animals were tagged.

The overall impression from the results of this study is that the movements of both male and female red crab tend to fit the nomadic pattern of behaviour described by Herrnkind (1980). This behaviour is not unexpected, because the habitat of the red crab has few of the controlling factors identified as giving rise to either the homing or migration patterns recognized by Herrnkind (1980).

A common element present in Herrnkind's description of both these behavioural patterns was the strong controlling influence of environmental conditions such as bottom surge, photoperiod and temperature changes. An assumed absence of these environmental influences in the deep has been suggested as the reason for *G. maritae* displaying a year-round reproductive cycle (Melville-Smith, in press). For the same reason, nomadism would be a logical behavioural option for a large deep-water scavenging crustacean.

The fact that large males (≥ 105 mm CW) have been shown to move significantly farther than small ones, may possibly be attributed to their greater size enabling them to cover distance with less effort. However, it cannot explain the extensive movements observed for mature female crabs, since the mature females which undertook the extensive movements recorded during this study, were virtually all smaller than large males.

Bennett & Brown (1983) noted for *Cancer pagurus* and Fee (1984) for blue crab (*Callinectes sapidus*) that mature females moved farther than other crabs of those species. In both cases the movements were migratory and appeared to be linked to their reproductive cycle. In the case of *G. maritae* the movements of mature female crabs have been shown by this study to be non-seasonal, often extensive and generally northward in direction. The movements do not appear to be associated with reproductive behaviour, because mating and ovigerous red crabs have been captured in both the northern and southern regions of the grounds.

One explanation which fits the above behaviour, is that mature females are particularly active foragers and therefore cover greater distances than the rest of the population. This hypothesis may be substantiated by the fact that a far greater percentage of mature females was recaptured in their first year of release than males and immature females (Figure 2). Since all recaptured animals were caught in baited traps, this implies a higher rate of foraging in mature females.

The trend displayed by mature female crabs to move in a generally northerly direction may be similarly explained. Commercial catch statistics for the red crab fishery show that catch per unit effort (in terms of numbers of crabs caught per trap) increases from south to north on the Namibian grounds (Melville-Smith unpub. data). This suggests that the environmental conditions (food availability, sediment type etc.) are probably more favourable for crabs in the north than in the south. Mature female crabs might be as likely to move in either of those directions when released, but those that moved north would be less likely to move away from the presumed more favourable environment, while those in the south would continue wandering in search of more suited conditions and would, in theory, ultimately move northwards.

The fact that red crabs are capable of wandering over considerable distances leaves no doubt that the Namibian and southern Angolan red crabs belong to a single stock. The results suggest that, although there is intermixing across territorial boundaries, it is of an exchange nature and does not appear to substantially benefit the crab fishery of either territory.

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PAPER 5:

A preliminary investigation into the possible causes of depth zonation by red crab (*Geryon maritae*), off Namibia

Sel. Pap. int. Comm SE. Atl. Fish.: in press.

A PRELIMINARY INVESTIGATION INTO THE POSSIBLE CAUSES OF DEPTH ZONATION BY RED CRAB (*GERYON MARITAE*), OFF NAMIBIA

R. MELVILLE-SMITH & G.W. BAILEY

Possible hydrological, sedimentological and biological factors responsible for causing the inshore and offshore depth distribution of red crab (*Geryon maritae*) off Namibia (18°S) are examined. Numerous possible factors, or combinations of factors responsible for the inshore distribution were identified, of which temperature and dissolved oxygen values appeared to be of particular importance. Factors responsible for the offshore distribution were less apparent, but sediment particle size may be a possible cause.

The red crab (*Geryon maritae* Manning & Holthuis) has been recorded as occuring in the east Atlantic Ocean between 23° 35'N off Spanish Sahara, to 27° 03'S off Namibia, at depths from 100 to 936 m (MacPherson 1983). Off the Namibian coast, the nearshore depth range of *G. maritae* would appear to be slightly more restricted than elsewhere on the African coast; the shallowest recorded depth of their capture in this region is 270 m (MacPherson op. cit.) and the deepest is 924 m (Melville-Smith, this study). The above depth ranges are extremities for the species off Namibia. Other studies (Beyers & Wilke 1980, Melville-Smith 1983, 1985 and this study) have all shown that red crab are generally restricted to a narrower depth zone between the 400 and 900 m isobaths.

The fact that *G. maritae* are to be found only within such a narrow and well defined depth range has led to some interest on this subject. The presence of distinct faunal zones in the deep-sea is well documented (*inter alia* Menzies *et al.* 1973, Haedrich *et al.* 1980, Rowe *et al.* 1982 and Carney *et al.* 1983), however these zones are usually considered to be areas of gradual replacement by one type of fauna with another. As far as can be ascertained from the literature, abrupt disappearences by dominant species as in the case of *G. maritae* have not been previously reported for a deep-sea animal.

The aim of this preliminary investigation was to ascertain the depths defining the boundaries to the crabs vertical distribution along latitude 18° 00'S (an area of relatively high red crab abundance (see Melville-Smith 1985)). Using these boundary depths, a number of hydrological, sedimentological and biological parameters were examined both inside and outside of the depths of the crab's occurrence. The results of these environmental parameters have been discussed in relation to the crab catches in an attempt to establish possible reasons for the depth boundaries to the crabs distribution.

METHODS

Sampling took place from the R.V. *Benguela* between 21 and 27 June 1986. Dropper lines with either one or two traps attached, were set at depths which were considered to be near to the extreme range of the species off Namibia (Table 1). The traps were left for approximately 18 hours before being hauled.

Using the catch from the traps as an indicator of crab abundance, the depth range of the crabs was successfully established. Hydrological, biological and sedimentological parameters were sampled in the vicinity of the depths indicated in Table 1.

Temperature and salinity were sampled using a Neil Brown C.T.D. Readings were taken over the whole water column, with particular emphasis on the depth nearest to the bottom. In most cases this was about five metres off the sea-bed. The C.T.D. was triggered to collect water samples at selected depths (5, 20 and 40 m from the surface and at 50 m intervals thereafter). Samples were analysed onboard for dissolved oxygen by Winkler titration and samples were frozen for later determination of nutrients by autoanalyser (Mostert 1983).

Sediment samples were taken using a shipek grab. Particle size was measured by settling tube, according to the method discribed in Brink and Rogers (1985). The textural properties of the sediment samples have been classified based on triangular gravel-sand-mud (silt) graphs (Buchanan and Kain 1971). Samples were further analysed by wet oxidation with dichromate (Strickland and Parsons 1972) to obtain the organic carbon content, after fuming over concentrated HCl to remove inorganic carbon.

Biological samples were taken using a small biology trawl (SBT) identical to the one described by Menzies (1962), covered by a nylon net with a mesh diameter of 0,5 mm. The gear was allowed to drag along the bottom for 10 minutes before being raised and was towed only by the drift of the ship. Further understanding of the biology at the various sampling depths was facilitated by photographs of the sea-bed which were taken at the various depths investigated.

RESULTS

(i) Trap fishing: Trap catches at various depths are presented in Table 1. The nearshore boundary was peculiar in that crabs were caught at 380, 400 and 517 m, but none were caught at the three depths that were fished in between 400 and 517 m. The true nearshore boundary zone is considered to be between 340 and 380 m. This boundary would also conform reasonably closely to that defined by trawling results presented in Beyers and Wilke (1980). Those authors failed to catch *Geryon maritae* in trawls conducted shallower than 324 m in the area between latitudes 19° 15'S and 20° 00'S. The offshore boundary fell between 924 and 970 m (Table 1). From the catch per trap results, it would appear that crabs were more abundant in the deeper zones.

TABLE 1: Details of trap settings and the number of <u>G. maritae</u> caught

Depth boundary	Date set	Position	Depth (m)	No of traps/ dropper line	Batch (number of red crabs)	Mean catch/ trap
Nearshore	21/6/86	17°58,5'S 11°23,7'E	344	1	-	-
	22/6/86	17°58,7'S 11°23,4'E	380	1	26	26
	21/6/86	17°59,5'S 11°23,2'E	400	1	28	28
	21/6/86	17°59,5'S 11°23,5'E	450	1	-	-
	23/6/86	17°57,2'S 11°22,3'E	456	2	-	-
	22/6/86	17°59,8'S 11°22,5'E	458	1	-	-
	22/6/86	17°59,7'S 11°22,2'E	517	1	8	8
Offshore	23/6/86	17°56,8'S 11°19,3'E	850	2	71	36
	26/6/86	17°56,4'S 11°17,0'E	887	2	300	150
	23/6/86	17°56,1'S 11°17,1'E	924	2	113	57
	24/6/86	17°58,6'S 11°16,8'E	970	2	-	-
	24/6/86	17°59,1'S 11°16,4'E	1 050	2	-	-

(ii) Hydrology: Temperature changed rapidly over the depths examined (Fig. 1). In the inshore area, the temperature ten metres off the sea bed (340 m) was 9,8°C, while by comparison the temperature 20 m off the sea bed in the offshore area (930 m) was 4,4 °C, a difference of some 5,4°C over a depth difference of approximately 600 m (Table 2).

The dissolved oxygen levels recorded over the study area (Table 2, Fig. 2), conform closely in most respects to other investigations which have covered this area (see Chapman and Shannon (1985)). The oxygen-deficient zone typically found between 200 and 400 m over a range of latitudes from 10° S to *ca*.25° S (Chapman and Shannon 1985), was recorded between 100 and 500 m (Fig. 2).

Salinity values were sampled throughout the water column, at the hydrological stations shown in Table 2. This variable is not considered to have been important in relating the distribution of red crabs to particular depths (Table 2), but the profile (Fig. 3) does give important indications as to the hydrological conditions over the study period.

A full range of nutrients were sampled (Table 2), but only two are presented as profiles (Figs 4 and 5). Both show elevated levels at approximately the depths (100-500 m) corresponding to those with low oxygen levels.

TABLE 2: Hydrological data near to the sea bed at 18°S

Variables	Depth at sea bed (m)								
	350	370	380	400	410	464	520	869	950
Depth sampled (m)	340	365	375	387	400	445	515	865	930
Temperature (°c)	9,80	9,14	8,65	8,21	7,25	7,79	5,99	4,52	4,40
Oxygen ($ml.l^{-1}$)	1,81	0,76	.....	0,84	.....	1,23	2,04	3,42	3,16
Salinity ($^{0}/oo$)	34,89	34,81	34,77	34,71	34,63	34,67	34,52	34,47	34,51
PO_4 -P	2,01	.....	2,19	.....	2,46	2,34	1,76	1,89	2,08
NO_2 -N	0,13	.....	0,21	.....	0,16	0,50	0,55	0,07	0,07
SiO_3	1,48	.....	1,66	.....	2,32	2,16	0,74	2,36	2,58
NO_3	3,10	.....	3,07	.....	3,67	3,56	2,21	2,44	2,82
NH_3	-	.....	-	.....	2,50	-	1,20	-	-

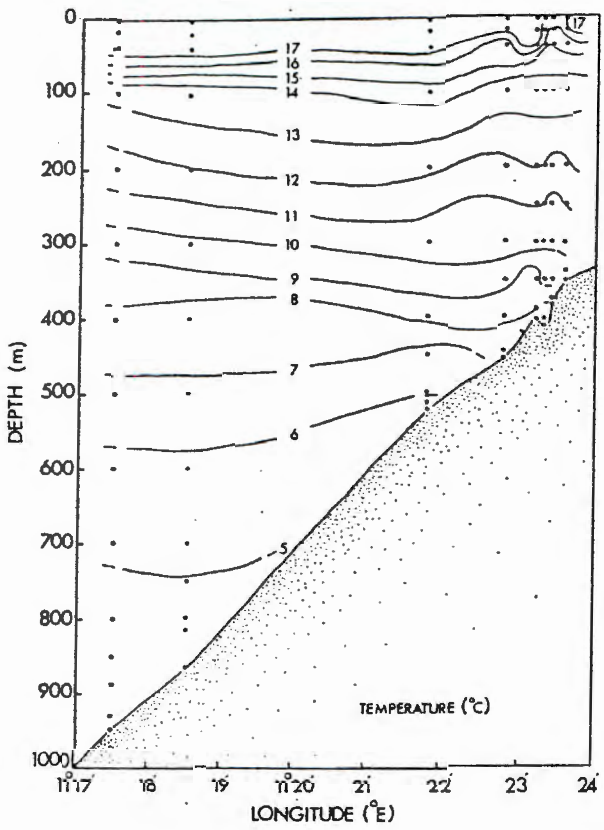

Fig. 1: Vertical distribution of temperature (°C)

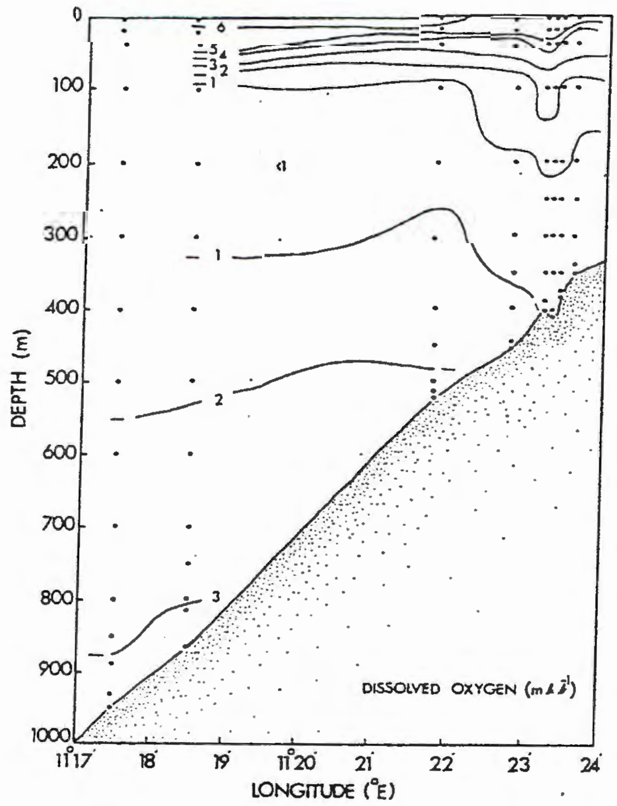

Fig. 2: Vertical distribution of dissolved oxygen ($ml.l^{-1}$)

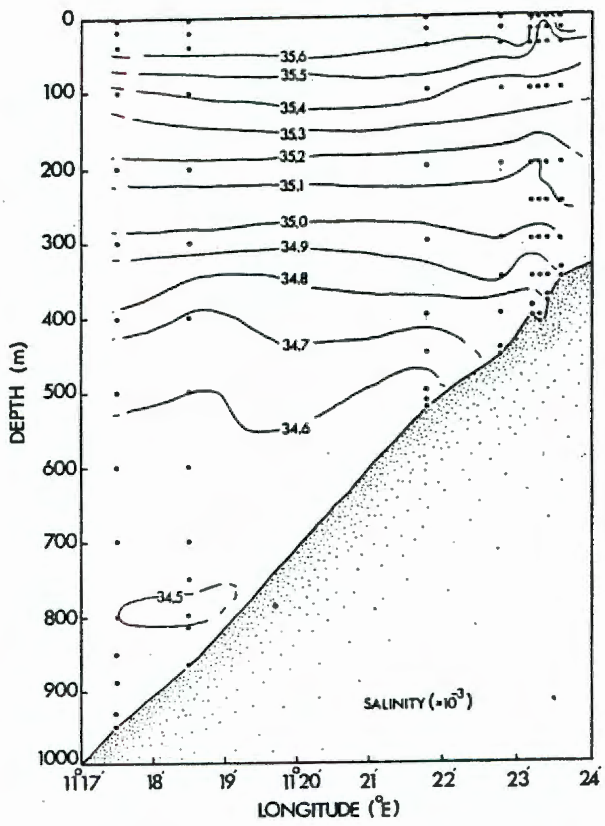

Fig. 3: Vertical distribution of salinity (‰)

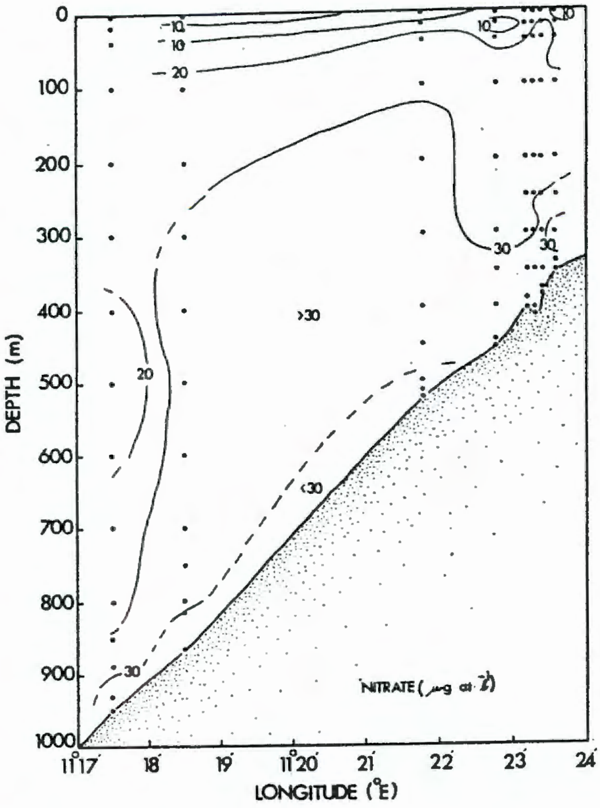

Fig. 4: Vertical distribution of nitrate (ug at.l^{-1})

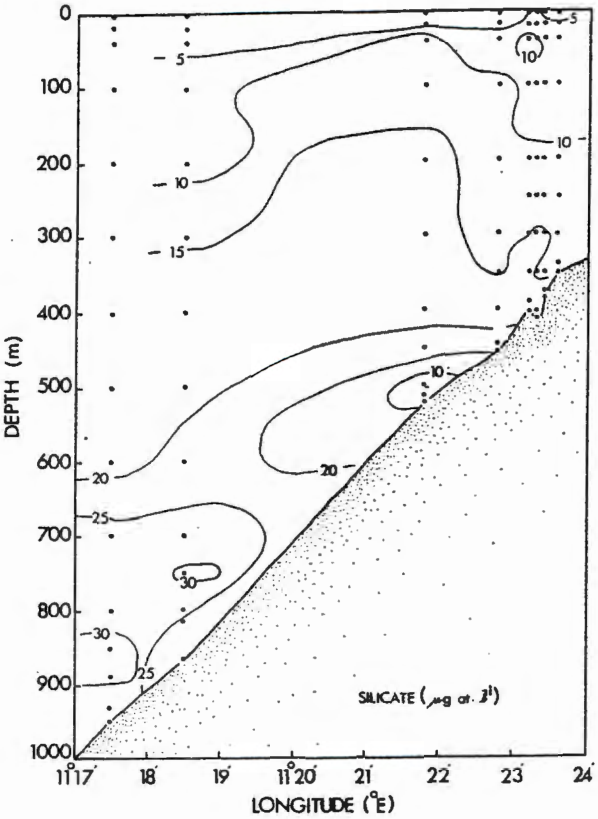

Fig. 5: Vertical distribution of silicate (ug at.l^{-1})

(iii) Sediment: The mud sand fraction at various depth intervals sampled is presented in Table 3. The sediment texture was fairly uniform between 350 and 450 m, however the three deepest depths sampled (520, 864 and 1 000 m) showed a rapid change from sandy to muddy substrate (compare 22 per cent at 350 m, with 85 per cent at 1000 m). These values correspond with the work of Bremner (1981) in the same area (Fig. 6). Values for

TABLE 3: Sediment texture and organic carbon content at seven depth intervals off latitude 18°S

Depth boundary	Depth (m)	Particle size fraction (percentage)			Textural facies	% organic carbon
		Mud (< 63μ)	Sand (> 63μ)	Gravel		
Nearshore	350	22,93	77,07	-	sand	1,09
	380	19,53	80,47	-	sand	0,34
	400	11,32	88,68	-	sand	1,90
	450	12,94	87,06	-	sand	1,91
	520	38,86	61,14	-	muddy sand	0,98
Offshore	864	74,79	25,21	-	sandy mud	1,34
	1 000	85,50	14,50	-	mud	2,64

organic carbon are presented in Table 3. The results show the sediment offshore to be both organically richer and structurally finer than inshore.

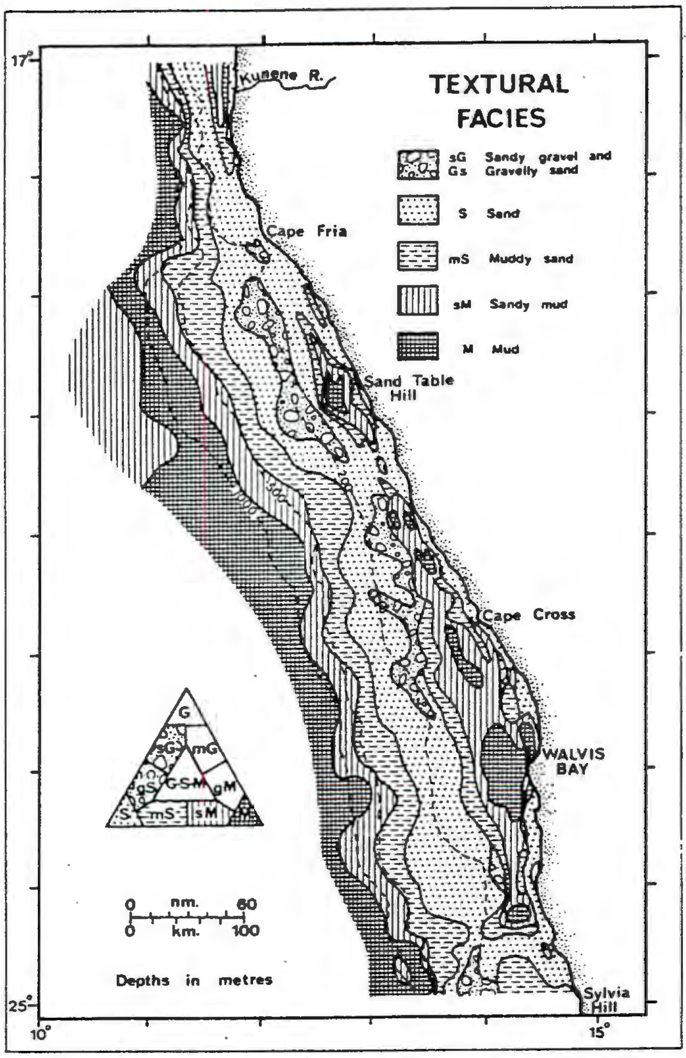

Fig. 6: Texture of surficial sediment on the Namibian continental margin (from Bremner 1981)

(iv) Biology: *Geryon maritae* have been shown by Melville-Smith (unpub. data), to be scavengers, consuming a wide variety of prey organisms. Items which frequently appeared in their gut contents such as small molluscs and polychaete worms, were present in all the dredge samples taken over the depth range 350 to 1 000 m. No attempt has been made to compare the catches of these microfauna at different depths, because the sampling method was not at all quantitative (the dredge was pulled by the drift of the ship).

Photography did allow some quantitative comparisons of the macrofauna. It was obvious that, for example, holes in the sediment (most of which are thought to have been caused by polychaete worms), were more plentiful at shallow than deeper depths. This was also the case with what are thought to have been solitary corals. They were abundant up to 500 m, but only one such animal was noted at 900 m and none were seen at 1 000 m. Numerous tracks, thought to be those made by red crabs, were seen at depths up to 906 m, but none were observed at the deepest camera station (990 to 1018 m).

It was mentioned under trap fishing results, that no red crabs were trapped in the depth range between 400 and 517 m. Photography in this depth range (440 to 466 m), did however record the presence of *G. maritae* in the area.

DISCUSSION

General conditions in the study area

Dissolved oxygen values at the sea bed are of particular relevance to this study. Conditions in Figure 2 best fit the situation described by Bubnov (1972), where an oxygen minimum exists at intermediate depths, overlaid by an oxygen-depleted layer formed on the shelf, thereby forming a continuous oxygen minimum layer between 100-500 m. Part of this oxygen deficient water develops on the shelf and according to Bubnov (op. cit.) moves offshore in a northwesterly direction. The vertical profile (Fig. 2) clearly shows the depressed oxygen levels in the water referred to above. Considering the origin of this water, one would expect it to have high nutrient levels. Figures 4 and 5 confirm this to have been the case during the study period.

Salinity and temperature remained stratified throughout the study (Figs 1 and 3) suggesting that upwelling of cold, lower salinity South Atlantic Central water did not occur over this period. More importantly , regarding the objectives of this study, one may deduce that the high salinity inshore water (Fig. 3) is indicative of southward incursions of high salinity, low nutrient Angolan water. Southward movement of Angolan water into northern Namibian waters is a well recorded phenomenon (*inter alia* Bubnov 1972, Visser 1969 and Moroshkin *et al*. 1970).

The above results, supported by the numerous references cited, suggest that the inshore waters over large areas of the Namibian red crab grounds are influenced by southward incursions of low oxygen, high salinity, low nutrient and therefore low potential for primary production Angolan water. This is considered to account for the generally lower organic carbon values inshore than offshore.

The above agrees with the findings of Bremner (1983). He showed the offshore area under question in this paper, to be one of the regions marked by high concentrations of diatoms, radiolarians and planktonic foraminifers. The same author (Bremner op. cit.), further suggested that the offshore advection of upwelled water near the coast prevented these planktofers from settling out on the shelf and resulted on them settling on the slope and thereby forming a food source for benthic scavengers. *Geryon maritae* would be one of the top predators in a presumed foodchain of these shelf scavengers.

Last of the environmental parameters deserving some explanation, is the sediment structure. The rapid change from sand to mud (Table 3) is thought to mainly be due to the effects of turbidity currents and slumping (Bremner *pers. comm*). These phenomena would be expected, due to the steeply shelving slope in this area.

Environmental and biological effects on crab distribution

It is clear from the results presented in Table 1 and from crab densities as calculated by photography (Melville-Smith 1983, 1985), that the density of *G. maritae* can decrease rapidly over a small difference in depth, particularly at the offshore limits of the species. Based on these results and those of the numerous studies which have investigated zonation in deep-sea fauna, it is possible to hypothesize as to some likely reasons for the well defined depth zonation of *G. maritae*.

In studies of this type, one seeks characteristics which stand out in setting the two zones apart. Beyers & Wilke (1980) showed a good correlation between the number of red crabs caught by trawling and the quantity of dissolved oxygen in the water. Since the depths forming the inshore boundary of the crab population are characterised by an oxygen minimum layer (as discussed above), it was felt that dissolved oxygen might be an important parameter in preventing *G. maritae* from colonising shallow waters. The fact that red crabs have been taken at depths where oxygen levels are as low as 0,45 to 0,65 ml l^{-1} have been recorded (Beyers & Wilke 1980) and that the bottom water at 340 m (considered by this study to have been the inshore limit of the crabs distribution) had 1,81 ml dissolved oxygen l^{-1}, suggests however that this is unlikely to be the main factor affecting their distribution.

Temperature may be another important variable affecting the crabs depth preference. Bottom waters dropped on average $2^{o}C$ between

300 and 400 m (Fig. 1) and from Table 2, it can be seen that the temperature changed very rapidly over what is considered to have been the inshore depth limit of the crabs (compare 9,8°C at 340 m with 9,14°C at 365 m and 8,65°C at 375 m. A full 1°C over a 30 m vertical depth difference).

The temperatures recorded between 300-400 m by this study, fall within the range documented for the same depths in the Cunene area by Stander (1964). Also apparent from the work documented by Stander op. cit.), is the fact that such temperatures are (within a small range) features of these depths. To an animal used to the constant environmental conditions of the deep-sea, this temperature change may be highly significant. Soto (1985), in an examination of the distribution of deep-water crabs off Florida, came to the conclusion that temperature was the factor that proabably most influenced the vertical range of various species. The archibenthal (deep-water) forms in his study, as with *Geryon maritae* in this investigation, all remained in waters colder than 10°C.

It is noteworthy that the near-shore boundary for *G. maritae* corresponds roughly with a zone that has been recognised as an area of faunal change by numerous deep-water zonation studies (*inter alia* Ekman 1953 (200-400 m), Menzies *et al.* 1973 (246-445 m), Haedrich *et al.* 1975 (285-393 m), Lagardère 1977 (400 m) and Haedrich *et al.* 1980 (283 m))

The above authors have all recognised a shallow zone, termed a shelf faunal province by Menzies *et al.* (1973), extending down to around 200 - 400 m. At around this depth they noted a different type of fauna which Menzies *et al.* named the archibenthal zone of transition (AZT). Though deeper zones have been recorded by a multitude of studies, this first transition is the most consistently recognised faunal change in deep-sea studies. Grassle *et al.* (1979) in observing this same fact, commented that boundaries between other depth zones were not obvious and could change continuously or discontinuously, depending largely on the methods of data analysis and presentation.

A relatively new theory that has been put forward by Somero *et al.* (1983) may go a long way towards explaining this transition zone. Their research has shown that enzymes of deep-water fish differ from those of cold-adapted shallow-living fish in that they are pressure insensitive. The insensitivity of these enzymes does however carry a serious disadvantage; namely that they have lower catalytic efficiencies than do the homologous enzymes in shallow-living fish. In effect this means that deep-water fish with pressure insensitive enzymes do not have the ability to compete with shallow water species possessing pressure sensitive enzymes.

Somero *et al.* (op. cit.) have suggested that pressures of only

50 to 100 atmospheres may be sufficiently stressful to enzyme function to favour selection for pressure insensitivity. They have shown that once evolved, pressure insensitive enzymes are theoretically capable of functioning efficiently to pressures of at least 476 atmospheres.

If this research on the effects of fish enzymes under pressure can be applied to other phyla, it would certainly help to explain the shelf faunal province/AZT zone. This zone falls slightly shallow of the depths which Somero *et al.* (1983) have postulated that animals would need pressure adapted enzymes. The fact that other depth zones are not obvious is substantiated by Somero *et al's* (1983) work, suggesting that pressure adapted enzymes are probably eurybaric. Deeper zones if present, would be caused by less predictable factors and would therefore be likely to show considerable depth variation for different areas.

The explanation also fits the observed near-shore depth distributions of *G. maritae* and a benthic brachyuran food competitor, *Bathynectes piperitus* (Manning & Holthuis). Melville-Smith (1985) has shown that both crab species can reach very high densities at the depths in which they commonly occur. There are zones (usually ~400-500 m) however, where they overlap in their distribution. It might be that *B. piperitus* has pressure sensitive enzymes, giving it a competitive advantage in the shallower depths over *G. maritae* which, being a deep-sea crab, would be expected to have pressure insensitive enzymes.

It would therefore appear that the near-shore distribution of *G. maritae* may be governed by more than one variable, which either singularly or together act to restrict red crab to its common depth limits.

Turning to the offshore depths bordering the limits of the crab's distribution, it is noteworthy that those depths falling inside the boundary should, in the majority of examples, have been areas of highest crab density (Table 1).

Bearing the above in mind, it would seem unlikely that the reasons which deter the crabs from colonising deeper depths are hydrologically related. It can be seen from Figures 1 and 2, that the characteristics of water at 924 m where crabs were present, are little different to those at 970 m where crabs were absent. Also, the differences in the physiological effects likely to have been experienced by crabs subjected to 97 as opposed to 92 atmospheres are small and would have been unlikely to have accounted for the observed distributional result.

Biological reasons, such as a lack of food availability or competition by some other organism might be suggested to explain the exclusion of crabs from depths greater than 920 m, but these explanations are not substantiated by the results. It is accepted that food available to benthic organisms decreases with distance from land and depth (the latter usually being closely related to the former). The horizontal difference between 920 and 970 m is only about 5 km (Table 1), a distance which is unlikely to result in such a drastic change in food availability as to result in the total exclusion of red crabs. Likewise, competition does not offer a solution to the depth zonation problem, because although it is possible that less food reaches 970 m than 920 m, there is (based on results from the dredge samples) still an appreciable macrofaunal food source. Those traps fishing outside the limits of the crabs distribution were brought up with their bait untouched, further dispelling any theory of an active competitor.

The only remaining explanation for the offshore distribution of the crabs is that the bottom topography may be unsuitable at depths deeper than 950 m. Grab samples (Table 3) have shown the sediment to change rapidly between 350 and 1000 m in the area 18° 00'S, with the mud fraction a full 11 per cent greater at 1000 m than at 864 m (compare 74,8 per cent at 864 m with 85,5 per cent at 1000 m). Thayer (1975) has mentioned that fine particles which are easly resuspended by currents and burrowing animals, may cause the feeding and respiratory structures of benthic organisms to become clogged. Certainly from photographic evidence, solitary corals which were observed at 900 m, were not seen in any of the exposures taken at 1000 m in the study area. Presumably the reason for the absence of the corals at 1000 m was related to the sediment clogging their feeding structures (their density had been steadily decreasing from 300 m). Likewise, it is possible that fine sediment might cause respiratory problems in the gills of red crabs, leading to their exclusion at the deeper depths.

Another possibility for the absence of crabs in the deeper depths may be attributed to the fact that muds typically have a high water content and that this can result in a structurally weak fluid surface. Bacescu (1971) suggested a number of adaptations common to animals occuring in muddy sediments. He noted that decapods, isopods and pyconogonids usually have long legs to help tham to expand their supporting surface. Red crabs do not have particularly long legs and it is therefore conceivable that they find difficulty in walking on the muddy surfaces at depths >930 m and therefore avoid those sediments.

Further sampling in different areas would be necessary to confirm the role played by sediment type in the distribution of red crabs. The texture of the surficial sediment at 18° 00'S as measured by this study, agreed closely with data presented by Bremner (1981) (Fig. 6). Figure 6 shows a general tendancy for sediment type to follow bathymetric contours (particularly the 500 and 1 000 m contours), suggesting that most depths off the Namibian coast between 17° and 23° S, have a similar sediment type to that found at 18° S by this study (Table 3).

The above observation supports the fact that while *G. maritae* have been taken at ~900 m on several occasions off Namibia, they have never been caught at 1 000 m, despite numerous attempts to capture them at that depth (Melville-Smith unpub. data).

Though this study has not provided conclusive evidence relating crab distribution at particular depths to specific environmental or biological factors, it has nevertheless succeeded in isolating some possible causes which may be responsible for this behaviour. Further more intense sampling along the same lines as in this report (possibly in several other areas of the crab grounds) will be necessary before firm conclusions can be made.

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PAPER 6:

Abundance of deep-sea red crab *Geryon maritae* in South West African waters from photography

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1983

ABUNDANCE OF DEEP-SEA RED CRAB *GERYON MARITAE* IN SOUTH WEST AFRICAN WATERS FROM PHOTOGRAPHY

R. MELVILLE-SMITH

The absolute density of red crab *Geryon maritae* at depths ranging between 375 and 700 m was studied photographically. These results (over 3 000 exposures were taken) were extrapolated to estimate the density between latitudes 19°30′ and 20°00′S, an area which forms a portion of the commercial red-crab fishing grounds off South West Africa. The depth range was divided into four zones: 375—399 m, 400—499 m, 500—599 m and 600—699 m. In the shallowest zone no crabs were photographed and the maximum density was calculated by a probabilistic method. For the other three zones, the densities in order of increasing depth were estimated as 22, 44 and 48 crabs·h^{-1} with coefficients of variation of 0,35, 0,24 and 0,23 respectively. Results are compared with published works on *Geryon* in which photography, trawling and trap fishing were used for estimating population density. The possible interaction between the photographic gear and the behaviour of crabs is discussed.

Die absolute digtheid van rooikrappe *Geryon maritae* op dieptes tussen 375 en 700 m is fotografies bestudeer. Die resultate hiervan (oor die 3 000 opnames is gemaak) is geëkstrapoleer om die digtheid te skat tussen suiderbreedtes 19°30′ en 20°00′, 'n gebied wat deel uitmaak van die kommersiële rooikrap-vanggronde teenoor Suidwes-Afrika. Die dieptebestek is verdeel in vier sones: 375—399 m, 400—499 m, 500—599 m en 600—699 m. In die vlakste sone is geen krappe gefotografeer nie en is die maksimum digtheid volgens 'n waarskynlikheidsmetode bereken. Vir die ander drie sones het die digthede toegeneem na gelang van die diepte, en is hulle geraam op 22, 44 en 48 krappe·ha^{-1}, met variasiekoëffisiënte van 0,35, 0,24 en 0,23 onderskeidelik. Resultate word vergelyk met gepubliseerde werk oor *Geryon*, waarin fotografie, fuikvangs en treil vir die raming van bevolkingsdigtheid gebruik is. Die moontlike wisselwerking van fotografiese uitrusting en die gedrag van die krappe word bespreek.

Although the red crab *Geryon maritae* has been commercially exploited in deep water off South West Africa (Namibia) since 1973, little is known about the size or density of the stock. Trawl surveys (Beyers and Wilke 1980, Melville-Smith unpublished data) have indicated crab densities of 1—6 crabs·ha^{-1} in 370—700 m water, the depths at which most of the commercial fishing takes place. However, with the yield to the fishery being in excess of 3 100 tons of processed product in 1981, this density value would appear to be a gross underestimate.

Standard mark-recapture methods for estimating stock size are difficult to apply to this crab, because the population is spread over an area stretching from the Angolan border to well south of Walvis Bay, thereby causing problems in ensuring random dispersion of tagged animals. In addition, commercial fishing is concentrated mainly in the shallower part of the depth range of the stock (*G. maritae* have been caught experimentally from 324 to 900 m). Consequently, recapture of tagged animals in any such survey would be subject to a bias.

Bottom photography has been successfully employed to census stocks of *Geryon quinquedens* on the east coast of the United States of America (Wigley *et al.* 1975), and the use of this proved method was therefore considered the logical solution to obtaining realistic estimates of stock density of red crabs in the commercially fished area off South West Africa.

Two members of the genus *Geryon* have been reported as occurring on the commercial fishing grounds off South West Africa, namely *Geryon affinis* and *G. maritae* (Manning and Holthuis 1981). The latter species has only recently been named and, according to these authors, was formerly confused with *Geryon quinquedens,* a species of the North American Atlantic coast. The confirmed distribution of *G. affinis* suggests that it is not common off West Africa, and Manning and Holthuis *(op. cit.)* state that most records of *G. affinis* or *G. quinquedens* from West Africa pertain to *G. maritae.* All literature dealing with West African red crab cited in this report refer to the crab in question as *G. quinquedens.* These references to *G. quinquedens* have been taken as belonging to *G. maritae* for the purposes of this report.

METHODS

A deep-sea photographic survey was conducted from the R.V. *Benguela* during July 1981. The area surveyed fell between latitudes 19°30′ and 20°00′S (Fig. 1) and was selected for two reasons. Firstly, information on crab density was available from a

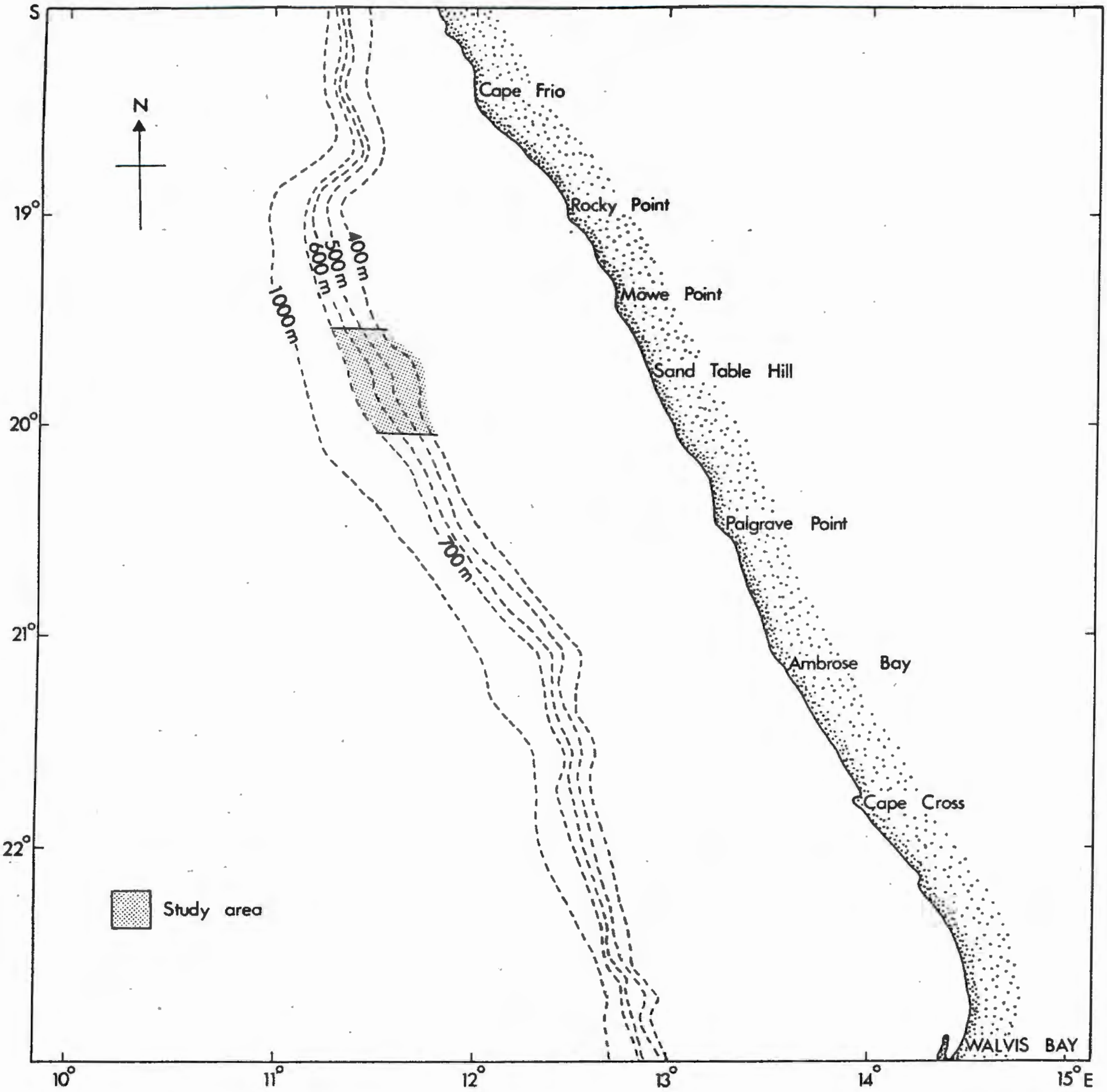

Fig. 1: The study area and bathymetry of the depths surveyed (after Bremner 1981) — station locations are presented in Table I

quantitative trawl survey of the stock conducted in this area by Beyers and Wilke (1980), and comparison of the two different survey methods was considered to be useful. The other reason for selecting this area was that, according to the official catch statistics supplied by commercial crab catchers for the 12 months immediately prior to this survey, more effort was expended there than in any other part of the commercial fishing grounds (± 12 per cent).

Red crabs are caught by commercial crab fishing vessels at depths of 400—900 m. Insufficient time precluded photography over the whole depth range

Table I: Film reference number, date, position and depth range at which exposed, and the number of red crab observed

Film number	Date	Depth range (m)	Position at start	Number of *Geryon maritae*	Total area successfully filmed (m²)
13	18.7.81	491 — 493	19°59,0'S 11°43,4'E	1	154,32
14	19.7.81	503 — 520	20°01,0'S 11°44,4'E	1	134,83
15	19.7.81	500	20°01,1'S 11°44,1'E	3	177,86
16	19.7.81	496 — 498	19°59,6'S 11°44,3'E	3	166,51
17	19.7.81	475	19°59,2'S 11°44,2'E		189,21
20	19.7.81	393 — 400	19°56,7'S 11°49,5'E		124,89
21	19.7.81	394 — 400	19°56,4'S 11°49,8'E		161,71
22	19.7.81	363 — 386	19°55,4'S 11°48,0'E		156,87
23	20.7.81	420 — 427	19°58,1'S 11°47,7'E		139,50
24	20.7.81	434 — 438	19°55,2'S 11°45,9'E		150,52
25	20.7.81	392 — 395	19°57,1'S 11°50,3'E		159,42
26	20.7.81	402	19°57,0'S 11°50,0'E		158,50
27	20.7.81	440	20°00,2'S 11°48,9'E		145,85
28	20.7.81	445 — 446	19°59,5'S 11°48,4'E		140,42
29	20.7.81	442	19°58,0'S 11°45,2'E		165,62
30	20.7.81	457	19°57,5'S 11°45,1'E		102,63
31	20.7.81	457 — 462	19°58,9'S 11°46,5'E		128,69
32	21.7.81	635 — 650	20°00,7'S 11°37,5'E		110,77
33	21.7.81	627 — 631	20°00,1'S 11°37,4'E		128,69
34	21.7.81	637 — 638	19°59,2'S 11°36,8'E		150,95
35	21.7.81	657 — 660	19°57,5'S 11°35,2'E		139,55
37	21.7.81	676 — 680	19°58,5'S 11°34,5'E		16,29
38	21.7.81	680 — 684	19°57,2'S 11°33,7'E		27,15
39	21.7.81	668 — 671	19°57,7'S 11°34,8'E		10,86
40	24.7.81	510 — 512	20°00,2'S 11°43,3'E		160,73
41	24.7.81	507 — 518	20°00,0'S 11°44,1'E	7	165,07
42	24.7.81	524 — 525	20°00,6'S 11°44,0'E	2	161,81
43	24.7.81	525 — 530	20°00,7'S 11°42,8'E		179,19
44	24.7.81	532 — 540	20°00,7'S 11°42,4'E		158,56
45	24.7.81	490 — 492	19°59,9'S 11°42,0'E		154,76
46	24.7.81	538 — 550	20°00,1'S 11°41,6'E		38,01
47	24.7.81	550 — 560	20°00,4'S 11°41,1'E		128,52
48	24.7.81	560 — 565	20°00,1'S 11°40,2'E		150,96
49	25.7.81	549 — 555	20°00,5'S 11°39,3'E		156,57
50	25.7.81	568 — 571	19°59,2'S 11°39,3'E		152,49
51	25.7.81	581	19°58,5'S 11°39,0'E	1	149,43
52	25.7.81	590 — 596	19°57,4'S 11°37,9'E		142,29
53	25.7.81	573 — 575	20°00,0'S 11°40,8'E		150,45
54	25.7.81	588 — 597	20°00,2'S 11°28,4'E		142,80
55	25.7.81	598 — 605	19°58,9'S 11°37,3'E	1	127,50
56	25.7.81	600 — 610	19°58,1'S 11°36,9'E		145,86
57	25.7.81	600 — 612	19°58,1'S 11°37,7'E		146,88
58	25.7.81	607 — 624	19°58,6'S 11°37,0'E		151,98
59	25.7.81	628 — 632	19°58,4'S 11°36,6'E		136,68
60	25.7.81	645	19°57,0'S 11°35,0'E		141,78
61	26.7.81	373 — 385	19°32,1'S 11°37,8'E		133,62
62	26.7.81	391 — 395	19°32,6'S 11°38,0'E		147,39
63	26.7.81	401 — 405	19°32,9'S 11°37,6'E		111,69
64	26.7.81	410 — 411	19°31,2'S 11°36,8'E		147,39
65	26.7.81	425 — 430	19°31,4'S 11°35,4'E		132,60
66	26.7.81	415 — 420	19°31,5'S 11°36,0'E		45,39
67	26.7.81	406 — 416	19°31,7'S 11°36,4'E		178,09
68	26.7.81	430 — 440	19°31,8'S 11°35,5'E	1	181,58
69	26.7.81	443 — 450	19°31,5'S 11°34,4'E		167,62
70	26.7.81	453 — 460	19°31,8'S 11°34,0'E		178,09
71	26.7.81	470	19°32,1'S 11°33,5'E	1	104,18
72	26.7.81	480 — 487	19°32,6'S 11°33,3'E	1	171,69
73	27.7.81	488 — 490	19°31,4'S 11°31,8'E		179,84
74	27.7.81	495 — 500	19°31,4'S 11°31,5'E	1	162,38
75	27.7.81	510 — 511	19°30,4'S 11°31,4'E		167,62
76	27.7.81	520 — 527	19°30,6'S 11°31,0'E		161,80
77	27.7.81	530 — 533	19°31,0'S 11°30,5'E		156,56
78	27.7.81	540	19°31,3'S 11°30,3'E		143,75
79	27.7.81	550	19°31,5'S 11°29,0'E	1	172,27
80	27.7.81	560 — 563	19°31,7'S 11°29,0'E		171,11
82	27.7.81	580 — 585	19°31,7'S 11°28,1'E	2	174,02
83	27.7.81	570 — 574	19°31,6'S 11°29,1'E		174,02
84	27.7.81	590 — 592	19°32,0'S 11°28,7'E		173,44
87	28.7.81	684 — 690	19°31,3'S 11°22,4'E	2	116,40
88	28.7.81	677 — 680	19°31,2'S 11°23,0'E	1	79,15
89	28.7.81	662 — 664	19°31,0'S 11°23,8'E	1	168,20
91	28.7.81	672 — 673	19°33,0'S 11°23,9'E	2	179,26
92	28.7.81	675 — 685	19°32,5'S 11°22,9'E	3	33,76
93	28.7.81	678 — 680	19°30,4'S 11°22,8'E		51,80
94	29.7.81	650 — 669	19°31,0'S 11°24,0'E		150,16
95	29.7.81	640 — 653	19°30,5'S 11°24,5'E	1	174,60
96	29.7.81	630 — 639	19°30,5'S 11°24,9'E		144,34
97	29.7.81	620	19°30,7'S 11°25,7'E	2	175,18
98	29.7.81	635 — 638	19°30,4'S 11°24,5'E	1	159,47
99	29.7.81	610	19°29,1'S 11°25,1'E	2	172,85
100	29.7.81	600 — 607	19°28,9'S 11°25,8'E	2	162,38
101	29.7.81	615 — 625	19°28,5'S 11°25,6'E		168,20
102	29.7.81	624 — 636	19°27,8'S 11°24,9'E		180,42
103	29.7.81	658 — 669	19°27,3'S 11°23,9'E	2	133,86
104	30.7.81	657 — 660	20°00,4'S 11°37,0'E		168,20
105	30.7.81	670	19°59,8'S 11°35,4'E		168,20
106	30.7.81	672 — 680	19°59,1'S 11°34,3'E		173,44
107	30.7.81	690 — 692	19°59,3'S 11°34,1'E	1	163,54

and, therefore, only the depths between 375 and 700 m were surveyed. Over the 12 months preceding the survey, these depths accounted for approximately 75 per cent of the total fishing effort actually expended within the survey area (Sea Fisheries Research Institute, unpublished data).

The photographic equipment consisted of a Benthos model 371 deep-sea 35-mm camera and Benthos model 381 deep-sea flash. The camera and the flash were mounted on a weighted metal frame which was suspended by wire from a winch on the research vessel. Each exposure was triggered by means of a Benthos model 394 bottom-contact switch, which activated the camera and the flash the moment that a weight hanging from the trigger touched bottom and released tension on the switch mechanism. The height from which the weight hung from the contact switch determined the area photographed (normally 5—6 m²).

The camera was restricted to standard 36-exposure film which, because of the feed mechanism employed, seldom gave more than 30 exposures per spool. Monochrome Ilford HP5 135 film, with a rating of 400 ASA was used. At the start and the completion of each spool, ship's position and any other relevant information were recorded (Table I).

The ship was allowed to drift during the whole photographic operation from the moment the camera was lowered until its return on board. The height of the gear above the sea bottom was monitored by means of echo sounding equipment, which recorded a 12-kHz signal emitted by a Benthos bottom-finding deep-sea pinger attached to the camera frame. A series of photographs was taken of the sea-bed by lowering and raising the camera equipment. Each time the trigger weight touched bottom initiating an exposure, a signal was relayed to the operator on the surface. The equipment would then be winched up to 15—20 m from the bottom and slowly lowered back down to the point of triggering.

The period between exposures was approximately one minute. This gave sufficient time for the ship to drift, thus preventing photographing the same area twice. It did happen that the same area was photographed twice on more than one occasion, but this was easily discovered from the photographs, because the sediment disturbance caused by the weight in triggering off the first exposure was evident in the second photograph. In these cases, the second exposure was ignored for calculation purposes.

Over 3 000 exposures were taken during the course of the survey, of which 2 270,4 frames (or portions of frames) were considered suitable for analysis. Insufficient illumination of the subject was the reason for most rejections. All the accepted frames were printed as contact prints and were examined as such, as well as in their negative form, under a ×40 stereomicroscope. The number of crabs observed on each spool was noted, together with the total area successfully photographed (Table I).

Data were collected along the two latitudinal boundaries of the study area. However, it proved difficult and impractical to sample exactly along the latitudes, and consequently the ship was allowed to drift, samples being taken up to a maximum of five nautical miles on either side of each boundary. The target was four film spools per 25-m depth interval along each boundary, and all data were ultimately pooled by mean depth surveyed into the depth zones 375—399 m, 400—499 m, 500—599 m and 600—699 m.

The mean area occupied per crab and the density of crabs per hectare in each depth zone were determined by simple calculation. Bathymetric charts supplied by the Hydrographic Survey Branch of the South African Navy permitted calculation with a planimeter of the area between 19°30′ and 20°00′S for each of the four depth zones. From the known density in each depth zone and the known area of that zone, it was possible to estimate the crab population in each.

The actual size (carapace width) of each crab photographed was determined directly from the negative with a ×10 calibrated eyepiece. The size measured on the negative was multiplied by a magnification factor derived from the square root of the calculated area actually photographed divided by 0,02929 m, the square root of the area of a negative.

ANALYSIS

Area photographed

The area photographed by the camera, at various distances from the subject, was determined in a salt-water swimming pool. The camera was triggered at six distances 0,5—3,0 m from the subject. The relationship between the distance of the camera housing from the subject and the area photographed was:

$$y = 0{,}5858\ x^{1{,}9554}\ (r = 0{,}9989),$$

where y is the area photographed and x is the distance of the camera housing from the subject (both in metre), and r is the correlation coefficient.

This relationship was used to calculate the area photographed per exposure from the length of the trigger cord employed. Multiplication of this area by the total number of successful exposures (including partly successful ones) gave the total area successfully photographed (Table I).

Sampling zones

The study area was divided into four depth zones (Tables II and III). The total area sampled photographically in each of the three deeper zones was roughly equal, the mean area being 3 920 m^2. In the shallowest zone (Table II), a considerably smaller area of 884 m^2 was sampled, because the depth range was only 25 per cent of that of the other zones.

CRAB DENSITY PER SAMPLING ZONE

The number of red crabs photographed per sampling zone (N) is recorded in Tables II and III. From these numbers and the total number of observations (n), a mean and standard deviation from the mean of the number of crabs per exposure in each zone were calculated (Table III). They were further used,

Table II: Data used to estimate the population size in the 375—399 m depth zone between latitudes 19°30′ and 20°00′S — three confidence levels are given, each representing the level at which it is certain that the population in this depth zone does not exceed the value given

Information sought		Result
Total number of exposures (n)		166,13
Number of red crab seen (N)		0
Area photographed (m^2)		883,90
Mean area per exposure (m^2)		5,32
Area of depth zone (square nautical mile)		103,2
Area of depth zone (ha)		35 440
Maximum population and (density of crabs·ha^{-1}):	95% certain	1 191 000 (33,61)
	80% certain	642 000 (18,12)
	50% certain	277 000 (7,82)

together with the total area sampled photographically, to estimate the density of red crabs per hectare in each depth zone.

The total area of each depth zone sampled was calculated in both square nautical miles and hectares (Tables II and III). In Table III, the calculated total area and the estimated density of crabs per hectare are used to predict the red-crab population in each depth zone. Three probability values were calculated for each depth.

No red crabs were observed in any of the exposures taken in the 375—399 m depth zone (Table II). This is misleading, because *G. maritae* is known to occur at this depth (Beyers and Wilke 1980). It is therefore incorrect to conclude that there were no red crabs in this zone at the time of the survey. The following argument, based on one used by Horwood (1981), has therefore been formulated to estimate the maximum size of the red-crab population in this zone, for three statistical values of certainty.

Table III: Data used to estimate the population size in three different 100-m depth zones between latitudes 19°30′ and 20°00′S

Information sought	Results per depth zone (m)		
	400—499	500—599	600—699
Total number of exposures (n)	626,3	701,3	776,7
Number of red crab (N)	8	17	21
Mean number of red crab per exposure ($\bar{x}$)	0,0128	0,0242	0,0270
Variance (S^2)	0,0126	0,0237	0,0289
Standard deviation	0,1124	0,1539	0,1701
Area photographed (m^2)	3557,07	3844,16	4358,35
Density of red crab per hectare and (coefficient of variation)	22,49 (0,35)	44,22 (0,24)	48,18 (0,23)
Area of depth zone (square nautical mile)	182,7	143,9	129,0
Area of depth zone (ha)	62 750	49 420	44 300
Red-crab population and (95% confidence limits)	1 411 000 (971 000)	2 185 000 (1 027 000)	2 135 000 (944 000)

The probability of photographing crabs in a depth zone where they are known to occur is proportional to the area photographed and the density of the crab population spread over that zone. If N is the number of crabs in the depth range, A is the area between the depth ranges being considered and a is the area photographed in a single exposure, then the probability of photographing a crab in one exposure is

$$\frac{N a}{A} .$$

Conversely, the probability p of photographing no crabs in n exposures is

$$p = \left(1 - \frac{N a}{A}\right)^n .$$

If the results in Table II are used in the above expression, the value that one is 95 per cent certain the population N does not exceed may be obtained as:

$$0{,}05 = \left(\frac{1 - 5{,}32\,N}{3{,}544 \times 10^8}\right)^{166.13}$$

and $N = 1\ 191\ 000$.

Some partial exposures contribute to the value of 166,13 used in this relationship and not all exposures are of areas of the same size, but the formula, though approximate as a result, is considered to be sufficiently accurate for the purpose for which it is used here.

Estimates of maximum N for other levels of certainty are included in Table II.

The density of red crabs increased with depth (Tables II and III) to a maximum of 48 crabs·ha^{-1} in the depth zone 600—699 m. At 500—599 m, the density was similar (44 crabs·ha^{-1}), but the estimated population was larger because its area was greater. In this respect, it should be noted that the area encompassed per unit depth decreased from east to west (Tables II and III, Fig. 1) as the sea-bed assumed a steeper gradient with depth.

The estimated sizes of the crabs, as calculated from the photographs, ranged between 41 and 123 mm (carapace width). However, it should be noted that

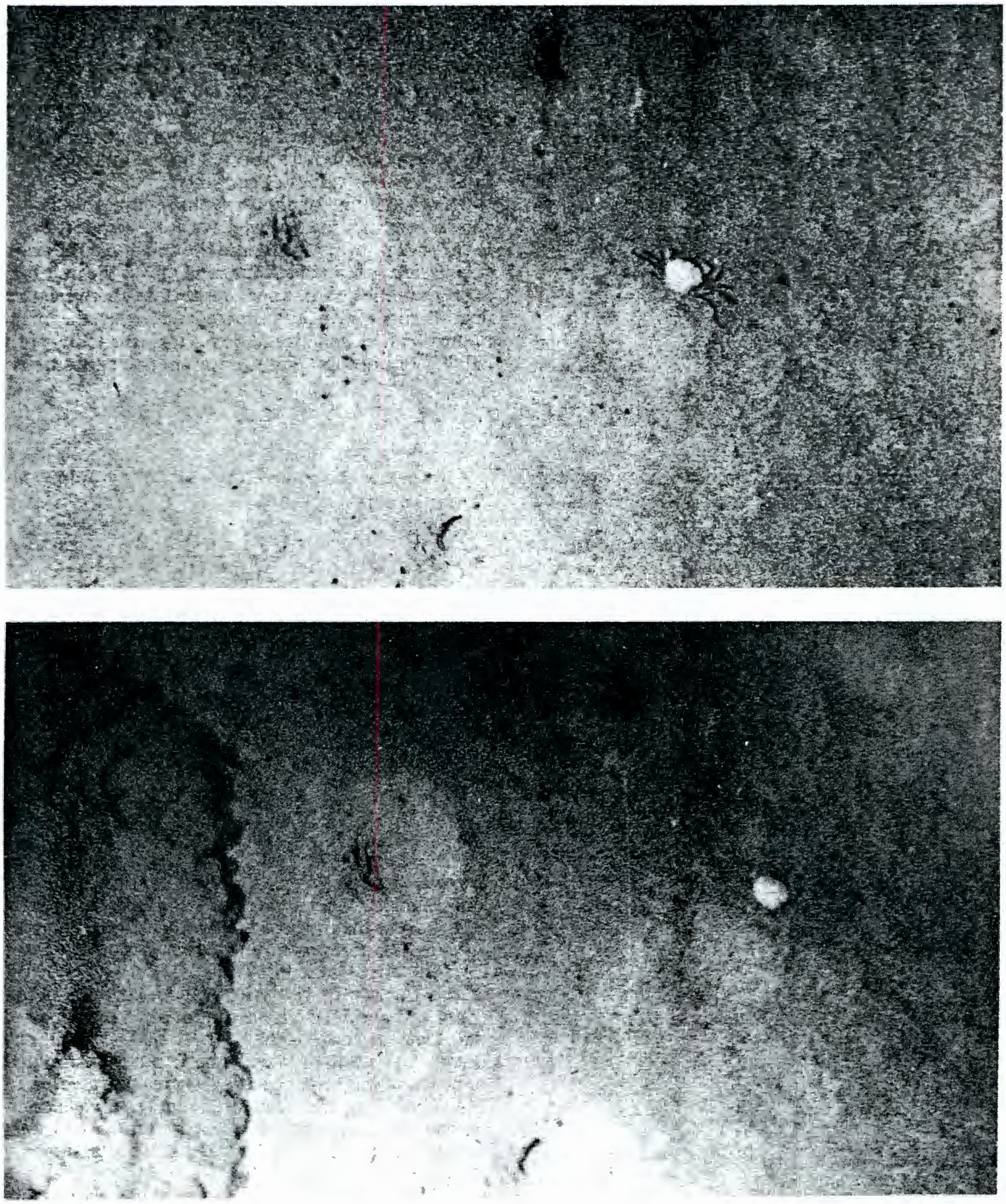

Fig. 2: A sequence of two exposures of the same area and crab taken within a short time interval — the lower photograph shows sediment disturbed while triggering the upper photograph

Fig. 3: A red crab *Geryon maritae* partially buried in silt (location — Film 95 in Table I)

measuring the size of a crab from a photograph can introduce error and therefore these estimated sizes should be viewed with caution.

DISCUSSION

It is not known how the red crabs behaved towards the physical disturbance caused by the camera gear during photography. Any active avoidance by the crabs in the area being photographed would obviously result in serious errors in the analysis of the data. Therefore, all the exposures in which crabs were photographed were closely examined in order to provide some clues in this regard.

None of the crabs appeared to be fleeing from the immediate vicinity in which they were photographed. This conclusion is drawn from the fact that any quick movement by a crab on a soft sediment bottom would have resulted in a trail of disturbance in the sediment. No such disturbance was observed in any of the photographs of crabs taken on this survey.

In one particularly unusual case, the camera photographed a crab and was hoisted up but, because the ship had not drifted, the gear came down in virtually the same place and photographed the same crab a second time (Fig. 2). The only reaction of the crab to the gear, as deduced from a comparison of the two exposures (Fig. 2), is that the crab apparently concealed its legs. This observation would suggest that the crab had either retracted its legs under its body, or it had succeeded in burying them under the silt. Either way, the result reinforces the assumption that crabs do not flee from the camera gear.

Several red crabs were photographed partially buried by sediment (Fig. 3). The extent to which the crabs are able to bury themselves could introduce an important source of error in a photographic survey. Further work is necessary, though it is considered unlikely that *G. maritae* burrow any deeper than the one shown in Figure 3. They possess none of the adaptations associated with burrowing crabs, e.g. flattened legs and modified respiratory openings. Also, crabs which were kept under laboratory con-

Table IV: Comparison of the estimated biomass values for *Geryon maritae* in five regions off the West African coast

Area	Biomass (kg·ha⁻¹)	Density (number·ha⁻¹)	Source of information
Ivory Coast	12,3 — 23,6		Cayré *et al.*(1979)
Congo	22,1 — 40,8		Cayré *et al.*(1979)
North Angola	8,6 — 16,6		Cayré *et al.*(1979)
South Angola	43,3 — 83,4		Cayré *et al.*(1979)
South West Africa	up to 6,9*	up to 23,0	Beyers and Wilke (1980)
South West Africa	up to 14,4*	up to 48,2	This study

* Estimated biomass determined from density values

Table V: Comparison of red-crab densities per depth zone obtained from trawling and photographic surveys of a similar area off South West Africa

Depth zone (m)	Mean density from trawling (number·ha⁻¹)#	Density from photography
375 — 399	1,2	<34*
400 — 499	3,7	22
500 — 599	7,5	44
600 — 699	3,4	48

* Value at 95-per-cent certainty
\# After Beyers and Wilke (1980)

ditions simulating their natural environment (except for pressure), frequently buried their limbs under sediment, but never their carapace.

There is very little quantitative information on the numerical abundance of red crabs off the West African coast. Published work (Dias and Machado 1973, Intès and Le Loeuff 1976, Le Loeuff *et al.* 1974, 1978) has mostly been semi-quantitative in nature, reporting on aspects of the biology and relative abundance of crabs as deduced from trap catches.

Two published studies (Cayré *et al.* 1979, Beyers and Wilke 1980) have attempted quantitative assessments of the abundance of West African red crabs. Cayré *et al.* (*op. cit.*) achieved their assessment by applying two sets of data derived from the stock off the United States of America to the West African stock. Raw catch-per-unit-effort information derived from trap fishing of *G. quinquedens* was related to the photographically determined densities of Wigley *et al.* (1975), and the biomass of *G maritae* (in kg·ha⁻¹) between 300 and 1 000 m for four regions of West Africa, all of them north of the South West African border, was derived by straight comparison (Table IV).

Beyers and Wilke (1980) estimated the density of West African red crabs over the same area as this study from trawl data. The density for each trawl was calculated from the number of crabs caught over the area trawled (Tables IV and V).

Comparison of results from this present study with those of Cayré *et al.* (1979) — see Table IV — is complicated by the difference in the units expressing the quantity of crabs per hectare.

Some comparison between the sets of data can be made by assuming the mean size of crabs in the 300—700 m depth range to be about 10,2 cm carapace width, as was found by Beyers and Wilke (1980). From the relationship between carapace width and whole mass established by the same authors, a red crab of 10,2 cm would have a mass of approximately 300 g. This figure was used to convert the density values recorded in Table IV to biomass.

The crab densities obtained in this survey were considerably higher than those obtained by Beyers and Wilke (1980) from trawling (Table V), sometimes by an order of magnitude. Assuming that the crab densities were similar during both surveys, the conclusions of other workers (Haefner 1978, Cayré *et al.* 1979) that trawl surveys are not effective in determining absolute densities of *Geryon* species would appear to be substantiated. Trawl surveys do, however, remain useful as an index of relative abundance and for obtaining biological information.

The present study is based on only a portion of the South West African red-crab grounds and must therefore be considered preliminary. More surveys are required to establish whether these density and biomass values are representative of the ground as a whole. Certainly, compared with other regions of the West African coast (Table IV), they are low.

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PAPER 7:

Density distribution by depth of *Geryon maritae* on the northern crab grounds of South West Africa/Namibia determined by photography in 1983, with notes on the portunid crab *Bathynectes piperitus*

S. Afr. J. mar. Sci. 3: 55–62
1985

DENSITY DISTRIBUTION BY DEPTH OF *GERYON MARITAE* ON THE NORTHERN CRAB GROUNDS OF SOUTH WEST AFRICA/NAMIBIA DETERMINED BY PHOTOGRAPHY IN 1983, WITH NOTES ON THE PORTUNID CRAB *BATHYNECTES PIPERITUS*

*R. MELVILLE-SMITH**

The density of red crab *Geryon maritae* between 18°00′ and 18°30′S and in depths of 350-1 000 m was quantitatively examined by photography. This area, estimated to be approximately 92 000 ha, is part of the commercial crab ground off South West Africa. The biomass of red crab, up to 55,5 kg·ha^{-1}, is one of the highest recorded off the African coast for the species. Density of red crab was highest in depths exceeding 600 m, the greatest density (350,2 crabs·ha^{-1}) being recorded in the 600-699 m depth zone. Another crab, *Bathynectes piperitus*, was also photographed in the shallower depths of the survey area (300-500 m), and some density estimates for this species at those depths are presented.

Die digtheid van rooikrap *Geryon maritae* tussen 18°00′ en 18°30′S en op dieptes van 350-1 000 m is deur middel van fotografie kwantitatief ondersoek. Hierdie gebied, wat volgens raming ongeveer 92 000 ha beslaan, maak deel uit van die kommersiële krapgronde teenoor Suidwes-Afrika. Die biomassa van rooikrap, tot 55,5 kg·ha^{-1}, is van die hoogstes wat langs die kus van Afrika vir die spesie opgeteken is. Die grootste digtheid van rooikrap is op dieptes benede 600 m aangetref, waar die hoogste syfer (350,2 krappe·ha^{-1}) in die dieptesone 600-699 m opgeteken is. 'n Ander krap, *Bathynectes piperitus*, is ook op vlakker plekke in die opnamegebied (300-500 m) gefotografeer, en 'n aantal digtheidsramings vir hierdie spesie op daardie dieptes word aangebied.

A short history of the commercial exploitation of red crab *Geryon maritae* off South West Africa (Namibia) has been given by Beyers and Wilke (1980). The stock continues to support a small but intensive fishery and, over the period 1981-1984, the total yield fluctuated between 3 100 and 3 600 tons of processed product.

Estimates of stock density for red crab off South West Africa are limited to a series of trawling surveys (Beyers and Wilke 1980) and a single photographic survey (Melville-Smith 1983), all conducted in the area 19°16′-20°01′S. The photographic survey suggested the method to be reliable for estimating the density of the species, but time limitations precluded surveying all but the shallower depths at which crab occur in commercial quantities (375-700 m).

The latest survey was aimed at quantitatively examining changes in crab density with depth over the full depth range at which the red crab occurs in commercial quantities.

Trawling and trap fishing (Sea Fisheries Research Institute, unpublished data) have shown, in semi-quantitative terms, that red crab are generally more abundant in the northern part of the known crab grounds. A second objective of the survey was therefore to compare quantitatively the variation in abundance of red crab in the area surveyed during this study (*c.* 18°00′-18°30′S) with that obtained in 1981 by Melville-Smith (1983). For this reason, the area selected for this latest survey was sited well north of the 1981 photographic survey area (Fig. 1.)

METHODS

A full account of the gear and the methods used to photographically assess stock density of red crab off South West Africa has been given by Melville-Smith (1983). The gear used for this latest survey, in August 1983, was essentially the same, although several improvements were made in order to optimize the area of coverage per exposure:

(i) an additional Benthos model 381 flash unit was added to improve the illumination capabilities;
(ii) the camera frame was extended to allow the flash units to be positioned approximately 1 m below the camera unit, thereby reducing unnecessary scattering of the flash beam by particles in the water;
(iii) the film used was 36-exposure monochrome Ilford XP-1 film, with a 400 ASA rating. Because of its wide exposure latitude, this film was found to be ideal for increasing the level of detail in the shadows, at the extremities of the area illuminated by the flashes.

By improving the quality of illumination, it was

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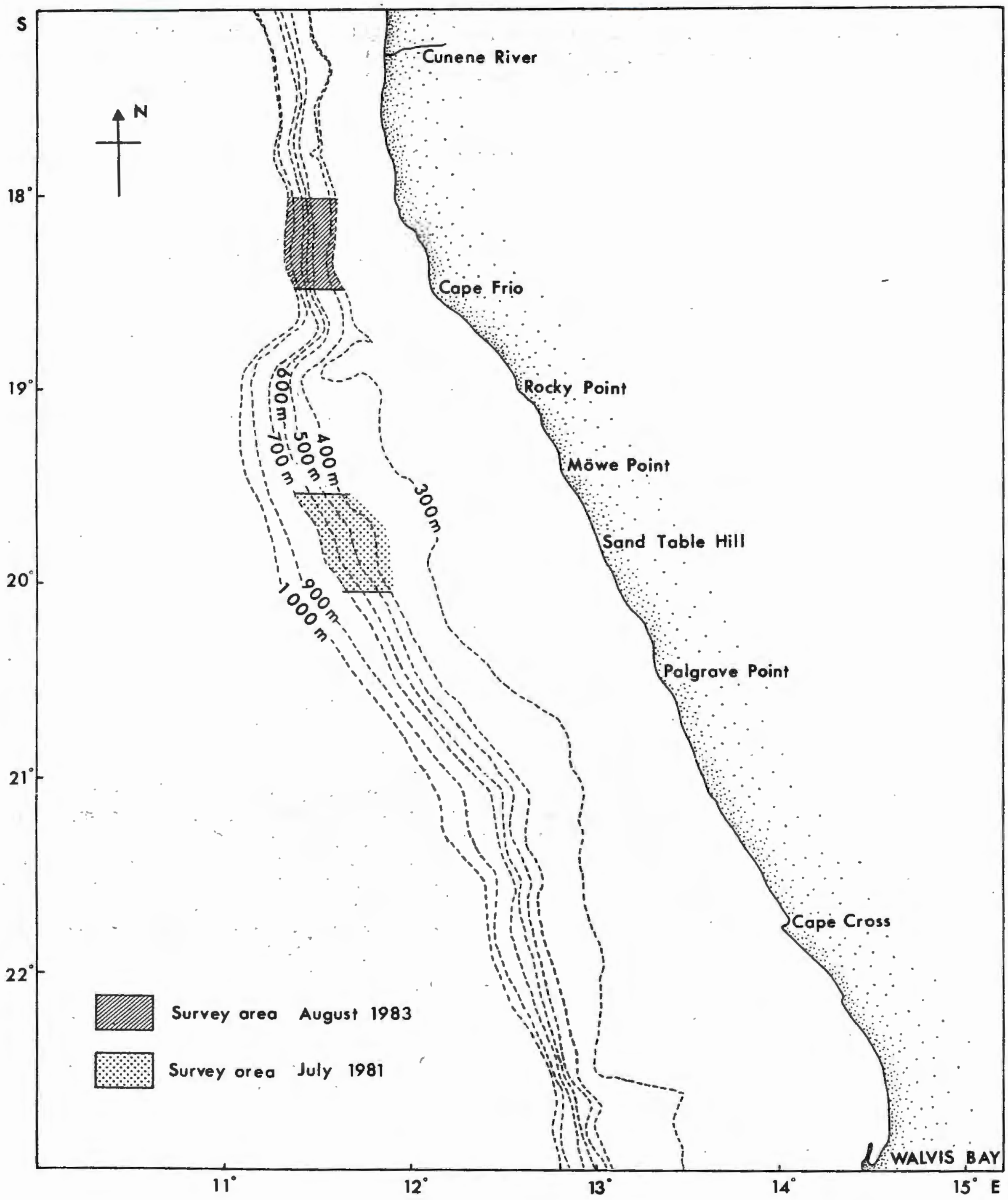

Fig. 1: The study area and bathymetry of the depths surveyed (after Bremner 1981) for this report and for that of Melville-Smith (1983) — station locations are presented in Table I

Table I: Film reference number, date, position and depth range at which exposed, and the number of *B. piperitus* and *G. maritae* observed

Film number	Date	Depth range (m)	Position at start		Number of *B. piperitus*	Number of *G. maritae*	Total area successfully filmed (m²)
1	23/8/83	394—400	18°30,0'S	11°26,5'E	10	0	194,7
2	23/8/83	940—949	18°27,0'S	11°17,0'E	0	0	103,5
3	23/8/83	864—920	18°29,0'S	11°18,0'E	0	9	185,0
5	24/8/83	400—419	18°29,8'S	11°25,5'E	2	11	184,2
6	24/8/83	425—438	18°30,0'S	11°25,5'E	1	2	252,1
7	24/8/83	454—468	18°30,3'S	11°25,7'E	1	1	220,7
8	24/8/83	475—487	18°29,0'S	11°24,0'E	0	3	216,8
9	24/8/83	494—508	18°29,0'S	11°23,0'E	0	1	177,4
10	24/8/83	534—562	18°29,0'S	11°23,0'E	0	2	164,6
11	24/8/83	550—569	18°29,0'S	11°23,0'E	0	1	179,9
12	25/8/83	575	18°29,6'S	11°22,7'E	0	6	215,2
13	25/8/83	596—602	18°29,6'S	11°22,5'E	0	3	183,3
14	25/8/83	642—646	18°29,1'S	11°21,8'E	0	4	180,2
15	25/8/83	650—660	18°28,7'S	11°21,3'E	0	8	178,8
16	25/8/83	657—682	18°28,6'S	11°21,1'E	0	4	178,2
17	25/8/83	705—723	18°29,5'S	11°20,6'E	0	5	203,8
18	25/8/83	758—759	18°30,0'S	11°19,7'E	0	1	156,5
19	25/8/83	736—752	18°30,7'S	11°20,0'E	0	1	162,0
20	26/8/83	770—810	18°29,9'S	11°19,0'E	0	3	205,3
21	26/8/83	800—848	18°29,8'S	11°19,5'E	0	0	191,3
22	26/8/83	821—858	18°29,6'S	11°18,9'E	0	4	217,8
23	26/8/83	848—852	18°29,5'S	11°18,9'E	0	3	159,6
24	26/8/83	884—899	18°30,0'S	11°18,0'E	0	11	214,5
25	26/8/83	900—965	18°29,9'S	11°18,8'E	0	0	228,8
26	27/8/83	837—874	18°00,1'S	11°18,3'E	0	15	212,0
27	27/8/83	901—997	18°01,0'S	11°17,5'E	0	0	229,1
28	27/8/83	890—912	17°59,8'S	11°18,0'E	0	0	250,4
29	27/8/83	847—850	17°58,8'S	11°17,9'E	0	9	251,3
30	27/8/83	890—906	17°57,5'S	11°18,3'E	0	0	239,2
31	27/8/83	825—864	17°58,5'S	11°19,5'E	0	14	287,3
32	28/8/83	736—768	17°59,9'S	11°18,7'E	0	6	283,7
34	28/8/83	720—800	17°59,1'S	11°20,2'E	0	10	250,5
35	28/8/83	696—768	17°58,7'S	11°19,9'E	0	6	260,3
38	29/8/83	600—604	18°02,1'S	11°22,5'E	0	1	13,6
39	29/8/83	604—620	18°00,1'S	11°21,9'E	0	4	219,2
40	29/8/83	637—640	18°01,5'S	11°22,1'E	0	8	211,3
41	29/8/83	680—692	18°00,9'S	11°20,9'E	0	8	165,9
43	29/8/83	575—605	18°00,2'S	11°21,7'E	0	0	230,7
44	30/8/83	548—572	18°00,8'S	11°22,7'E	0	0	205,6
45	30/8/83	651—691	18°01,1'S	11°22,1'E	0	11	223,3
46	30/8/83	520—548	17°59,5'S	11°21,8'E	0	0	177,1
47	30/8/83	500—516	17°59,2'S	11°22,6'E	0	0	200,1
48	30/8/83	475—520	18°00,1'S	11°23,9'E	0	0	251,7
49	30/8/83	448—500	17°58,8'S	11°22,6'E	0	0	225,2
50	30/8/83	425—458	18°00,1'S	11°23,5'E	0	0	289,0
51	30/8/83	712—740	18°01,1'S	11°21,6'E	0	7	227,3
52	30/8/83	912—981	18°00,4'S	11°18,5'E	0	0	232,4
54	30/8/83	390—420	17°59,3'S	11°23,5'E	1	5	289,9
55	30/8/83	350—370	18°00,4'S	11°24,4'E	4	0	302,2
56	30/8/83	442—474	18°01,4'S	11°24,5'E	1	0	296,5

possible to photograph at distances of up to 4,6 m from the subject. The area photographed per exposure was calculated from the relationship derived by Melville-Smith (1983):

$$y = 0{,}5858\ x^{1{,}9554},$$

where y is the area photographed and x is the distance of the camera housing from the subject (both in metre).

The improved lighting caused an increase of 28,1 per cent in mean area photographed per exposure, from 5,7 m² in July 1981 to 7,3 m² on this survey.

Because of the emphasis placed on increasing the area of coverage per frame, many of the exposures were poorly illuminated at their extremities. These

Table II: Data used to estimate the population size in seven different 100-m depth zones between latitudes 18° 00′ and 18° 30′S

Information sought	Results per depth zone (m)						
	300*—399	400—499	500—599	600—699	700—799	800—899	900—999
Total number of exposures (*n*)	59	284	267	210	231	265	139
Number of red crab (*N*)	0	22	13	48	39	65	0
Mean number of red crab per exposure ($\bar{x}$)	—	0,0775	0,0487	0,2286	0,1688	0,2453	—
Standard deviation	—	0,3162	0,2324	0,4537	0,4294	0,4887	—
Area photographed (m²)	496,9	2 226,1	1 733,9	1 370,5	1 749,4	1 958,0	1 044,2
Density of red crab per hectare and (coefficient of variation)	—	98,83 (0,24)	74,98 (0,29)	350,24 (0,14)	222,93 (0,17)	331,97 (0,12)	—
Area of depth zone (square nautical mile)	32,67	54,89	41,21	37,25	38,43	33,42	30,65
Area of depth zone (ha)	11 220	18 850	14 150	12 790	13 200	11 480	10 520
Red crab population and (95% confidence limits)		1 863 000 (885 000)	1 061 000 (607 000)	4 480 000 (1 203 000)	2 943 000 (965 000)	3 811 000 (914 000)	

*No depths shallower than 350 m were surveyed underexposed (and therefore rejected) areas were calculated for each of the affected frames with a KONTRON Videoplan electronic digitizer board, and the area of ground covered credited to each exposure was readjusted by subtracting the percentage of the exposure area rejected.

No attempt was made to estimate the actual size of the crabs photographed. Although it is possible to measure the size of the crabs in the photographs, the degree of error is considered to be too large to use this method.

RESULTS

The area exposed for each of the 56 films taken on this survey is shown in Table I. For ease of analysis, the study area was subdivided into 100-m depth zones (from 300 to 999 m), and each film was assigned to a single one of these depth zones. Where a film traversed two depth zones, a mean of the depth at the start and end of filming was taken, and the entire film was categorized as the depth zone indicated by the mean.

Crab density per sampling zone

All relevant data used to estimate the density of crabs per depth zone are given in Table II. The number of exposures taken per zone was approximately equal (200–300) except for the shallowest (300–399 m) and deepest (900–999 m) zones. No red crabs were observed in these latter two zones and, because the object of the study was to examine the crab density in the productive area of the grounds, less effort was expended on photographing in these zones of obviously low crab density.

Although the data are skewed with a large proportion of the photographs not recording any crabs, the high number of replicates used to establish the crab density in each zone ($n = 200–300$) makes the central limit theorem applicable. Under these circumstances the estimated mean density of crab may be considered to be normally distributed around the true mean.

Some quantitative information is available on the abundance of red crab in areas off the West African coast (Table IV of Mellville-Smith 1983). Those data are given in units of biomass (kg·ha^{-1}) and, for comparison with the results of this study, it was necessary to convert the values of crab density determined by photography to biomass values.

The mean size of crabs in the area of this survey was determined from trawling data collected over the same area and depths in August 1982. The mean carapace width for all depths for the sexes combined was 8,2 cm. From the relationship between carapace width and whole wet mass given by Beyers and Wilke (1980), a single live male red crab with a carapace width of 8,2 cm could be assumed to weigh 158,6g. Hence, a density of 350,2 crabs·ha^{-1} would amount to a biomass of 55,5 kg·ha^{-1}. The comparative biomass data are listed in Table III.

Table III: Comparison of the estimated biomass values of *Geryon maritae* in six regions off the West African coast

Area	Biomass (kg·ha^{-1})	Density (number·ha^{-1})	Source of information
Ivory Coast	12,3—23,6	—	Cayré *et al.* (1979)
Congo	22,1—40,8	—	Cayré *et al.* (1979)
North Angola	8,6—16,6	—	Cayré *et al.* (1979)
South Angola	43,3—83,4	—	Cayré *et al.* (1979)
South West Africa (17°58'S—18°30'S)	up to 55,5*	up to 350,2	This study
South West Africa (19°27'S—20°01'S)	up to 14,4*	up to 48,2	Melville-Smith (1983)

*Estimated biomass determined from density values

DISCUSSION

The results (Table II) suggest that *G. maritae* are only abundant along a depth corridor of 400-900 m. The species has been recorded much shallower (270 m) off South West Africa and even shallower (100 m) elsewhere in the Atlantic Ocean (MacPherson 1983). the deepest recorded capture of *G. maritae* was 936 m (MacPherson op. cit.), a figure close to the maximum depth at which red crabs were recorded during this study (Films 23, 24, 26 and 29 — see Table I).

Comparison of data from this survey with information from an area 90 nautical miles further south sampled in 1981 (Melville-Smith 1983) shows that, because of the narrower continental shelf in the north (Fig. 1), the area per depth zone in this survey was approximately 3,4 times smaller than in the earlier survey. Also, the area photographed and upon which the density calculations per zone were made was 1,5-3,2 times smaller. The crab density was higher in the area surveyed in this study (Table IV) and, as a result, the accuracy (as gauged from the coefficient of variation) was correspondingly better. Even though

Table IV: A comparison of *Geryon maritae* photographic stock density assessment data for two areas of the South West African red-crab grounds

Parameter	Results per depth zone (m) per survey period*					
	400—499		500—599		600—699	
	1981	1983	1981	1983	1981	1983
Area photographed (m^2)	3 557,1	2 226,1	3 844,2	1 733,9	4 358,4	1 370,5
Density of red crab per hectare	22,49	98,83	44,22	74,98	48,18	350,24
Coefficient of variation	(0,35)	(0,24)	(0,24)	(0,29)	(0,23)	(0,14)
Area of depth zone (ha)	62 750	18 850	49 420	14 150	44 300	12 790
Red crab population and (95% confidence limits)	1 411 000 (971 000)	1 863 000 (885 000)	2 185 000 (1 027 000)	1 061 000 (607 000)	2 135 000 (944 000)	4 480 000 (1 203 000)

*1981 data from Melville-Smith (1983); 1983 data from this survey

the area per depth zone on the more southern of the South West African grounds was far greater than that found during this survey, the greater crab density in the lower latitudes resulted in the estimated number of crabs per depth zone being higher in two of the three zones compared in Table IV.

In addition to that from photography, the observation that *G. maritae* are more abundant in the more northerly areas of South West Africa has also been made from trawling and trap fishing (Sea Fisheries Research Institute, unpublished data). Examined in its geographical perspective, this observation presents an interesting trend in the biomass of red crab off West Africa (Table III). Moderate values have been recorded in survey areas in the north (Ivory Coast) and south (southern survey area off South West Africa), with maximum values in between off southern Angola. The only data that do not fit this distribution pattern are those from off northern Angola (Table III).

The crabs tended to be more abundant in the deeper zones (cf. < 600 m and > 600 m). This observation contrasts with the results obtained off Angola by Dias and Seita Machado (1973) and the Ivory Coast (Intès and Le Loeuff 1976, Le Loeuff *et al.* 1978). These studies concluded that best catches (in terms of numbers of crabs caught) were made in depths of 400–600 m (Ivory Coast) and 400–500 m (Angola).

There is no obvious reason for the difference in crab density at depth though, on the South West African grounds, where commercial crab fishing has taken place since 1973, the depth-related densities might be attributed to fishing pressure as well as to biological or hydrological factors, or indeed to a combination of all three.

On both this and the 1981 surveys, the high 300- and low 400-m depth zones tended to be dominated by a portunid crab *Bathynectes piperitus* (Tables I and V). These crabs, which are smaller than red crabs, are caught in considerable numbers in crab traps set in the shallower water, often together with *Geryon maritae.* The two species could therefore be food competitors. Though it is unlikely that the dominance of *B. piperitus* in the lesser depths is the only cause for the shoreward boundary in the distribution of *G. maritae,* the competition generated by the former species may be a contributing factor.

Although the two species overlap in distribution, the obvious shell markings of *B. piperitus* make it easily distinguishable from the red crab (Fig. 2), even in poorly illuminated photographs. *B. piperitus* frequently appears to hide itself by burrowing or by closely associating with any objects lying on the bottom. In consequence photographic density estimates of this species may be biased, but they have nevertheless been included in Table V because they do give an indication of the high density of the species where it overlaps with the red crab.

Table V: Mean density of *Bathynectes piperitus* and *Geryon maritae* by depth zone in two areas of the South West African red-crab grounds

Depth zone *(m)*	Mean density (number·ha^{-1}) on each survey			
	B. piperitus		*G. maritae*	
	1981	1983	1981	1983
*300—399	294,15	281,76	0	0
400—499	44,98	26,95	22,49	98,83
500—599	0	0	44,22	74,98

* No depths shallower than 350 m were surveyed

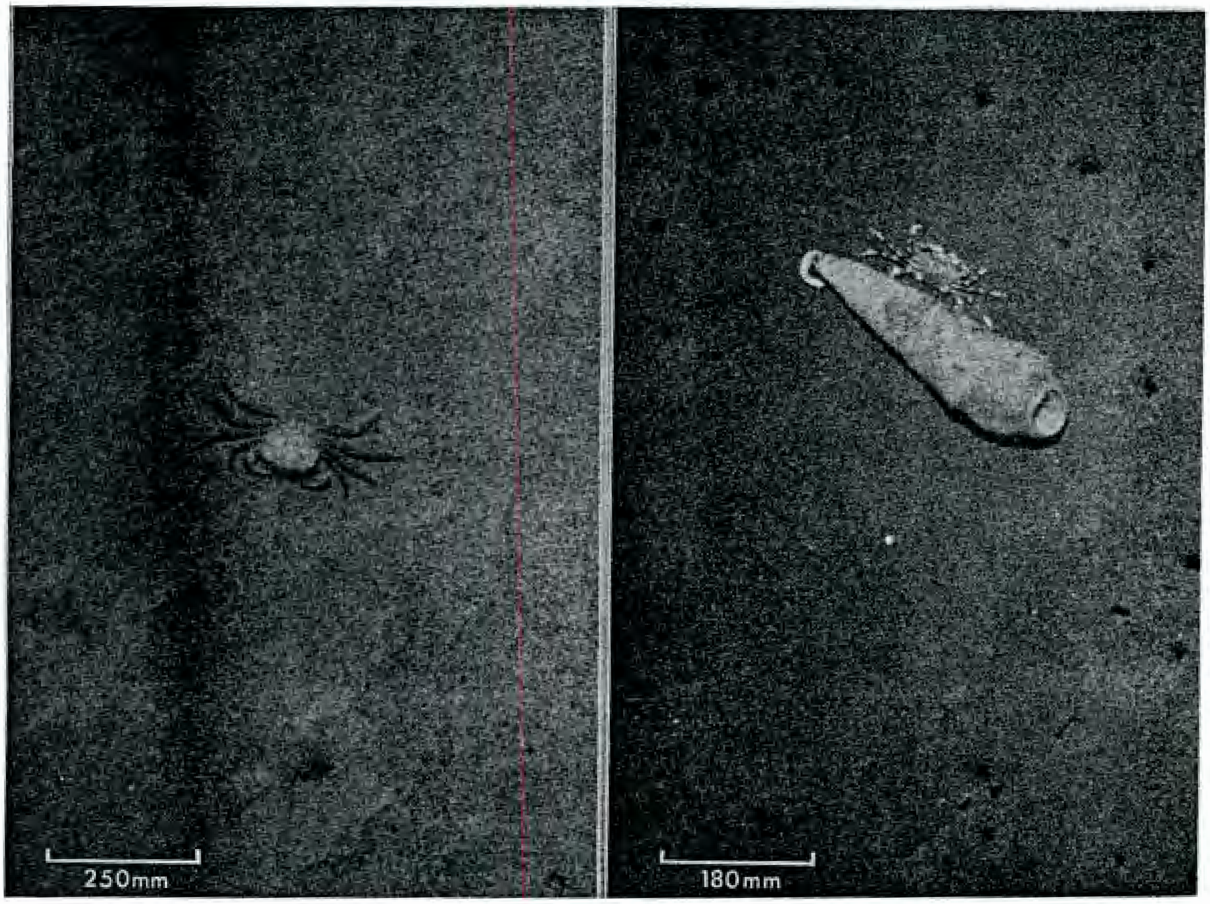

Fig. 2: Obvious dissimilarity between *Geryon maritae* (left) and *Bathynectes piperitus* (right), the latter sheltering next to a sponge of the genus *Suberites*

Photography appears to be the most adequate means available at present of assessing the stock density of *G. maritae*. It is, unfortunately, a time-consuming technique, and consequently the area that can be covered in a survey is severely limited. Future work will attempt to combine photography with trap fishing, in order to establish a relationship between trap catches and crab density. If such a relationship does exist, research and commercial trap-fishing data can be combined, thus allowing rapid estimates of red crab density to be made over a wide area.

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PAPER 8:

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
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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

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The mean effective fishing area (EFA) of a Japanese-type crab trap fishing for *Geryon maritae* on the northern South West African red-crab grounds was calibrated as 2 160 m². The commercial fishery uses traps covered with 90-mm mesh. In order to be able to use the density results obtained by this survey from traps covered with 60-mm mesh, a preliminary mesh selectivity study was carried out. The carapace width at 50-per-cent retention for 90-mm mesh was estimated as 72 mm. Based on the EFA results, it seems that most commercial fishing takes place in areas of crab density varying between 46 and 231 crabs·ha^{-1}, but that densities can reach ~510 crabs·ha^{-1}. It is suggested that crab traps would fish more efficiently on the northern South West African crab grounds if longlines were set across the depth contours rather than in a longshore direction.

Die gemiddelde effektiewe vanggebied (EVG) van die Japannese tipe van krapfuik wat *Geryon maritae* gevang het op die rooikrapgronde teenoor noordelike Suidwes-Afrika, is as 2 160 m² gekalibreer. Die kommersiële vissery gebruik fuike wat met 90-mm-maas bedek is. Ten einde gebruik te kan maak van die digtheidsresultate verkry uit hierdie opname van fuike met 60-mm-maas, is vooraf 'n maasselektiwiteitstudie gedoen. Die geraamde rugdopwydte by behoud van 50 persent vir 90-mm-maas was 72 mm. Op grond van die EVG-resultate wil dit voorkom asof die meeste handelsvangste plaasvind in gebiede waar krapdigtheid van 46 tot 231 krappe·ha^{-1} wissel, maar dat digthede ~510 krappe·ha^{-1} kan bereik. Daar word aan die hand gedoen dat vangste met krapfuike op die krapgronde teenoor die noordelike deel van Suidwes-Afrika doeltreffender sou wees indien langlyne, eerder as in 'n kuslangse rigting, dwarsoor die dieptekontoere geplaas sou word.

During recent years attempts have been made at the Sea Fisheries Research Institute to achieve reliable estimates of stock density for the deep-sea red-crab fishery off South West Africa (Namibia). Recognized methods such as trawling (Beyers and Wilke 1980), photography (Melville-Smith 1983, 1985) and tagging have been employed with varying degrees of success to this end.

Trawling has been shown to introduce large errors possibly due to the net bouncing on the bottom and thus allowing crabs to escape underneath the ground rope. Photography is a reliable but slow method, so that only relatively small areas can be covered. Tagging has yet to be fully assessed, but tentative results suggest that problems may be posed by unknown tagging and natural mortalities, as well as by movements of crabs in and out of the tagging area.

Miller (1975) estimated the density of the crab *Chionoecetes opilio* by calibrating the effective fishing area (EFA) for a single trap. Once this factor has been established, it is possible (making several assumptions) to estimate the density of crabs in a particular area if the mean catch per trap in that area is known. This technique has been used subsequently on red crab by Le Loeuff *et al.* (1978), Stone and Bailey (1980), McElman and Elner (1982) and Barea and Defeo (1984).

The present study was aimed at calibrating the effective area fished by a conventional crab trap of the Japanese type on the South West African red-crab grounds, with a view to substantiating future estimates of stock density. It had the additional aim of examining whether any inferences could be made from these results of benefit to the deployment of traps by the commercial fishery.

METHODS

The EFA trap calibrations were conducted over seven days from 23 to 29 June 1985. Two areas were chosen, one of known high crab density (~18°00'S, 11°21'E, 520–570 m) and the other of low crab abundance on the periphery of the commercial red-crab grounds (~21°00'S, 12°16'E, 620–640 m). For reasons outlined later, data obtained from the latter area were not used in the EFA calculations.

To derive an estimate of EFA, two variables, crab density and mean crab catch per trap, are needed. Two research ships were used to estimate these variables. The photographic work (to estimate crab

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density) was undertaken by the R.S. *Benguela* and trap fishing was done simultaneously by the P.V. *Caroline*.

Photography

Crab density was calculated in a fashion similar to that described by Melville-Smith (1983). The photography was carried out with a deep-water camera unit built at the Sea Fisheries Research Institute and fitted with a 24-mm wide-angle lens and a double set of flash housings, each with a flash unit of 110 watt-second output.

The area defined for the photographic density estimate fell between latitudes 18°00′ and 17°55′S and depths of 520 and 570 m. The ship was allowed to drift over the survey area while exposures were taken of the bottom. During the survey, the trigger of the camera was set to trip at several different distances off the bottom. The areas covered by the resultant exposures were calculated by means of the following equation derived for the system:

$$y = 0{,}76\, x^{2{,}0},$$

where y is the area photographed and x is the distance of the camera housing from the subject (both in metres). The correlation coefficient (r) was 0,996. The distance of the camera from the bottom found to be most suitable as regards area of coverage and dissipation of flash lighting was 2,4 m (for Ilford XP 1 film). Substituting this distance in the above equation gives an area of coverage of 4,38 m^2 per exposure.

The camera had a bulk-film loader, which gave it the capacity to take 250 exposures without raising the gear to the surface. This capability was not used to full advantage, because on most occasions the ship drifted beyond the boundaries defining the study zone.

Trap fishing

Commercial-sized, conical crab traps, measuring 136 and 78 cm in diameter at the base and the top respectively and 60 cm in height, were set on longlines of 15 traps per line spaced 10 fathoms (~18,2 m) apart. The traps were baited with horse mackerel and left for 16–19,5 hours (except for a single line which was only set for 6,5 hours) in an area close to that being photographed (i.e. between 17°54′ and 18°02′S and in the depth range 526–566 m). The mean number of crabs caught per trap was calculated for each longline.

Standardization of research and commercial gear

The research traps were fitted with 60-mm mesh netting in contrast to the 90-mm mesh used by the commercial fishery, resulting in somewhat different size compositions.

In order to standardize the commercial and research results, six commercial crab samples ($n = 1\ 808$) taken close to the research area during March and May 1985 (all within 15 nautical miles of 18°00′S), were analysed and compared with the six research samples obtained on this survey ($n = 1\ 688$). Both the commercial and the research data were standardized to reflect the expected catch per 100 traps for each size increment of a millimetre carapace width (CW). A selection curve was calculated by the method described by Gulland (1969), which allowed the research sample to be adjusted to the size composition to be expected with 90-mm mesh.

Analysis

The fishing area of a single crab trap was estimated by means of the formula

$$\mathrm{EFA} = \mathrm{C}\left(\frac{\text{Catch (crabs}\cdot\text{trap}^{-1})}{\text{Density of crabs}\cdot\text{m}^{-2}}\right)$$

derived by Miller (1975) and modified for this study by the addition of a mesh constant (C) to compensate for the selectivity of different mesh sizes.

RESULTS

As already stated, the EFA was examined in two areas of very different crab densities. In the area around 21°00′S (low density), only one crab was identified in the 2 560 m^2 area photographed. Obviously no valid conclusion could be drawn from this result regarding crab density, and therefore the results from this area are not presented.

Photography

The area photographed and numbers of crabs seen in each film are presented in Table I. Only the

Table I: Details of photographic work and the number of *G. maritae* observed

Film	Date	Depth range (m)	Position at end	Number of *G. maritae*	Area filmed (m²)
13	26/6/85	538–552	17°58,7'S, 11°21,5'E	5	468,3
14	26/6/85	556–568	17°57,5'S, 11°21,3'E	4	442,1
15	26/6/85	560–570	17°58,5'S, 11°20,7'E	0	91,9
17	27/6/85	520–524	17°58,1'S, 11°20,9'E	4	144,4
18	27/6/85	552–570	17°59,9'S, 11°21,3'E	3	236,4
19	27/6/85	530–549	17°59,1'S, 11°21,0'E	1	293,3
20	27/6/85	540–573	17°58,1'S, 11°21,5'E	3	319,5
21	27/6/85	540–570	17°56,2'S, 11°20,7'E	1	232,0
22	27/6/85	533–550	17°59,2'S, 11°20,8'E	1	14,2
23	28/6/85	532	17°57,9'S, 11°21,7'E	1	21,9
24	28/6/85	550–560	17°59,7'S, 11°22,2'E	1	183,8
25	28/6/85	544–548	18°00,2'S, 11°22,6'E	1	70,0
26	28/6/85	540–544	17°54,6'S, 11°20,2'E	24	857,9

Table II: Data used to estimate the density of crabs in the study area

Information sought	Results
Total number of exposures	857
Number of red crab	49
Mean number of red crab per exposure	0,0572
Standard deviation	0,2323
Area photographed (m²)	3 375,7
Density of red crab per hectare	145,16
Coefficient of variation	0,14

positions at the end of each film have been listed, because those at the start of filming were all within half a nautical mile of 18° 00'S. The results are further summarized in Table II, and the density of crabs per hectare in the study area (18°00'–18°05'S, 520–570 m) has been estimated as 145,2 crabs·ha^{-1}.

All the crabs photographed were measured and were estimated to range from 56 to 110 mm CW, though measurements are not very accurate because of the distortion caused by the wide-angle lens.

Trap fishing

Trap-fishing data for the area 17°56,5'–18°01,7'S are shown in Table III. An obvious feature is the large variation in the number of crabs caught per trap (13,5–51,1). The mean catch of 31,4 crabs·trap^{-1} was comparable to recent commercial catches in the same area, although some crabs in the research catches were smaller than would be expected from a commercial catch sample (Fig. 1).

Standardization of research and commercial gear

A comparison of the number of crabs caught in each millimetre size increment for the research and the commercial gear shows that the traps with 60-mm mesh retained more small-sized crabs than those with 90-mm mesh (Fig. 1). Assuming that the research gear retained all crabs caught of the smaller size classes, the percentage of the catch that escaped through the 90-mm commercially used mesh could be calculated for each size increment as described by

Table III: Details of research trap fishing, showing number of crabs caught and mean number of crabs caught per trap on each longline

Longline number	Date (m)	Depth (m)	Position	Soak time (h)	Number of traps	Number of crabs caught	Catch rate (crabs·trap^{-1})
5	26/6/85	535	18°00,9'S, 11°22,6'E	16,0	15	202	13,5
6	26/6/85	546	18°01,2'S, 11°23,8'E	16,5	15	767	51,1
7	26/6/85	557	18°01,7'S, 11°24,1'E	17,0	14	461	32,9
8	27/6/85	526	17°59,0'S, 11°20,9'E	16,5	13	592	45,5
10	27/6/85	566	17°54,5'S, 11°21,6'E	19,5	15	336	22,4
12	29/6/85	546	17°57,6'E, 11°20,4'E	6,5	14	339	24,2
Mean							31,4

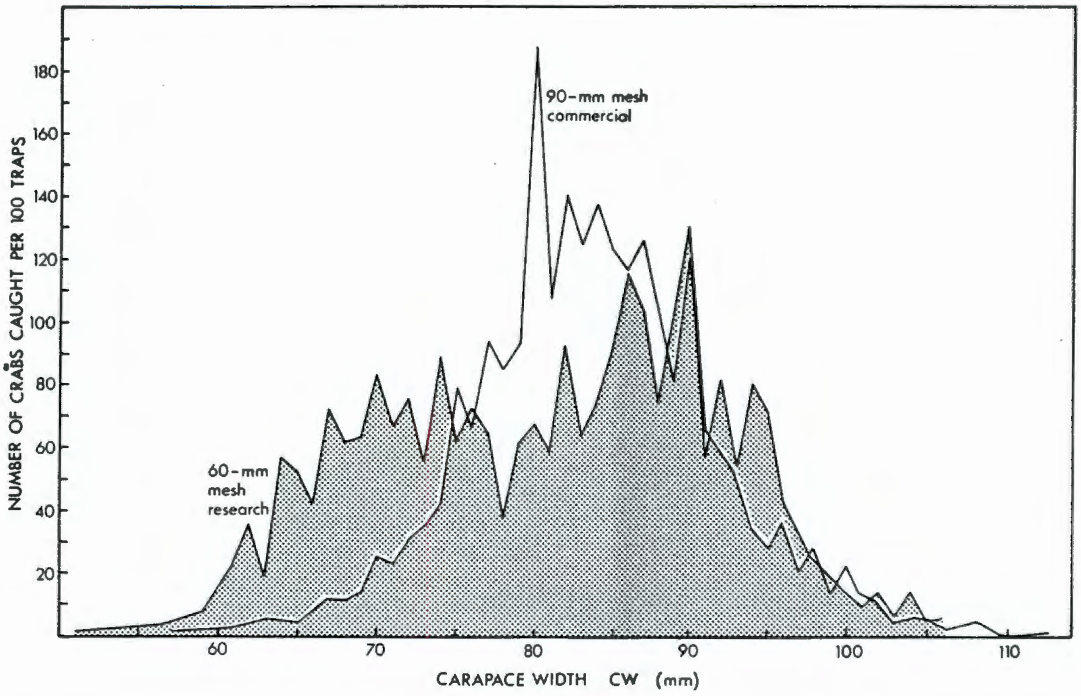

Fig. 1: Size composition of crabs caught during this survey (with 60-mm mesh) and by a commercial vessel fishing in the same area (with 90-mm mesh)

Gulland (1969) and plotted (Fig. 2). From Figure 2, it would appear that, for the 90-mm mesh, 50- and 100-per-cent retention are at some 72 mm and 75 mm CW respectively.

From the estimated retention percentage by 90-mm mesh for each size increment less than 72 mm CW, the results from the research traps (*r*) have been adjusted to the number of crabs which would have been expected to have been caught had 90-mm mesh been used (*r1*). Minimum, maximum and mean catches per trap for research traps plus the calculated mean number that would have been caught by commercial traps are presented in Table IV.

Table IV: Maximum, minimum and mean number of crabs caught per trap with 60-mm mesh, and estimates of expected mean catch for 90-mm mesh and mean mesh constant

Mesh (mm)	Minimum	Maximum	Mean
60 90	13,5	51,1	31,4 (= *r*) 24,4 (= *r1*)
Mesh constant C			1,287

Effective fishing area

The maximum, minimum and mean EFA of a crab trap, calculated by means of the formula given earlier, are presented in Table V. The catches per trap used in the EFA calculations were taken from Table IV and the density of crabs per square metre was taken as 0,01452, the figure deduced from photography (Table II).

In calculating the EFA for 60-mm mesh, it was assumed that all the crabs photographed would have been retained by the traps (i.e. a 56-mm-CW crab, the smallest photographed, would not have been able to pass through that mesh). Therefore, no mesh constant was necessary for estimating the research EFA. However, in the case of the 90-mm mesh 10–30 per

Table V: Calculated minimum, maximum and mean EFA for baited 60-mm mesh Japanese crab traps

	Effective fishing area (m^2)	
Minimum	Maximum	Mean
930	3 520	2 160

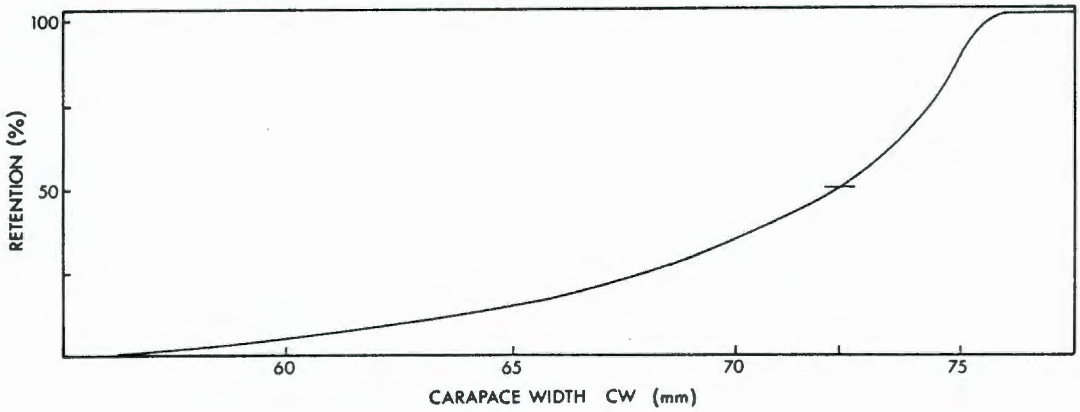

Fig. 2: Provisional selectivity curve for *Geryon maritae* constructed for traps covered with 90-mm mesh

cent of the crabs would have been lost as a result of the selectivity of the larger mesh (Table IV). Assuming that the EFAs for 60- and 90-mm-mesh traps are the same, the mesh constant C can be assumed to be the ratio of the mean number of crabs caught per trap with 60-mm mesh and the mean number caught with 90-mm mesh (i.e. $r/r1$). The mean value of C for 90-mm mesh has been calculated as 1,287 in this study (Table IV).

DISCUSSION

It must be realized that the EFA of a trap is only an approximate statistic, dependent upon a wide variety of variables such as the soaking time of the traps, the type and quantity of bait used per trap, the size of the trap, the distance between traps and the trap mesh size. Naturally, the more variables that can be standardized, the more reliable is the end result. In calculating the EFA of a trap, it is necessary to assume that all the crabs within the fishing area of a trap are caught. This assumption is unlikely, so that the calculated EFA of a trap is probably an overestimate. By the same token, the longer the soaking time of a trap, the greater the likelihood that it would catch crabs entering into the EFA of that trap, thereby inflating the calculated EFA.

The EFA is also dependent on the accuracy of the photographic estimate of density. In this survey the estimated density for the area 18°00'S, 520–570 m was 145,2 crabs·ha^{-1}. By comparison, for a photographic survey undertaken during August 1983 in the same area and over a similar depth range (500–600 m) the crab density was estimated as 75 crabs·ha^{-1} (Melville-Smith 1985). The similarity of the two estimates, bearing in mind statistically acceptable error, inspires confidence in the accuracy of the technique and it is likely that this is the most justifiable portion of the EFA estimation.

One of the unexplained aspects of red-crab sampling (trawling, photography and trap fishing), during this and other surveys, has been the scarcity of juvenile crabs. The smallest crab photographed during this survey was estimated to have had a carapace width of 56 mm and, from the 60-mm trap catches, only one crab smaller than 55 mm CW was measured out of a sample of 1 688 animals.

The standardization of research and commercial trap samples permitted construction of a selectivity curve for 90-mm mesh (see Fig. 2). Note should be taken that this curve was derived from a relatively small sample of crabs ($n = 3\ 496$) and from catches in close, but nevertheless different, areas. The mesh selectivity figures presented in this report should therefore be considered as preliminary, until a separate investigation can be undertaken. A further point of caution that should be observed is that the 90-mm mesh constant presented in Table IV can only be used to calculate density from the EFA formula (see section on analysis in Methods) when the population size composition is similar to the research trap data shown in Figure 1 (i.e. when the ratio of crabs photographed $<$ 72-mm CW is ~30:70).

The size frequency distribution of crabs caught by research gear (Fig. 1) was unexpected in that it was bimodal instead of normal. Such an anomaly permits another possible interpretation of the retention capabilities of 90-mm mesh. The trough of the 60-mm mesh size frequency graph (Fig. 1) could be scaled to fit the 90-mm mesh size frequency over the size range

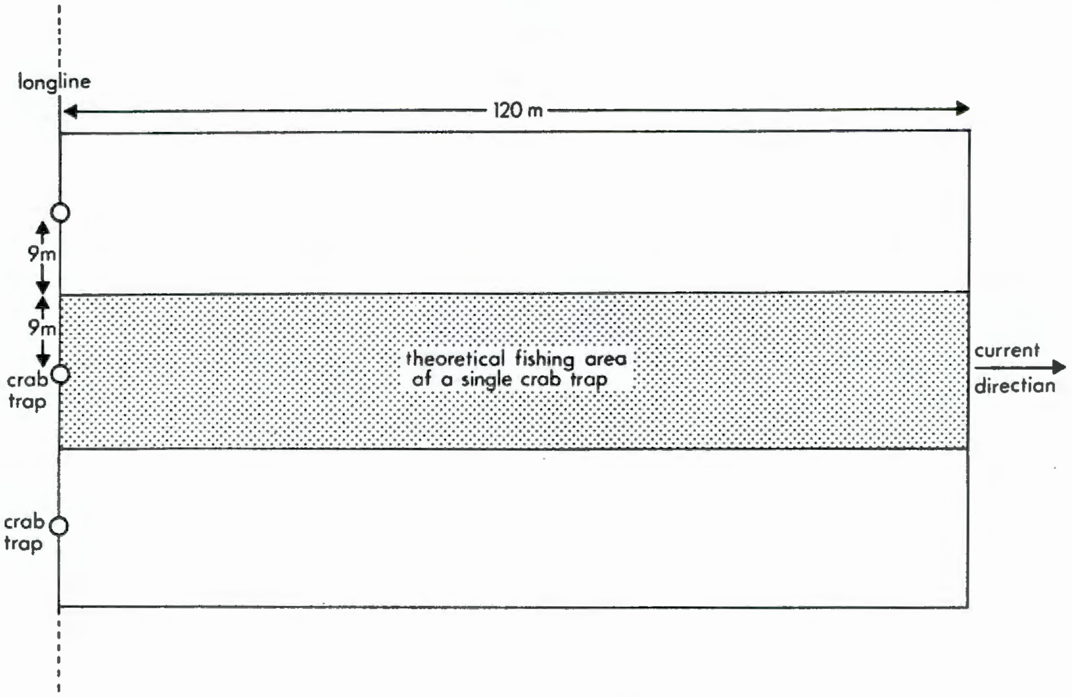

Fig. 3: Theoretical fishing area calculated in this study for crab traps fishing 18 m apart

75–85 mm CW, in which case the 50- and 100-per-cent retention of 90-mm mesh would be larger than the present estimate. Though consideration was given to carrying out such procedure, it was felt that there was not sufficient justification to apply a raising factor. The two sets of data in Figure 1 are considered to fit closely for sizes greater than 85-mm CW, and the bimodal nature of the research catch therefore appears to have resulted from lack of availability of some size crabs over the sampling period rather than by a failure of the research traps to retain those sizes.

At present there exists no legal minimum size for red crabs locally, so that all crabs, irrespective of size or sex, caught by the 90-mm trap mesh are utilized by the commercial fishery. It therefore follows that, from the point of view of stock assessment, the most useful density estimates would be for crabs > 72-mm CW. The most accessible data source is generally catch per trap as obtained from commercial catch statistics, thereby limiting the usefulness of the mesh constant.

Although the number of crabs caught per trap during the research fishing varied considerably (Table III), similar quantities were caught per trap by commercial crab vessels off northern South West Africa over this same period. For example, the catch per trap of the six commercial samples used to standardize the research and commercial mesh sizes varied between 17,4 and 31,7 and the soaking times between 48 and 72 hours. Commercial catches are generally 10–50 crabs per trap, and therefore crab densities in these commercially viable areas are probably about 46–231 crabs > 72-mm CW per hectare. The most crabs caught per trap recorded during commercial sampling was 110 (January 1983, 18°08'S, 11°24'E, 485 m). These figures would suggest that densities of crabs > 72 mm-CW can reach as much as 510 crabs·ha^{-1}.

Stone and Bailey (1980) and Barea and Defeo (1985) have used the estimated EFA of a trap to suggest an optimum distance between traps on a longline, to prevent the traps from fishing competitively. This distance has been calculated, assuming that a trap fishes a circular area, by the formula

$$R = 2(\sqrt{A/\pi}),$$

where R is the optimal distance between traps and A is the estimated trap EFA.

In this study, application of this formula would result in a recommended spacing of 52,4 m for traps not to influence each other. Commercial traps are at present spaced at 18-m intervals or 34,4 m closer than the optimal fishing spacing estimated. However, at the relatively great depths on the crab grounds, where current flow is likely to be unidirectional or at least not highly variable in direction, the area fished by a trap is unlikely to be circular. The attractive stimulus of bait is apparently carried by currents and the crabs move upstream to the trap, as has been noted by Miller (1981) for crabs observed under laboratory conditions and by Thurston (1979) for deep-water amphipods. If this were the case, it would be more realistic to imagine a trap attracting crabs within a theoretical shape, essentially triangular or possibly rectangular (Fig. 3). The actual shape would depend on the strength of the prevailing currents, for which there is no available information.

Assuming that the currents are slow and therefore that the theoretical fishing area is virtually rectangular, the path of attraction to a trap would have a width corresponding to half the distance of its nearest neighbour on either side (Fig. 3). Using the mean EFA for 90-mm mesh (Table V), this would imply that the distance of attraction to a trap is 120 m. By comparison, Brêthes *et al.* (1985) estimated from the results of short-time tagging and recapture experiments (carried out in water shallower than during this study) that the maximum extent of the influence of bait odour on the crab *Chionoecetes opilio* was in the range of 100–140 m for two different regression models.

In attempting to maximize trap catches, an important consideration should therefore be that the line of traps lies perpendicular to the water currents. Literature dealing with deep-water currents off South West Africa is limited to that dealing with generalized movements of water masses in a longshore direction (e.g. Hart and Currie 1960, Stander 1964, Visser 1969), rather than localized current movements, which might have shown some lateral components. There is a possibility of lateral current movement onto the shelf associated with tidal Kelvin waves moving southwards along the shelf edge. The top part of the wave would tend to spill onto the shelf, but the velocities associated with this process would be small (G. Nelson, Sea Fisheries Research Institute, pers. comm.). On the assumption that the current movements are only in a plane corresponding to the depth contours, it is interesting to speculate as to whether the traps would not fish more efficiently if set across a depth contour rather than with the contours as is the present commercial method of setting them.

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PAPER 9:

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
1988

COMPARATIVE POPULATION SIZE ESTIMATES FOR A PORTION OF THE RED CRAB *GERYON MARITAE* STOCK OFF THE SOUTH WEST AFRICAN COAST

*R. MELVILLE-SMITH**

The size and the density of the red-crab population between latitudes 19°20′ and 20°10′S and depths 400 and 900 m are estimated by a tag-recapture technique. Results are compared with estimates of stock density in the same area by three other methods (trawling, photography and effective fishing area [EFA]). Tagging and photography yielded similar estimates of crab population size (21,6 and 19,5 million crabs respectively) whereas trawling (1,9 million) and EFA techniques (81,4 million) apparently under- and overestimated stock size respectively. Fishing mortality (based on the ratio of crabs returned to those tagged) is estimated as 0,24 for males and 0,41 for females.

Die grootte en die digtheid van die rooikrapbevolking tussen breedtegrade 19°20′ en 20°10′S en dieptes 400 en 900 m word geskat volgens 'n tegniek van merk en weer vang. Resultate word vergelyk met skattings van stapeldigtheid in dieselfde gebied volgens drie ander metodes (treil, fotografie en effektiewe visvanggebied [EVG]). Merk en fotografie het soortgelyke skattings van krapbevolkingsgrootte opgelewer (onderskeidelik 21,6 en 19,5 miljoen krappe), maar treil (1,9 miljoen) en EVG-tegnieke (81,4 miljoen) het blykbaar die stapeldigtheid onderskeidelik onder- en oorskat. Visvangmortaliteit (gegrond op die verhouding van herwonne tot gemerkte krappe) word geskat op 0,24 vir mannetjies en 0,41 vir wyfies.

Reliable estimates of stock density (and therefore number of individuals) have obvious practical applications to fisheries management. In the case of the red-crab stock off South West Africa (Namibia), three methods have been used in the past to estimate crab density, trawling (Beyers and Wilke 1980), photography (Melville-Smith 1983, 1985) and the technique of effective area fished per trap (Melville-Smith 1986). The object of this paper is to report on the results obtained by a fourth method, that of tag recapture, and to compare these results with those obtained in the same area from the other three techniques.

In addition to providing an estimate of stock abundance, the tag-return data presented in this report have also been used to estimate fishing mortality (*F*) in the study area. Though red crabs have been fished since 1973, this is the first estimate of *F* for this area.

METHODS

The tagging survey described in this report was conducted from 10 to 18 October 1982 between latitudes 19°30′ and 20°00′S (Fig. 1). This particular study area was chosen on the basis of existing information on crab densities deduced from trawling and photographic surveys.

Trap lines (18 traps per longline) were set along latitudes 20°00′S and 19°30′S at 100-m intervals from 400 to 1 000 m. On both lines of latitude, the 400- and 1 000-m depths yielded no crabs and these depths were therefore considered as the limits of the stock. All depths in between yielded crab catches. All crabs caught, excluding those in a condition approaching moult or immediately post-moult, were tagged with spaghetti-type dart tags inserted through the epimeral suture of the carapace. A full description of the tagging methods and the information recorded at tagging has been documented in Melville-Smith (1987).

The crab catch from the first nine traps was placed into separate holding tanks from those caught by the balance of the traps, thereby approximately halving the catch. The catch from the first set of traps was released on the latitude and depth of capture and that from the remaining nine traps at the same depth 10 miles north in the case of the 20°00′S line, or 10 miles south for the 19°30′S line. This method was employed to achieve a more random distribution of crabs over the area surveyed.

It has been shown by numerous studies (e.g. Dias and Seita Machado 1973, Cayré *et al.* 1979, Beyers and Wilke 1980) that female *G. maritae* generally live

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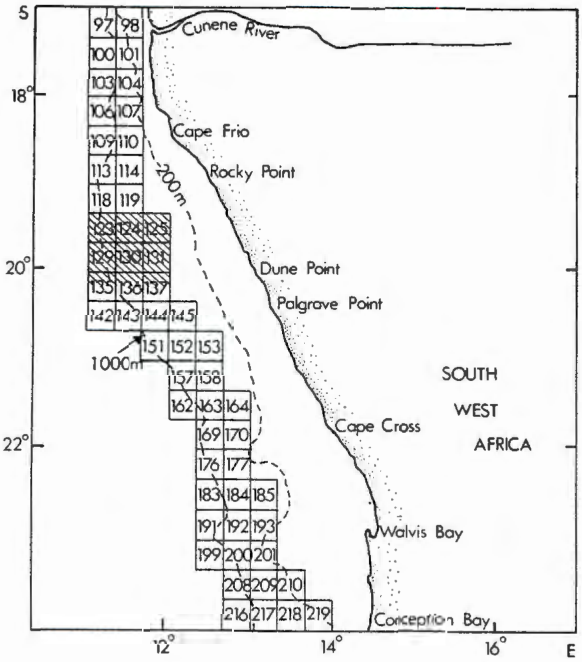

Fig. 1: The study area, showing the catch-reporting grid

in shallower water than males. Furthermore, Beyers and Wilke (op. cit.) and Melville-Smith (1987) have shown that small red crabs tend to occur deeper than large ones. It was therefore important to release the crabs as near as possible to their depth of capture and, with this in mind, a cage was constructed in which the tagged crabs could be lowered to within 50–100 m of the bottom before being released. The release of crabs in this manner had another advantage in that it prevented them, to a large extent, from being attacked by predators before reaching the bottom.

The present study has been restricted to analysis of returns of tagged crabs recorded within one year of their release (i.e. to 10 October 1983). During this period the crab grounds off South West Africa were fished by five Japanese vessels, but only a small portion of their effort (16,5 per cent—Melville-Smith, unpub. data) was directed in the area where the crabs had been released. The fishermen were requested to return any tagged crabs to the Sea Fisheries Research Institute together with details of the time, depth and position at recapture. All relevant information on the recaptured crabs was coded and computerized for eventual analysis.

It has been established that red crabs (particularly mature females) are capable of moving considerable distances (Melville-Smith 1987). In order to allow for some movements by the tagged crabs within the study area, its "boundaries" have been taken as latitudes 19°20′ and 20°10′S. These borders include the horizontal row of grids (Grid rows) 123–125 and 129–131, but only half of Grid row 135–137 (Fig. 1). As a result, it has been assumed that half of all the commercially reported catch statistics for Grid row 135–137 were made within the study area and, where catch statistics for this row have been used, they have been halved.

Commercial catch statistics provided information on the number of crabs caught in the areas in which the tagged crabs were released. Catch forms are completed by commercial crab-fishing vessels detailing the position of each longline set according to the grid shown in Figure 1, the depth at which the line was set, the number of traps used and the quantity of processed crab packed for that line. Conversion factors (Melville-Smith in press a) were applied to convert packed product mass to whole crab mass caught in each grid row during the year 10 October 1982–10 October 1983.

Size compositions and sex ratios are necessary to estimate the quantities that each size class contributed to the commercial catch. The size composition of crabs caught in the three grid rows covered by this survey was not uniform and it was therefore necessary to consider each row separately. All data used in this analysis were from commercial and research samples collected during the year of study.

The stock size for the study area was estimated from Bailey's (1951) modification of the "Lincoln Index":

$$\hat{N} = \frac{T(C+1)}{R+1} ,$$

and the sampling variance was estimated by

$$V(\hat{N}) = \frac{\hat{N}^2 (C-R)}{(C+1)(R+2)} \text{ (Bailey 1951),}$$

where $\hat{N}$ is the population size in numbers, T is the number tagged, C is the catch by number, R is the number of tags returned and $V(\hat{N})$ is the sampling variance for N.

An estimate of the fishing mortality (F) was made for crabs fully recruited to the fishery, i.e. > 75 mm carapace width (CW), by comparing the proportion of tags returned during the first year after release with the original number tagged.

As stated earlier, three other methods have been used to estimate the population size and density of

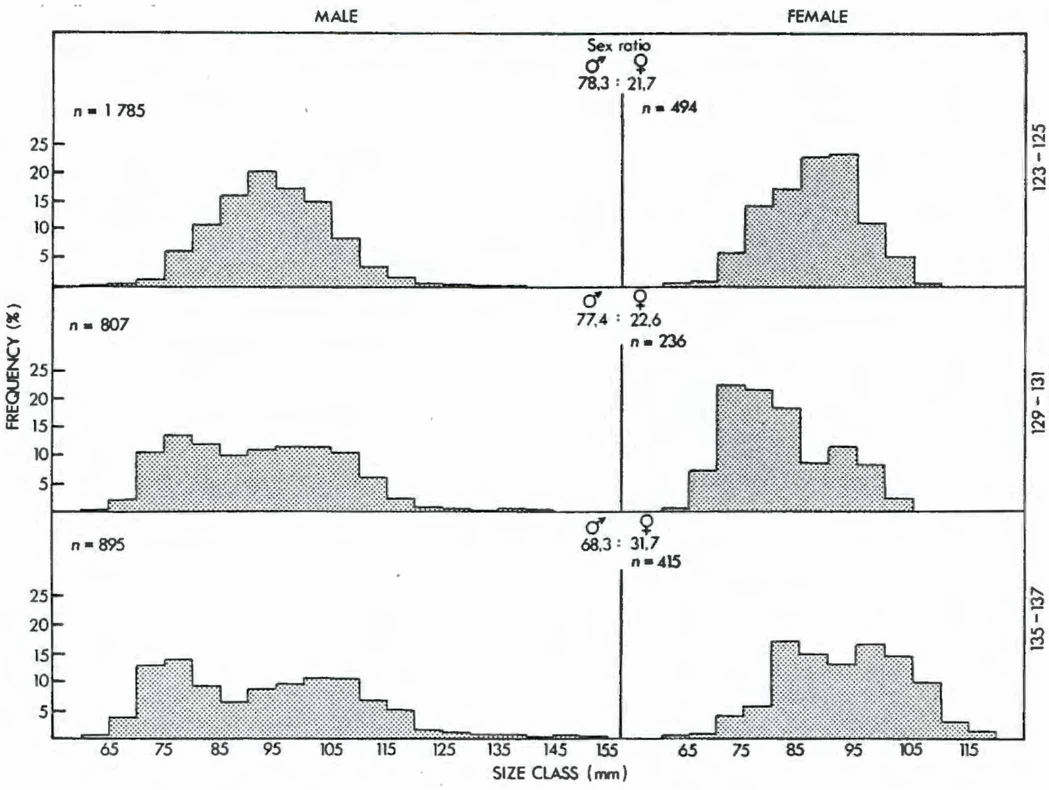

Fig. 2: Size composition of catch samples taken from the grids between 19° 20′ and 20° 10′S

red crabs between 19° 20′ and 20° 10′S. The methods used to derive these estimates are fully documented in Beyers and Wilke (1980) for trawling, Melville-Smith (1983) for photography and Melville-Smith (1986) for the effective fishing area per trap technique (EFA). All methods have estimated the population size by the same general principle, namely

$$\hat{N} = \frac{Ax}{a} ,$$

where $\hat{N}$ is the population size in numbers, a is the area sampled, x is the number of crabs observed in the area sampled and A is the area for which the population size is being estimated. The variance of $\hat{N}$ has been estimated as

$$V(\hat{N}) = \left(\frac{A}{a}\right)^2 x .$$

In order to determine A, depth contours were drawn onto South African Navy bathymetric charts of the region and the area within each depth zone was determined on a KONTRON electronic digitizer board.

RESULTS

Population size/density from tagging

The size compositions of commercial and research catches combined in Grid rows 123–125, 129–131 and 135–137 are presented in Figure 2. Although the female size composition was fairly constant throughout the area, the size of males increased noticeably in the south. All crabs caught during the survey were tagged, and it is therefore assumed that the size composition of the tagged animals was similar to the actual size distribution of the commercial stock in those areas.

From the catch statistics and the conversion

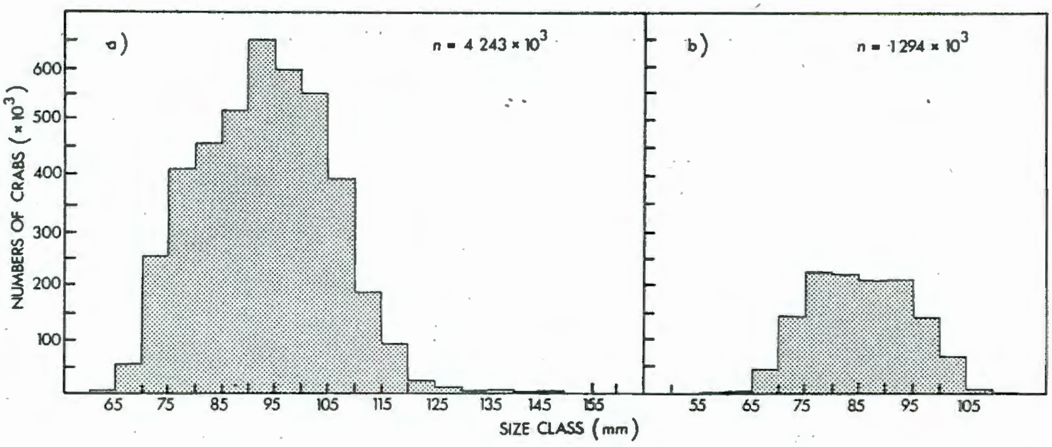

Fig. 3: Estimated number of crabs (by size class) caught between 19° 20′ and 20° 10′S during the study period (a) males and (b) females.

factors described in the previous section, it is estimated that totals of 4,2 million males and 1,3 million females were caught between 19° 20′ and 20° 10′S during the year of study. The size composition data presented in Figure 2 may be used to estimate the total number of animals caught in each size class over the study period (Fig. 3).

The numbers of crabs tagged and the proportion recaptured are presented in Table I. The percentage of returns in the smaller size classes was lower than for the larger sizes. In a preliminary study conducted by Melville-Smith (1986), it was suggested that 100-per-cent mesh retention is attained at a size of 75 mm CW, which would explain the low returns for sizes smaller than 75 mm CW. The low percentage returns in the 75–84 mm CW size classes may be real, i.e. in the bounds of sampling error, or the result of less obvious causes, such as the smaller crabs not being able to climb into the traps as readily as the larger ones.

From tagging data (Table I) and the estimated number of crabs caught in the tagging area during 1982/83 (Fig. 3), the population sizes between 19° 20′ and 20° 10′S are estimated (with 95-per-cent confidence limits) as $18{,}3 \times 10^6 \pm 1{,}9 \times 10^6$ males and $3{,}3 \times 10^6 \pm 4{,}6 \times 10^6$ females of sizes $\geqslant 75$ mm CW (i.e. for animals fully recruited to the fishery). Based on an estimated area between 400 and 900 m of 427 600 ha, the mean density of such a population would be approximately 50,5 crabs·ha^{-1}. For the whole population, it is notable that the sex ratio appears to be strongly biased in favour of males (5,5 : 1) but, in commercial catch samples, such a disparity is not so clear (Fig. 2 and Table I).

From the data presented in Table I, the instantaneous rate of fishing mortality (F) for fully recruited male crabs in the study area was estimated as 0,24 and for females as 0,41.

Population size/densities from EFA

Catch statistics supplied by commercial crab-fishing vessels for the period October 1982–October 1983 revealed that all fishing was carried out between depths of 400 and 900 m. The mean catch per trap for the various depths fished between Grids 123 and 137 (Table II) varied between 7,8 and 16,0 kg, with a general tendency to increase from shallow to deep.

The mean mass of a commercial-sized crab was

Table I: Numbers of crabs tagged and proportion returned after one year at large

Size class (mm)	Males tagged	Number returned	% return	Females tagged	Number returned	% return
60– 64	3	—	—	1	—	—
65– 69	11	—	—	4	—	—
70– 74	33	1	3,0	31	5	16,1
75– 79	102	16	15,7	76	14	18,4
80– 84	154	22	14,3	89	26	29,2
85– 89	214	44	20,6	138	47	34,1
90– 94	319	65	20,4	150	64	42,7
95– 99	301	76	25,2	80	30	37,5
100–104	268	55	20,5	25	6	24,0
105–109	188	42	22,3	2	1	50,0
110–114	88	26	29,5	1	—	—
115–119	46	11	23,9			
120–124	13	3	23,1			
125–129	7	2	28,6			
130–134	4	1	25,0			
135–139	2	1	50,0			
140–144	. . .	. . .	. . .			
145–149	1	—	—			
Total	1 754	365	20,8	597	193	32,3

Table II: Population size and density of red crab at different depth intervals between latitudes 19°20′ and 20°10′S, as calculated by the EFA method

Depth (m)	Catch rate		Density (crabs·ha^{-1})	Area (ha)	Population size (millions)	95% confidence limits (millions)
	(kg·trap^{-1})	(no·trap^{-1})				
Grids 123–125						
400–499	8,27	30	139	41 587	5,786	2,067
500–599	9,93	36	167	36 797	6,133	2,003
600–699	10,86	40	185	30 925	5,727	1,767
700–799	11,96	44	204	28 529	5,811	1,717
800–899	13,60	50	231	26 316	6,092	1,689
All depths				164 154	29,549	4,152
Grids 129–131						
400–499	7,75	31	144	47 260	6,783	2,388
500–599	10,07	40	185	34 865	6,456	2,001
600–699	10,52	42	194	31 382	6,102	1,845
700–799	11,94	48	222	30 292	6,732	1,904
800–899	13,38	54	250	30 833	7,708	2,056
All depths				174 632	33,781	4,578
Grids 135–137						
400–499	11,44	42	194	18 396	3,577	1,082
500–599	9,63	35	162	16 031	2,598	0,861
600–699	9,71	36	167	16 956	2,826	0,923
700–799	12,61	46	213	18 005	3,834	1,108
800–899	16,00	59	273	19 422	5,305	1,354
All depths				88 810	18,140	2,413
Totals						
400–499					16,146	3,338
500–599					15,187	2,959
600–699					14,655	2,722
700–799					16,377	2,793
800–899					19,105	2,985
All depths					81,470	6,625

calculated from the length frequencies and sex ratios in each grid row (Fig. 2). These figures were divided into catch rates for the respective grid rows (Table II) to predict the mean number of crabs expected to have been caught per trap at each depth. This figure has been divided by 2 160 m^2 (the estimated EFA of a baited commercial crab trap — Melville-Smith 1986) to give the estimated density of crabs per hectare (Table II).

The areas between the depth intervals surveyed have been multiplied by the figures for the crab densities at those depths to yield an estimate of the respective population sizes (Table II).

Population size/density from photography

The results for the estimated densities between latitudes 19°30′ and 20°00′S and depths of 400–699 m have been taken from Melville-Smith (1983) and are reproduced in Table III.

The density of crabs in depth zones 400–499, 500–599 and 600–699 m tended to increase with depth in a manner similar to that of the densities calculated by the EFA technique (Table II). With the photographic technique, the difference between the 400–499 and 500–599 m zones was considerably greater than that derived by means of the EFA method (Table IV), but this might be ascribed to the fact that photography covered the whole depth zone whereas the EFA result was based on commercial trap catches only, catches which would have been confined to the best fishing areas. The best fishing would have tended to be deeper (450–499 m), resulting in a possibly inflated density value for this zone.

The EFA and photographic techniques showed the densities in the 600–699 m zone to be 6 and 9 per cent higher respectively than those in the 500–599 m zone

Table III: Population size and density of red crab at three depth intervals between latitudes 19°20′ and 20°10′S, as calculated by photography. Information taken from Melville-Smith (1983)

Information sought	Results per depth zone (m)		
	400–499	500–599	600–699
Total number of exposures	623,3	701,3	776,7
Number of red crabs	8	17	21
Mean number of red crabs per exposure	0,0128	0,0242	0,0270
Area photographed (m²)	3 557,07	3 844,16	4 358,35
Density of red crab per hectare	22,49	44,22	48,18
Area of depth zone (ha)	107 243	87 693	79 263
Population size (millions)	2,412	3,878	3,819
95% confidence limits (millions)	1,671	1,844	1,633
Total population size between 400 and 699 m (millions)			10,109
95% confidence limits (millions)			2,977

Table IV: Percentage difference in crab density between depths using the EFA method, with estimates for photography (after Melville-Smith 1983) in parentheses based on the EFA increments

Depth range (m)	Mean density (EFA method) crabs·ha⁻¹	Percentage difference between each depth range	Mean density (photography) crabs·ha⁻¹	Percentage difference between each depth range
400–499	159	107,5	22,5	196,4
500–599	171	106,4	44,2	109,0
600–699	182	117,0	48,2	(117,0)
700–799	213	117,8	(56,4)	(117,8)
800–899	251		(66,4)	

(Table IV). Had the crab densities in the 700–799 and 800–899 m zones followed trends by depth similar to the mean values measured by the EFA method, their values would have been as shown in Table IV.

Population size/density from trawling

Several red-crab trawling surveys have been conducted on the South West African commercial crab grounds. During the course of these surveys, which were executed during July and September 1978 (Beyers and Wilke 1980) and April 1980, September 1981 and August 1982 (Melville-Smith, unpub. data), the area between 19°20′ and 20°10′S in the depth range 300–849 m was extensively covered (72 trawls in all).

The fact that the crabs were trawled over a five-year period has resulted in these data being less comparable than those from tagging, EFA and photography, all of which were collected during 1982/83. However, red-crab catch rates for Grids 123–137 have shown very little change over the period 1980–1983 (Melville-Smith 1988), so that it is not unreasonable to assume that the density estimates from the trawling data presented in this paper are at least reasonably comparable with those given for the other three techniques.

Data from the 72 trawls were separated into 100-m depth intervals and the mean density of crabs at each depth was calculated. The results are presented in Table V. As would be expected, the density value for the 300–399 m depth zone was very low (0,45) and has been omitted for purposes of comparison with the other methods.

DISCUSSION

Tag recapture is a well documented technique for estimating animal population sizes (Gulland 1969, Ricker 1975, Jones 1976). Though the rationale of the technique is simple, there are a number of principles which need to be adhered to in order to obtain a valid population estimate (Ricker op. cit.). Many of these principles are difficult to comply with in practice, particularly in a marine situation. Naturally, it must be accepted that the less strictly they are followed, the more chance there is that the population size estimated might misrepresent the true figure.

Numerous population estimates of marine animals have been made by means of tag-recapture techniques (e.g. Hancock 1963, Kelly and Barker 1963, Pollock 1981). In most cases, as with this study, some of the basic principles upon which the technique relies were either disregarded or compensated for in some manner in order to obtain the result. Because of this, the results documented are always open to critical examination.

The population estimate derived in this tag-recapture study has not taken tag loss into consideration, because it is considered to be significant only at ecdysis, when the exoskeleton is soft and the tag can easily tear through the membrane. During the period of study, no male crabs and only 9 per cent of the female crabs returned had moulted. This suggests that tag loss did not contribute to any notable extent to possible errors which might have been made in the population estimate.

It has also been assumed that all tagged crabs caught by the fishing fleet were reported. This is not considered to be an unreasonable assumption, because there were only five vessels fishing during the

Table V: Population size and density of red crab at different depth intervals between latitudes 19°20′ and 20°10′S, as calculated from trawling

Depth range (m)	Number of trawls (N)	Area trawled (ha)	Number of crabs trawled	Density (crabs·ha^{-1})	Estimated area (ha)	Population size (millions)	95% confidence limits (millions)
300–399	20	314,84	141	0,45	...	...	...
400–499	15	232,75	794	3,41	107 243	0,366	0,025
500–599	15	228,28	1 500	6,57	87 693	0,576	0,029
600–699	10	158,13	423	2,68	79 263	0,212	0,020
700–799	8	132,45	546	4,12	76 826	0,317	0,027
800–899	4	54,03	311	5,76	76 571	0,441	0,049

Total population size between 400 and 900 m (millions) 1,912
95% confidence limits (millions) 0,071

study period and all were co-operative towards the programme. In the course of processing the catch, it is necessary to handle each crab individually and, consequently, it is unlikely that any tagged animals were overlooked.

Obviously, the tagging method should not lead to mortality or alter an animal's susceptibility to capture. The type of tag used in this study is unlikely to have resulted in either of these two possibilities, except at ecdysis, as discussed earlier. However, in respect of method, the crabs were kept in holding tanks prior to their being tagged and released and these conditions may conceivably have led to some subsequent stress-related mortalities. Based on observation of the liveliness of the tagged animals when they were released, it is considered that, if any mortalities for this reason did occur, their numbers would have been very low.

This study also failed to observe the principle that the tagged animals should be randomly dispersed over the study area, for the reason that the large area of ocean which would have had to be covered made it impracticable in the time available.

The tagged crabs were released at 10-nautical-mile (18 km) intervals and, during their first three months at large, male and female crabs were recorded as moving 13 and 25 km respectively from their point of release (Melville-Smith 1987). Distances moved by crabs that had been at large for a longer period were even greater, an observation which suggests that the crabs quickly distributed themselves in a random fashion. By sheer chance, their distribution was assisted by the fact that only 3,6 per cent of the fishing effort recorded for the full year took place in the study area during the first two months after tagging.

As a result of their movements, a significant proportion of the tagged crabs returned by the fishing fleet (6 per cent of the males and 35 per cent of the females) were recaptured outside the borders of the area being assessed. Such recapture information has been included in the calculations of population size and fishing mortality, because it was deemed reasonable to assume an equal exchange of animals into and out of Grids 123–137 (i.e. the effects of immigration and emigration counteracted each other).

No doubt, some natural mortality would have taken place over the study period, but this would have affected tagged and untagged crabs equally. It would not, therefore, have influenced the population estimate to any extent.

Recruitment of juvenile crabs into the fishery has not been taken into account in the estimate of population size. Data for red crabs (Melville-Smith in press b) have shown that the growth rate is slow, and none of the crabs considered in this study would have moulted more than once during the year (a crab of 72 mm CW has an estimated intermoult period of over two years). From the same growth data (Melville-Smith op. cit.), it may be deduced that any small crabs entering the fishery during this study period would have moulted from the premoult size range 60–74 mm CW to a post-moult size about 15–16 mm longer (i.e. 75–90 mm CW). An influx of small crabs into the fishery would have led to an overestimate of the total population. Bearing in mind the slow growth rate and the relatively small size range affected by recruitment, any resultant overestimate of total population size is deemed unlikely to have exceeded 5–10 per cent.

From this discussion of tagging results, it can be seen that, whereas the likely sources of error are difficult to quantify, all are thought to be relatively small. All identified sources of possible "system" errors would have led to population overestimates. Two errors of a "sampling" nature, first the assumption that the crabs dispersed themselves randomly and second that immigration and emigration counteracted each other, could have led to either an over- or

Table VI: Comparison of the population size of red crab as estimated by four methods in the area 19°20′–20°10′S and depths of 400–900 m

Technique	Population size (millions)	95% confidence limits (millions)	Ratio between estimates
Tag recapture	21,608	1,936	1
EFA	81,470	6,633	3,8
Photography	19,526	*	0,9
Trawling	1,912	0,071	0,09

* Not possible to calculate confidence limits

an underestimate of the population size. As most of the errors would have led to overestimates, it must be concluded that the population estimates derived from tagging in this study refer to the maximum population levels.

Caution must be exercised when estimating fishing mortality from such data, because F is higher in the northern part of the grounds than in the south (Melville-Smith 1988). As a substantial number of the recaptured females had moved north outside the study area, their higher (and probably less reliable) F value may be explained. Fishing (F) and natural (M) mortality act on a population simultaneously, but the latter has here been ignored in the calculation of F. Had M been known and taken into account, the F value would have been slightly higher than that calculated. Also, no allowances were made for any possible tagging mortalities or for tagged animals that went unreported. If any errors of this type had occurred, they would have resulted in an artificially low value of F.

Estimates of population size for the study area, made by the four different techniques mentioned in this paper, are presented in Table VI. The values derived by photography and tag recapture were particularly close (10 per cent difference), and these two methods appear, from the discussion herein, to be the most reliable. There is no doubt that trawling methods severely underestimate red-crab population size, a fact that has been noted previously (Melville-Smith 1983). The extent to which red-crab population size may be underestimated from trawling is apparent from the fact that it produced an estimate an order of magnitude lower than the lowest of the other three methods (Table VI). The estimate of crab population size using the EFA technique was about four times greater than those from photography and tagging and is considered to have been an overestimate of the true value. This conclusion has been gained from the following considerations. The mean number of crabs caught per trap as measured from 14 commercial and research samples taken on vessels fishing in the study area during 1982/1983 was 20 crabs·trap^{-1}, with a standard deviation of 14,0. In contrast, the mean number of crabs caught per trap as estimated by this study and upon which the EFA density estimate was based (Table II), was twice as large (41 crabs·trap^{-1}). A number of conversion factors were used to arrive at the estimates of catch per commercial trap listed in Table II. It is possible that the suggested error with this technique may be the cumulative effect of the numerous assumptions used in its calculation.

Had the commercial trap-catch figure been used rather than that based on the catch statistics of the fishing vessels, the estimated population would have been considerably closer ($39,593 \times 10^6$ crabs) to those derived from photography and tagging (19,526 and $21,608 \times 10^6$ respectively).

Two of the methods used to estimate population sizes of red crabs (trawling and photography) included some crabs smaller than those available to the commercial fishery (i.e. < 75 mm CW). It can be estimated from the data of Beyers and Wilke (1980, Fig. 4) that trawling included about 16 per cent of animals smaller than 75 mm CW. Though it is not possible to quantify what proportion of the crabs used to derive the photographic assessment were < 75 mm CW, it is unlikely to have been very different from that made with the trawling method. For some as yet unexplained reason, small crabs do not appear in the photographs in quantity (Melville-Smith 1986).

The results of this study have suggested that the methods of photography and tag recapture are the most reliable for estimating density of red crabs. Further, the tag-recapture method was the most cost-effective in terms of the area that could be covered in a research cruise. Probably the single most important drawback of this method is its reliance on the co-operation of commercial fishermen.

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PAPER 10:

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
1988

THE COMMERCIAL FISHERY FOR AND POPULATION DYNAMICS OF RED CRAB *GERYON MARITAE* OFF SOUTH WEST AFRICA, 1976-1986

*R. MELVILLE-SMITH**

Commercial catch statistics for red crab *Geryon maritae* caught off South West Africa (Namibia) since 1980 and some historical data for the previous four years showed that crabs were much smaller in the northern areas than in the south. Catch per unit effort (cpue) was aseasonal and unaffected by soaking times of 24–120 h. Catches decreased from north to south, little fishing therefore taking place south of 22°S. Total catches increased from 1980, reaching a peak of over 10 000 tons (whole crab mass) in 1983, but subsequently falling to 7 000–8 000 tons between 1984 and 1986. Cpue, too, has decreased in recent years. The current size at first entry to the fishery is below that at which females mature, a situation which could lead to overfishing of the spawner stock. Analyses of yield per recruit for males (assuming instantaneous natural mortality rates of 0,05, 0,10 and 0,15) have shown that the present age at first capture is considerably less than that at which the yield for that sex would theoretically be optimal. Management options aimed at improving the long-term outlook of the fishery are suggested.

Handelsvangstatistieke vir rooikrap *Geryon maritae* teenoor Suidwes-Afrika (Namibië) gevang sedert 1980 en ook enkele historiese gegewens vir die vorige vier jaar het aangetoon dat krappe in die noordelike vanggebiede veel kleiner as in die suide was. Vangs per pogingseenheid (V.P.P.E.) het nie seisoenmatig gewissel nie en is ook nie geraak deur weektye van 24–120 h nie. Vangste het van noord na suid afgeneem; gevolglik is daar maar min suid van 22°S gevis. Totale vangs het sedert 1980 toegeneem, 'n hoogtepunt van meer as 10 000 ton (heelkrapmassa) in 1983 bereik, maar daarna tussen 1984 en 1986 gedaal tot 7 000–8 000 ton. Ook die V.P.P.E. het in onlangse jare afgeneem. Die grootte by toetrede tot die vissery is tans benede dié waarby wyfies geslagsryp word, 'n toedrag van sake wat tot oorbevissing van die kuitskietstapel kan lei. Ontleding van die opbrengs per rekruut vir mannetjies (met aanname van koerse van oombliklike natuurlike mortaliteit van 0,05, 0,10 en 0,15) het aangetoon dat die huidige ouderdom waarop krappe vangbaar word, aansienlik laer is as dié waarby die opbrengs vir daardie geslag teoreties optimaal sou wees. Bestuursopsies gemik op verbetering van die voortuitsig van die vissery op die lang termyn word aan die hand gedoen.

There are several species of *Geryon*, commonly known as deep-sea red crab, in the Atlantic Ocean, but only four are commercially exploited. *G. quinquedens* and *G. fenneri* both occur off the western Atlantic seaboard. *G. quinquedens* is fished commercially off the north-eastern United States (Lux *et al.* 1982) and on the edge of the Canadian Scotian shelf (R. W. Elner, Government of Canada, Fisheries and Oceans, pers. comm.) and *G. fenneri* is fished in the Gulf of Mexico (Manning and Holthuis 1984). The other two commercially exploited species are both found off the West African coast. *Geryon maritae*, which closely resembles *G. quinquedens* and was in fact presumed to be the latter species until 1981, when it was described as a new species (Manning and Holthuis 1981), occurs from Spanish Sahara to South West Africa (Manning and Holthuis 1981) and has been commercially fished off South West Africa, the Ivory Coast (J. P. Hie Dare, Centre de Recherches Océanographiques, Abidjan, pers. comm.) and Angola. *G. erythiae* is only found in a localized area of the Walvis Ridge (MacPherson 1984) and has been erratically exploited since late 1986.

The *G. maritae* fishery is unquestionably the largest of the four *Geryon* fisheries, and by far the most fishing effort for that species occurs off South West Africa between latitude 22° S and the Angolan border (Fig. 1). This report deals with an examination of catch trends in that area over the period 1976–1986, with the object of assessing the state of the *Geryon maritae* stock at its current level of exploitation and determining any conservational requirements.

Beyers and Wilke (1980) gave a brief history of the South West African red-crab fishery from its inception in 1973 to 1979. Since then, exploitation by South West African vessels has ceased (in late 1979) and Japanese fishing effort (in terms of number of ships on the grounds) has stabilized at five vessels (Table I). As most of the catch data presented in this report deals with the Japanese catch statistics collected since 1980, some description of their fishing method is necessary.

The fishermen use standard Japanese crab traps, as described by Beyers and Wilke (1980), covered with 90-mm mesh (one vessel used traps with 60-mm mesh

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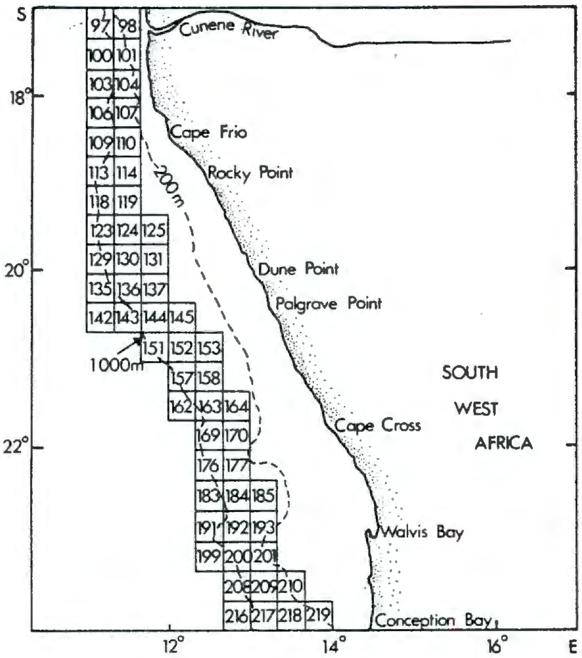

Fig. 1: The coastline of South West Africa showing the grid areas used in the statistical reporting of commercial crab catches

during 1985 and early 1986, before moving into Angolan waters). The traps are attached to longlines at 18-m intervals, and usually between 750 and 1 500 are hauled per day. The number of traps per longline is highly variable, but it is usually in excess of 250 and can be up to 1 500, in which case the line would extend some 30 km along the sea-bed. Traps are mostly left for periods of between 20 and 120 h before being hauled. Soaking times (the period for which a crab trap is left before being hauled) of longer than 120 h usually occur only when the ships put into port for some reason.

Fishing is conducted throughout the year. There is no minimum size limit and consequently all crabs caught by the traps are retained for processing.

METHODS

Commercial catch sampling

Prior to 1982 there was little sampling of commercial catches. On three occasions between 1978 and 1980, scientists from the Sea Fisheries Research Institute in Cape Town visited commercial crab vessels at sea and measured catch samples on board. Those data have been used in this report as they give an idea of the size composition of the catch during the earlier years of the fishery. In 1982 a regular commercial catch sampling programme was initiated, whereby it was attempted to visit each vessel fishing on the grounds at least once per quarter. Random catch samples of 200–300 crabs were taken from each line hauled during the day spent on board the vessel.

Table I: Number of vessels fishing for red crab off South West Africa since fishing commenced in 1973

Year	Nationality			Total
	Japanese		South West African	
	Private	Taiyo Fishing Co.		
1973	3			3
1974	16	1		17
1975	1	1		2
1976	4	2	1 (Sep.–Dec.)	7
1977	3	2	2 (Oct.–Dec.)	7
1978	3	2	2 (Jan.–Dec.)	7
1979	3	2	2 (Jan.–Oct.)	7
1980	3	3	1 (Jan.–Apr.)	7
1981	2	3		5
1982	2	3		5
1983	2	3		5
1984	2	3		5
1985	2	3		5
1986	2	3		5

From each animal sampled, the sex, the carapace width CW (measured across the widest part of the shell to the nearest millimetre), whether it was ovigerous, the state of the exoskeleton (Beyers and Wilke 1980) and whether it was sexually mature (Melville-Smith 1987a), were recorded. The method of determining whether the animals were sexually mature or not was only established after 1982 and consequently there are no data on this parameter prior to that year.

Commercial catch statistics

Though the South West African (SWA) red-crab stock was fished from 1973, the Institute only started collecting catch statistics from the local (SWA) vessels in 1976 and from the Japanese vessels in 1980.

Each vessel is supplied with a book of statistical forms and the skipper is requested to supply, for each longline hauled, the date, the soaking time (h), the grid position (see Fig. 1), the depth of the set, the number of traps per line and the catch of red crab expressed as kilogramme of each product packed for that line. There is also space on the form for information on catches of stone crab (Lithodidae) incorrectly termed "spider crab" by fishermen.

Catch report forms are collected when the ships return to port (i.e. about every 2–3 months) and the data are entered onto computer. The raw data on product mass are converted to whole crab mass by means of a series of conversion factors calculated for each product.

Product preparation

A description of the on-board product preparation is given in order to acquaint the reader with the various products packed and reported by the commercial crab vessels. All vessels that have fished for crab off SWA have used the same method of handling the crabs up to the point of cooking, but thereafter each operating company produces a slightly different range of products. The size of the crab generally determines the product for which it is used.

The butchering of crabs first entails removing the carapace (which is discarded into the sea as offal), after which two sets of legs attached together by the fleshy shoulder region are left. Each of these is known as a "section" (Fig. 2). The gills and any remaining viscera are removed manually on a rotating nylon brush and the sections are then packed into categories according to size. On the Japanese vessels there are three such categories, but on the SWA vessels only crabs larger than 115 mm CW were retained for processing and therefore there was no separation of sections of different size. As the Japanese produce a large range of products these are discussed in more detail.

The three size categories, small (< 95 mm CW), medium (95–110 mm CW) and large (> 110 mm CW) are cooked for approximately 15 minutes in boiling seawater. After cooking, the sections are placed into a second tank of cool circulating surface seawater (16–22°C) for a further 20 minutes before being processed, packed and frozen to −30°C. Five products are produced, some of the products having more than one variation.

Section product — This is the most basic product packed, and only crabs larger than 110 mm CW are packed in this manner (Fig. 2). Although smaller crabs are cooked as sections, they are always processed further into one of the products described below before being packed.

Leg product — This product is usually produced from medium-sized crabs (95–110 mm CW). Each of the two companies involved in the fishery produce their own version of leg product and the two methods are:

(i) the legs are cut close to the shoulder with secateurs and are broken at the joint between the carpus and merus (see Fig. 2). The meat is extracted from the shell of the merus and packed. The shell is discarded;

(ii) the merus is broken at its points of attachment to the shoulder and carpus and is packed with the flesh still encased by the shell.

Claw product — Only chelipeds of over 20 g are retained for this infrequently packed product. As crabs more than 100 mm CW are the only ones with claws of this mass, and because crabs larger than 110 mm CW are generally used for section product, the claw product is usually restricted to crabs of 100–110 mm CW. The claws are broken at the first joint and are packed unshelled.

Arm product — Only one of the two companies at present fishing for red crab packs this product, also infrequently. It is usually produced from the same crabs as were used for claw product and consists of the merus and carpus joints of the first leg (Fig. 2).

Flake product — By mass, this is by far the most important product produced by the Japanese commercial crab vessels. It is manufactured by a machine which separates meat from shell by the action of a piston repetitively crushing the crab portions through a sieve of holes. These holes vary in diameter from 1 to 10 mm depending on the coarseness of the product desired. The two companies fishing for crab use different hole sizes and therefore produce different flake products.

One company uses a machine with a 9-mm diameter hole, but the other company uses three different machines. Usually a third of the catch (though this can vary considerably) passes through a machine with 5-mm diameter holes and the balance passes through machines with 10-mm holes. The offal left behind after it has passed through the machine with 10-mm holes is then passed through a machine with 1-mm holes. This last machine is only used in conjunction with the 10-mm and never with the machine with 5-mm holes.

The size of crab and the appendages used for this product are particularly variable. All the sections from small crabs (< 95 mm CW) are used, as well as those parts of the medium-sized crabs not used for leg, claw and arm product. As already stated, those products are only packed infrequently and consequently are often included in the flake. On other rare

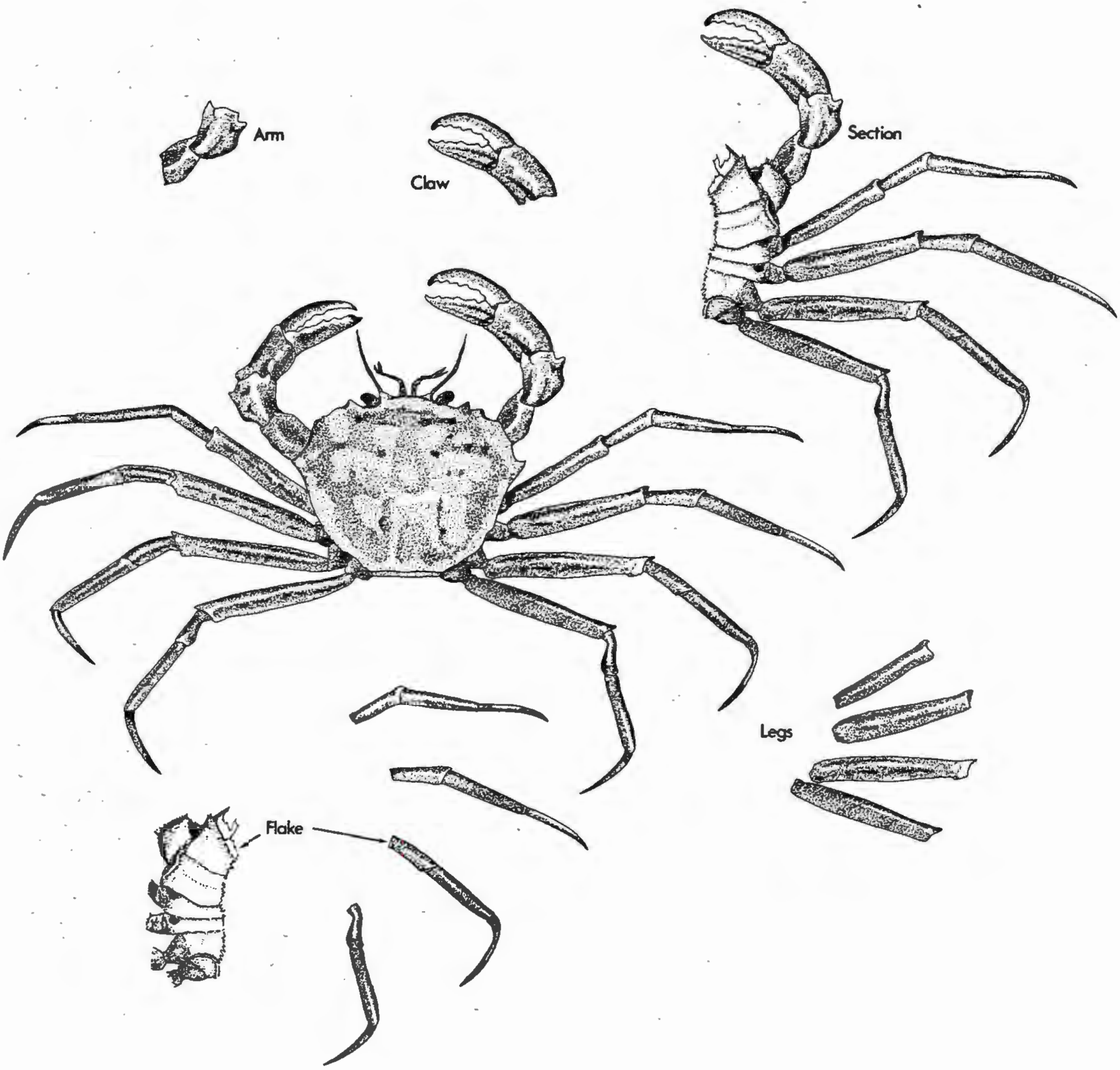

Fig. 2: Products produced from red crab caught off South West Africa

occasions, on demand from Japan, the whole catch irrespective of the size of the crabs is used for flake.

The factors for converting product mass to whole live crab mass are presented elsewhere (Melville-Smith in press a), together with the methods used for obtaining them.

Catch per unit effort (cpue)

Before annual cpue trends could be examined, it was necessary to establish the relationship between catch and soaking time, the influence of fishing area on cpue and whether cpue was influenced by season.

Only data supplied by the three ships belonging to the Taiyo Fishing Company were used in the computations, because that information was believed to be most reliable and also because the three vessels all packed and reported similar products.

A relationship between catch and soaking time was established by calculating the cpue (measured as kg whole crab mass per trap) for Grids 97–114 (17°20′–19°S) for several time periods. The calculations were limited to those grids because observations made on the abundance of crabs caught per trap and carapace-width frequency trends in those areas (Fig. 3) suggested that the various values in those grids might be reasonably similar. Such speculation is shown later to be justified (see the section "cpue differences with area" later).

Fluctuations in catch per unit effort were then further examined by area and by month for each of the grid rows fished between 1980 and 1986. Based on results obtained for different soaking times (see later), only catches where lines were set for periods of 24–119 h were used in the calculations.

Yield-per-recruit analysis

Yield-per-recruit models are very dependent on the estimated natural mortality (*M*) of a stock. In the case of *Geryon maritae*, sampling of the catches only started some years after the commencement of commercial fishing and, consequently, estimates of *M* from the "catch curve" method (Gulland 1969) are not possible owing to the bias of fishing mortality (*F*). However, the method has been used to estimate total mortality (*Z*) for males in different areas of the SWA grounds and, by assuming several different likely values of *M*, some indication of current (1986) *F* values has been gained.

The data used in the catch-curve calculations in this paper were collected during routine quarterly commercial sampling during 1986. Because there were insufficient data for the area 20–21°S, commercial sampling information for 1985 was combined with that for 1986 to derive the estimate of *Z* in that area.

A series of yield-per-recruit estimates for male crabs have been made for different *F* and *M* values according to the model of Thomson and Bell (Ricker 1958). This model requires a knowledge of mass at age, but available data (Melville-Smith in press b) are presented as age, carapace width and mass at instar number. The data have been adapted in Table II to a format appropriate to their use in this study. It should be noted that growth increments in red crab are not annual (Melville-Smith op. cit.) and that the predicted increments in Table II are therefore theoretical. The assumptions made by the yield-per-recruit model are that recruitment is constant each year and is complete at 5 years of age, that knife-edge selection takes place at the age of first capture and that natural mortality remains constant over the ages considered by the model.

Table II: Theoretical relationship between mid-year age at size and mass for male *G. maritae* (information adapted from Melville-Smith in press b)

Age (years)	Weight (g)	Carapace width (mm)
0+	Unreliable data	13
1+		23
2+		33
3+		43
4+		52
5+	70	60
6+	105	69
7+	154	78
8+	200	84
9+	255	91
10+	320	98
11+	385	104
12+	445	109
13+	515	114
14+	583	118
15+	652	123
16+	720	127
17+	790	130
18+	860	134
19+	928	137
20+	997	140
21+	1 065	143
22+	1 134	146
23+	1 202	149
24+	1 267	151
25+	1 332	154
26+	1 397	156
27+	1 459	158
28+	1 524	160
29+	1 590	163
30+	1 653	165

The yield-per-recruit estimates have been plotted as a two-dimensional yield isopleth. The resulting diagram has been used to gauge the value at which fishing mortality or age at first capture would best optimize yield per recruit for male crabs. Based on these results, yield trajectories have been constructed for the sexes combined, modelling the expected changes in yield per recruit at different possible values of mortality and age at first capture.

A model has also been constructed showing changes that would be likely to follow a lowering of *F*. In both of the above models, recruitment and natural mortality have been assumed to be constant,

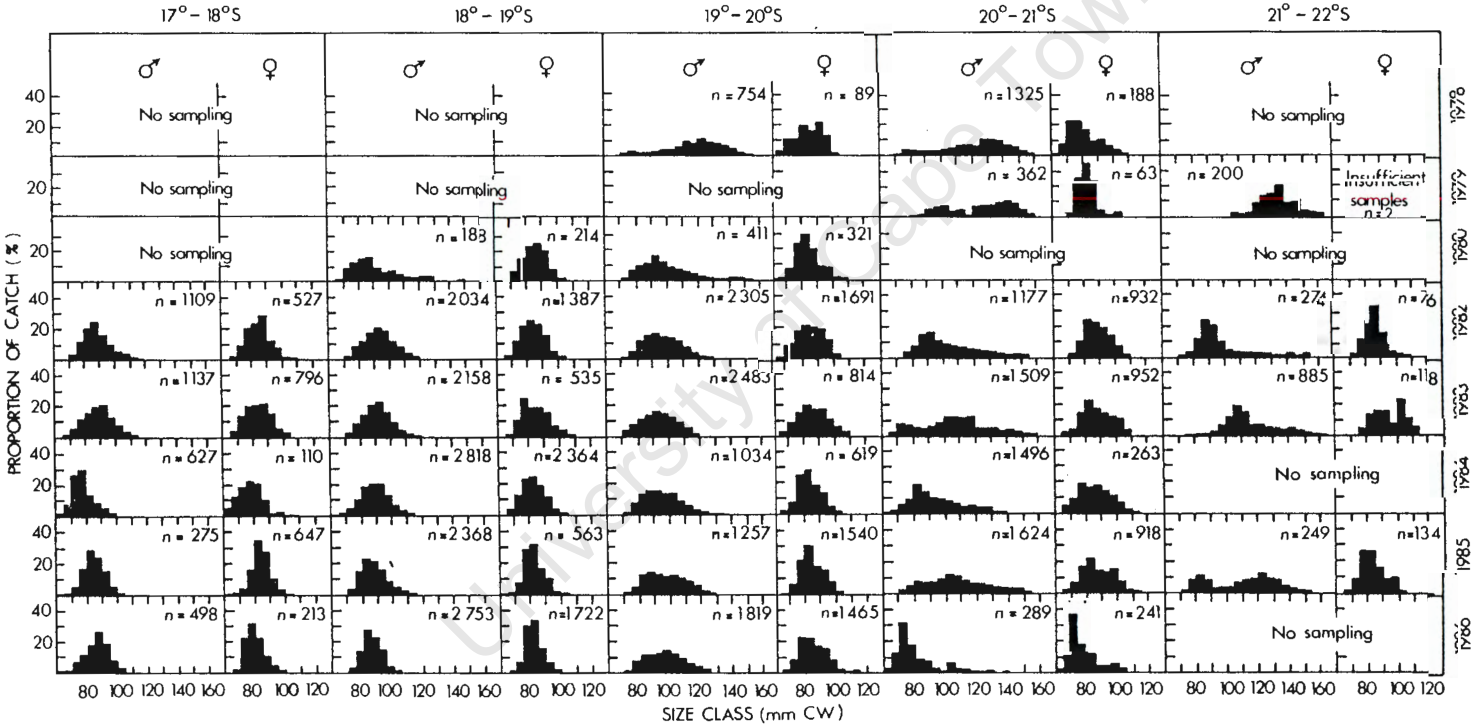

Fig. 3: Size frequencies of the commercial catch of male and female red crab by latitude, 1978–1986

age at first capture has been taken to be 6 years, 50 per cent of the female crabs have been assumed to mature (and therefore effectively cease growing) at 9 years (91 mm CW) and 100 per cent at 12 years (109 mm CW).

RESULTS

Size frequency and sex ratio

Size composition data for samples taken from commercial catches are presented in Figure 3. From the first commercial sample taken in 1978 until the present, it has been evident that crabs were larger but fewer in the south and plentiful but smaller in the north. In keeping with this observation, the data have been presented separately in Figure 3 for each degree of latitude (~110 km) over the commercial grounds.

The size composition of males in the south has varied over the years whereas that of males in the north has not changed much since the first samples were taken. The present disparity in size composition of male crabs in the north compared with those on the southern grounds must be due either to fishing mortality or movement/migration. The fact that Melville-Smith (1987b) has shown that tagged male crabs generally do not move far from their point of release would suggest that the former hypothesis is the more likely. In the case of females, there has been no variation in size composition of the magnitude observed for males (Fig. 3), because relatively few female crabs grow larger than 100 mm CW. As 100-per-cent selection by the meshes falls at approximately 75 mm CW (Melville-Smith 1986), there is little room for a shift in the modal peak.

Sex ratios, as calculated from commercial samples taken over the five-year period 1982–1986, are shown in Table III. The data have been presented by 100-m depth interval and by degrees of latitude. The most obvious trend is the predominance of male crabs at depths > 500 m and their secondary importance in shallower water. Males dominated all crab catches irrespective of depth south of 21°S.

Catch per unit effort (cpue) trends

RELATIONSHIP BETWEEN CATCH AND SOAKING TIME

The effect of soaking time on cpue is shown in Table IV. Traps are usually set for periods of 24, 48, 72 or 96 h. It appears that soaking time does not affect cpue (Table IV), except where traps are left for periods longer than 156 h (most of the data in this category were for traps left considerably longer than 156 h). This hypothesis was tested by applying a two-factor ANOVA test on the five soaking periods for which there were substantial data (namely 24–35, 48–59, 72–83, 96–119 and > 156 h). There is a significant difference in the catch with soaking time when data for periods > 156 h are included ($p < 0{,}01$), but not when periods > 156 h are excluded ($p > 0{,}05$). Presumably some of the crabs in the catch manage to escape when traps are left for periods longer than 156 h.

Table III: Sex ratios of commercially caught red crab at five depth intervals for five degrees at latitude, 1982–1986

Depth (m)	Parameter	Value by latitude, grid and sex									
		17–18°S		18–19°S		19–29°S		20–21°S		21–22°S	
		97–104		106–114		118–131		135–153		157–170	
		♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
⩾ 800	Percentage *n*	94,1 396	5,9 25	92,5 1 105	7,5 90	92,3 661	7,7 55	88,7 345	11,3 44	No data	
700–799	Percentage *n*	74,1 234	25,9 82	78,3 4 198	21,7 1 161	82,4 1 607	17,6 344	83,7 1 116	16,3 218	No data	
600–699	Percentage *n*	63,2 216	36,8 126	54,7 1 727	45,3 1 428	62,5 3 568	37,5 2 141	69,5 1 145	30,5 503	89,7 703	10,3 81
500–599	Percentage *n*	68,7 1 338	31,3 610	54,1 2 005	43,9 1 574	49,9 2 593	50,1 2 599	69,0 2 116	31,0 954	83,1 182	16,9 37
400–499	Percentage *n*	35,8 416	64,2 743	57,5 4 023	42,5 2 981	35,7 583	64,3 1 050	47,0 1 284	53,0 1 445	61,0 131	39,0 84

Table IV: Catch rates (cpue) over a five-year period for various soaking times. Only data for Taiyo Fishing Co. vessels and Grids 97–114 are included

Soaking time (h)	Catch rate (kg·trap^{-1})				
	1981	1982	1983	1984	1985
0– 11	· · ·	· · ·	· · ·	· · ·	· · ·
12– 23	· · ·	· · ·	11,94	13,43	· · ·
24– 35	11,85	11,40	12,95	10,84	11,18
36– 47	13,72	12,37	11,76	11,62	10,83
48– 59	12,93	11,90	11,76	11,18	10,64
60– 71	· · ·	11,48	10,32	9,99	· · ·
72– 83	13,84	10,92	11,67	9,99	7,23
84– 95	· · ·	· · ·	· · ·	· · ·	· · ·
96–119	12,44	12,05	11,68	11,25	6,98
120–143	· · ·	· · ·	11,81	12,59	7,76
144–155	· · ·	· · ·	· · ·	14,31	7,48
⩾156	9,00	7,36	8,97	9,91	7,50

· · · No data

DIFFERENCES IN CPUE WITH AREA AND BY MONTH

There is a general decrease in cpue between the northern and southern areas (Table V), a trend which is apparent in the results for each year except 1980. The fact that this trend was not apparent in the 1980 results is probably due to data for the northern areas (north of 19° S) in that year being based on very little effort (Table V).

For the previous section, the calculation was based on Grids 97–114. There is generally a cpue difference of about 2,0–2,5 kg·trap^{-1} between the maximum and minimum values measured for these grids. This observation may possibly account for some of the variation in cpue for different soaking times recorded within a single year (Table IV).

Limited monthly cpue trends (1981–1986) are presented in Figure 4. There is no seasonal variation in catch per trap, a not unexpected observation given the environmentally non-seasonal conditions at the depths inhabited by the crabs.

CATCH PER UNIT EFFORT TRENDS, 1976–1986

South West African fishery, 1976–1979 — The earliest available catch-and-effort data were derived from log books completed by ships fishing for a South West African company which exploited red crab intermittently between 1976 and 1979. These data are not comparable with those of the Japanese (see next section) for two reasons, first that the South West African company only processed crabs > 115 mm CW and second that they concentrated their fishing effort in the southern areas only (generally Grids 135–170). In contrast, the Japanese have always retained smaller crabs and have fished more widely over the grounds (see Table VI).

Catch rate is plotted for the South West African vessels on Figure 5. There was a clear decline in cpue over the period fished and, towards the end of the 1979, fishing was terminated because of uneconomic yields. The apparently low catch rate toward the end of 1979 (Fig. 5) should be viewed in the knowledge that three years of exploitation had taken place on what was originally virtually virgin fishing ground. The large, slow-growing animals had soon been eliminated and, had fishing continued, catches would have been expected to have eventually stabilized at a point at which catch and recruitment were in equilibrium.

Japanese fishery, 1980–1986 — Earlier it was shown that cpue varies markedly between different areas. Under normal circumstances, annual trends in cpue could be analysed without taking fishing area into account, because there is usually no reason for fishermen to work in areas where the catch rate is low. However, in this fishery, the incentive to fish in areas of low cpue (e.g. the south) comes from the size of crab, and therefore the product produced, being different from that in those areas in the north where cpue is high. The area where effort is applied is consequently partially dictated by market demand, rather than solely by cpue. As a result, effort is spread throughout the grounds (Table V and VI). Because of this fact, cpue trends are examined separately for different areas. The trends in cpue in three grid rows, situated in the northern (Grids 103–104), central (123–125) and southern (169–170) areas are reflected in Figure 6.

Catch rate has fluctuated considerably in the south (Fig. 6), largely because the annual values there are based on very little effort (Table V). In the northern and central areas, catch rate peaked in 1983 and declined for the next two years. In virtually all fishing areas in 1985, cpue was at its lowest since catch statistics were first submitted, but there was a slight improvement in 1986 (Table V, Fig. 6).

Summaries of the effort and the estimated whole mass of crab caught by (i) Taiyo Fishing Co. vessels and (ii) all vessels fishing off South West Africa since 1980 are presented in Figure 7. Total effort between 1981 and 1985 was reasonably constant at around $1,1 - 1,3 \times 10^6$ traps set per annum. During 1986 this figure decreased considerably because three of the five vessels which had previously been fishing on the South West African grounds left. The estimated total catch peaked in 1983 at over 10 000 tons (whole crab mass) but decreased thereafter. The Taiyo

Table V: Catch-and-effort data for Grids 100–180 by grid row for Taiyo Fishing Co. vessels, 1980–1986. Only catches with soaking times of 24–119 h were used in the calculations

Grids	1980			1981			1982			1983		
	Effort (traps hauled)	Catch (kg whole mass)	cpue (kg·trap^{-1})	Effort (traps hauled)	Catch (kg whole mass)	cpue (kg·trap^{-1})	Effort (traps hauled)	Catch (kg whole mass)	cpue (kg·trap^{-1})	Effort (traps hauled)	Catch (kg whole mass)	cpue (kg·trap^{-1})
100–101	...	...	...	30 471	411 824	13,52	14 748	200 865	13,62	19 907	252 271	12,67
103–104	...	...	...	59 044	759 655	12,87	32 995	429 788	13,03	45 560	651 587	14,30
106–107	250	536	2,14	55 131	761 897	13,82	46 247	601 665	13,01	46 497	559 901	12,04
109–110	750	2 273	3,03	55 344	749 008	13,53	60 501	651 793	10,77	59 239	691 435	11,67
113–114	3 000	22 911	7,64	62 802	725 659	11,55	78 080	874 331	11,20	55 488	576 071	10,38
118–119	35 650	383 268	10,75	39 763	458 350	11,53	89 260	1 040 465	11,66	48 976	563 408	11,50
123–125	65 800	730 180	11,10	73 800	594 462	8,06	65 823	590 760	8,97	68 198	802 106	11,76
129–131	65 965	647 197	9,81	31 700	231 492	7,30	24 092	177 205	7,36	36 678	392 111	10,69
135–137	47 015	614 574	13,07	8 398	72 850	8,67	28 395	242 587	8,54	37 409	429 611	11,48
142–145	54 452	720 980	13,24	10 961	131 828	12,03	10 946	106 021	9,69	26 820	268 678	10,02
151–153	31 908	373 399	11,70	2 229	20 197	9,06	16 470	197 768	12,01	32 560	316 698	9,73
157–158	249	1 912	7,68	250	2 973	11,89	11 494	118 112	10,28	35 455	313 735	8,85
162–164	...	...	...	2 480	27 951	11,27	5 250	31 290	5,96	9 780	69 962	7,15
169–170	...	...	...	2 980	35 663	11,97	4 500	15 741	3,50	7 248	51 346	7,08
176–177	...	...	...	999	4 157	4,16	1 250	5 657	4,52	4 495	31 155	6,93
Total	305 039	3 497 230	11,46	436 352	4 987 966	11,43	490 051	5 284 048	10,78	534 310	5 970 075	11,17

Table V: *continued*

Grids	1984			1985			1986		
	Effort (traps hauled)	Catch (kg whole mass)	cpue (kg·trap^{-1})	Effort (traps hauled)	Catch (kg whole mass)	cpue (kg·trap^{-1})	Effort (traps hauled)	Catch (kg whole mass)	cpue (kg·trap^{-1})
100–101	35 963	475 860	13,23	29 831	321 068	10,76	30 438	287 668	9,45
103–104	31 677	373 922	11,80	46 577	475 519	10,21	61 206	652 058	10,65
106–107	49 422	529 327	10,71	57 146	566 602	9,91	59 386	614 185	10,34
109–110	72 961	738 272	10,12	57 586	523 714	9,09	53 073	529 394	9,97
113–114	66 881	716 860	10,72	82 828	719 421	8,69	81 077	840 595	10,37
118–119	48 596	396 503	8,16	96 346	643 755	6,68	78 251	792 744	10,13
123–125	39 327	410 926	10,45	85 435	548 565	6,42	41 575	316 878	7,62
129–131	65 705	818 860	12,46	54 761	361 535	6,60	45 260	346 565	7,66
135–137	43 708	338 520	7,75	33 217	238 760	7,19	31 574	205 122	6,50
142–145	32 466	198 705	6,12	29 553	172 851	5,85	11 390	65 855	5,78
151–153	20 062	110 630	5,51	12 099	65 135	5,38	11 891	57 955	4,87
157–158	4 786	30 101	6,29	9 612	39 382	4,10	2 400	10 145	4,23
162–164	3 500	19 343	5,53	9 592	32 518	3,39	...	...	...
169–170	1 250	4 168	3,33	9 597	30 927	3,22	...	...	...
176–177	...	...	...	5 393	15 596	2,89	...	...	...
Total	516 304	5 161 997	10,00	619 573	4 755 348	7,68	507 521	4 719 164	9,29

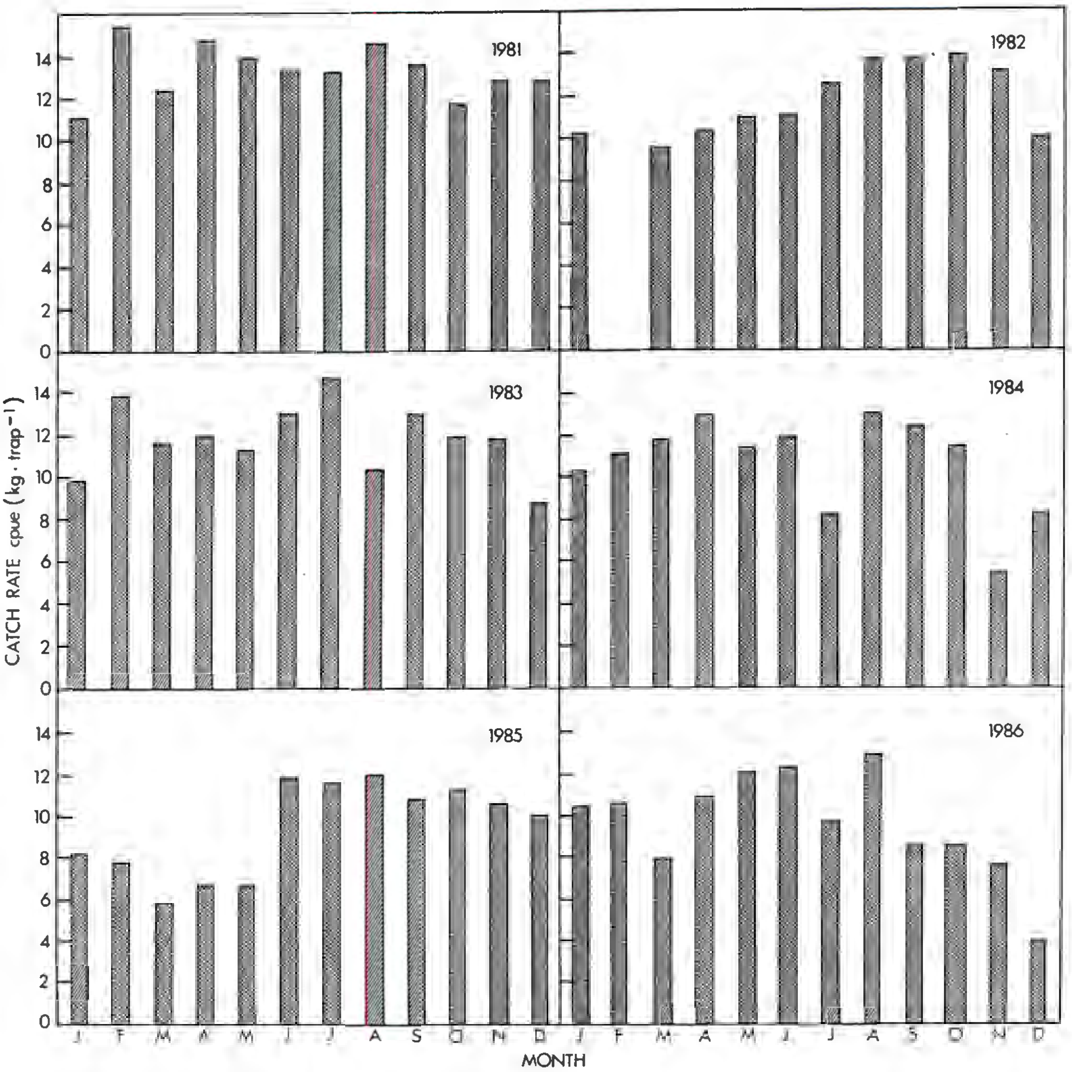

Fig. 4: Monthly trends in red-crab cpue for vessels of Taiyo Fishing Co. fishing in Grids 100–114, 1981–1986. Data only from catches made with soaking times of 24–119 h

Fishing Co. recently increased its effort considerably in an attempt to maintain its total annual catch (Fig. 7), apparently successfully. Since 1986, there have been no vessels on the South West African crab grounds other than those of the Taiyo Fishing Co.

Another apparently changing trend over the years is in the masses of the different products packed (Table VII). Whereas section mass has decreased, flake mass has remained more or less constant, probably a reflection of the drop in size of crabs available in the various grid areas (see Fig. 3). As already mentioned, large crabs (> 110 mm CW) are generally packed for the section product, whereas small crabs are processed as flake product. By 1986 the proportion of section product relative to the total mass of section and flake had decreased from

Table VI: Japanese effort, expressed as a percentage, by latitude, 1980–1986

Latitude (Grid rows)	Effort (%)						
	1980	1981	1982	1983	1984	1985	1986
< 17°S				0,2	6,6		0
17–18°S (Grids 97–104)	11,2	23,7	23,5	30,2	11,4	21,1	20,4
18–19°S (Grids 106–114)	17,3	23,0	30,7	28,3	29,2	29,0	33,8
19–20°S (Grids 118–131)	38,1	32,9	26,8	24,1	27,2	31,9	33,6
20–21°S (Grids 135–153)	31,6	18,5	16,4	11,8	19,9	12,3	11,5
21–22°S (Grids 157–170)	1,4	1,7	2,4	5,1	2,9	5,1	0,6
22–23°S (Grids 176–193)	0,4	0,2	0,1	0,3	2,8	0,6	0
> 23°S (South of Grid 199)	–	0,1	–	–	0,1	0,1	0

almost 40 per cent to only 7 per cent.

Yield-per-recruit analysis

Values of total mortality (Z) have been determined for males by the catch-curve method and are presented in Table VIII. The slopes of the plots in Figure 8, from which the values were calculated, vary considerably for different areas of the grounds.

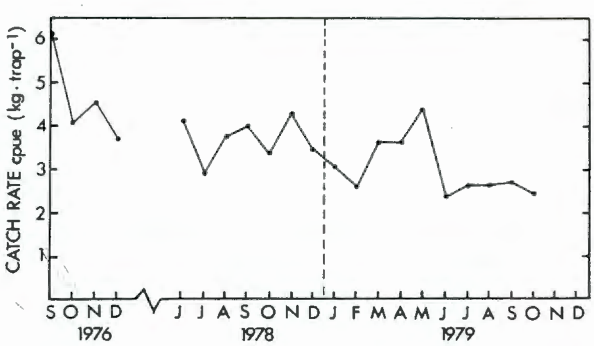

Fig. 5: Catch rate of red crab by South West African vessels, September 1976 – October 1979. Data only from catches made with soaking times of 24–119 h

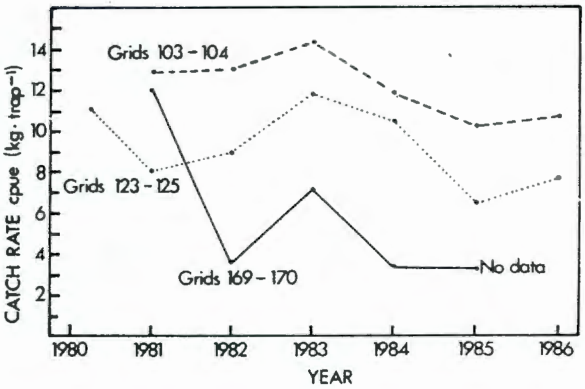

Fig. 6: Catch rate of red crab by Taiyo Fishing Co. vessels in three areas of the South West African fishing grounds, 1980–1986. Data only from catches made with soaking times of 24–119 h

With the limited information, there is no way of accurately calculating what portion of Z is made up by natural mortality M (Table VIII). Also, there is very little comparative information on decapod natural mortality in the literature. Most studies of cold-water crabs and lobsters have used an assumed or roughly calculated low value, 0,1 (Thomas 1973) and 0,02 (Ennis 1979) for *Homarus americanus*, 0,1 for *Jasus edwardsii* (Annala 1980), and 0,14 for *Cancer pagurus* (Bennett 1979). For warmer water lobsters, M has tended to be quoted as higher, 0,14–0,52 for *Panulirus argus* (Munro 1974 quoted by Cobb and Wang 1985) and 0,226 for *Panulirus cygnus* (Morgan 1977).

G. maritae is slow growing (Melville-Smith in press b) and lives in cold water at temperatures of 4,5–10,4°C (Beyers and Wilke 1980). Furthermore, size frequency analysis of the catch (Fig. 3) reveals that large crabs are abundant in areas where the rate of commercial exploitation is low. These factors suggest that the rate of natural mortality is low. Therefore, calculations involving M in this paper have been made with three values of M, 0,05, 0,10 and 0,15, the true value (which is unlikely to be constant over the whole grounds), probably lying somewhere within that range.

Yield-per-recruit estimates for male crabs with M of 0,05, 0,10 and 0,15 have been made and the results plotted (Fig. 9) in the form of yield isopleths. The models can be used to predict either the optimum age (and therefore size) at first capture or the theoretical level of F at which the stock should be fished.

There are data available on both current age at first capture and fishing mortality on the South West African red-crab grounds. Melville-Smith (1986) estimated, from a preliminary mesh selectivity study, that 50- and 100-per-cent selectivity for 90 mm mesh

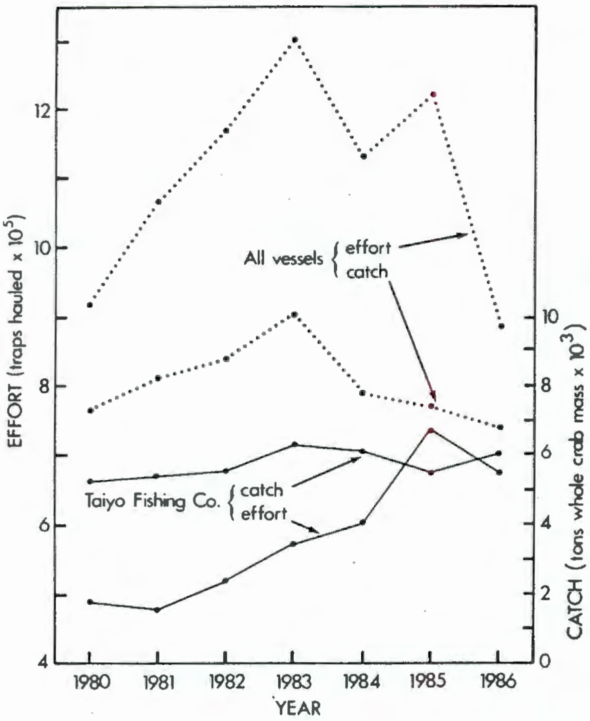

Fig. 7: Total catch and total effort and catch and effort by the Taiyo Fishing Co. on the South West African red-crab grounds, 1980–1986

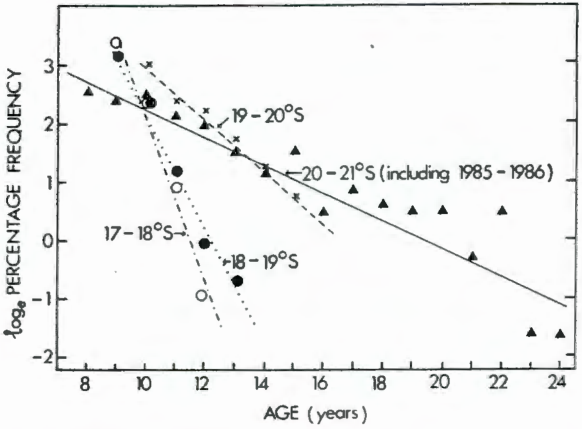

Fig. 8: The relationship between the log of the percentage frequency and age of male red crabs in four areas off South West Africa

is at 73 and 75 mm CW respectively. A crab of this size would be expected to be between six and seven years old (see Table II).

The values of F given in Table VIII have been estimated for males in different areas of the South West African crab grounds by subtracting an estimated M of 0,15 from the Z values obtained for each area in Table VIII. The estimate for F between 19 and 20°S (0,30) is reassuringly close to the estimate of 0,24 for males and 0,41 for females made during 1982–1983 for roughly the same area by another technique (Melville-Smith 1988).

Comparing the estimated F values with the results of the yield-per-recruit models (Fig. 9), it is evident that the present age at first capture (T_c) for males is considerably less than optimal. Based on the yield curve with the highest natural mortality (Fig. 9c), it is clear that the present fishing mortality in the important northern areas of the grounds (Table VIII, 17°20′–19°S) is in excess of the optimum. According to Figure 9c, F values could theoretically be indefinitely maintained at the above levels only if the age at first capture was greater than 11 years (or an estimated 104 mm CW). The curves based on lower rates of natural mortality (Figs 9a, b) show the fishery to be in a considerably more precarious position than is exemplified by Figure 9c. Those curves suggest that t_c should be considerably higher than 11 years.

Changes in yield per recruit (both sexes combined) expected if the age at first capture were to be increased to 9 or 12 years have been modelled for three rates of F and are presented in Figure 10. The F values selected (1,4, 0,98 and 0,30) correspond to those estimated for 17°20′–18°S, 18–19°S and 19–20°S respectively (Table VIII).

An alternative management option is to limit fishing effort. Based on the male yield isopleths (Figs 9a–c), the optimal level of F, under the present fishing conditions where all sizes larger than 6,5 years (75 mm CW) are retained, is between 0,20 and 0,25 at $M = 0,15$ and less where $M < 0,15$.

Table VII: Total production and proportion of section mass, 1980–1986

Year	Section mass (kg)	Flake mass (kg)	Total section and flake (kg)	Section as percentage of total (kg)
1980	1 104 780	1 706 873	2 811 653	39,3
1981	790 683	2 169 791	2 960 474	26,7
1982	781 896	2 305 158	3 087 054	25,3
1983	462 169	2 681 150	3 143 319	14,7
1984	309 345	2 384 346	2 693 691	11,5
1985	351 326	2 051 996	2 403 322	14,6
1986	153 297	2 030 630	2 183 927	7,0

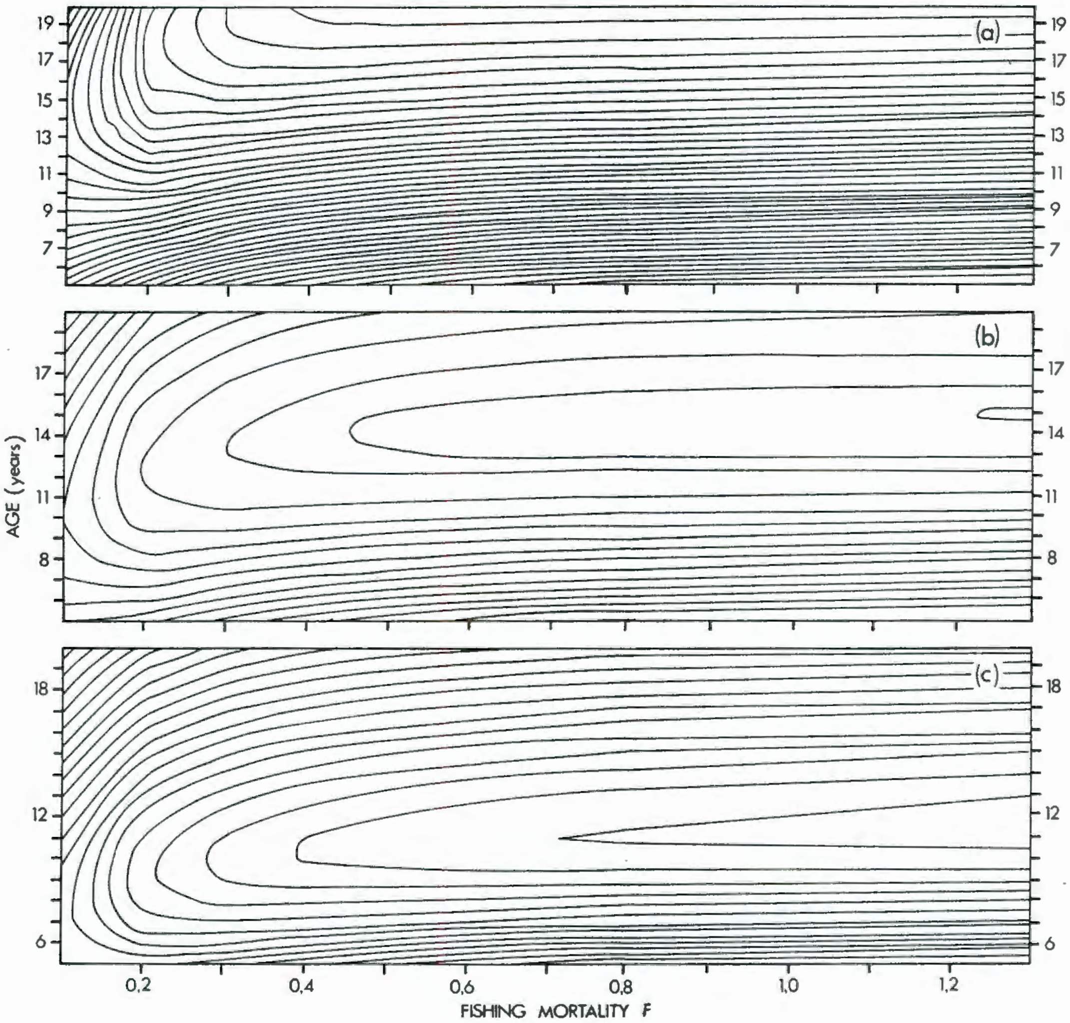

Fig. 9: Male crab yield isopleths for three values of natural mortality M, (a) 0,05, (b) 0,10 and (c) 0,15

DISCUSSION

The yield-per-recruit computations in Figure 9 have only taken male crabs into consideration. Limited information for female growth (Melville-Smith in press b) has shown that their growth appears to be similar to, or even slightly faster than for males, at least until maturity is attained. After maturity, their intermoult periods become lengthy and, judging by the small percentage of females that were recorded by Melville-Smith (op. cit.) as moulting after attaining maturity (1,6 per cent), it is quite likely that post-maturity moults are rare. In effect therefore, growth virtually ceases once maturity is reached. If the reproductive potential of female crabs is disregarded and a size is adopted at which an optimal yield per recruit for that sex would result, it is likely that the size would be at, or close to, the size at which sexual maturity is attained, i.e. at least 84 mm CW or a probable age of 7–9 years (see Table II). Female data have therefore been excluded from the yield computations (Fig. 9) because of their predictable effects on yields once age at maturity is attained (i.e. raising the

Table VIII: Estimated total (Z) and fishing (F) mortalities for various areas as calculated from Figure 8 using data for males. Natural mortality assumed = 0,15

Area	Ages analysed in catch curve (years)	Regression equation	r	Total mortality Z	Fishing mortality F (= Z − 0,15)
17 - 18°S	9-12	$y = -1{,}40x + 16{,}05$	0,99	1,40	1,25
18 - 19°S	9-13	$y = -0{,}98x + 11{,}92$	0,99	0,98	0,83
19 - 20°S	10-15	$y = -0{,}45x + 7{,}44$	0,98	0,45	0,30
20 - 21°S	8-24	$y = -0{,}24x + 4{,}64$	0,89	0,24	0,09

F and lowering the t_c values at which yield per recruit could be optimized). The approach used has been to establish an optimal t_c or F for males and then to discuss what effect that would have on the expected yields and changes in population structure of both sexes.

Evidence presented in the form of length frequency data (Fig. 3, Table VII), cpue (Table V, Figs 6 and 7) and mortality values (Table VIII) shows that the South West African red-crab stock has been, and still is being, heavily fished over much of its distribution. This fishing pressure must undoubtedly have had a considerable impact on the egg production of the population because, as noted earlier, 100-per-cent retention by commercial fishing gear is at only 75 mm CW, 9 mm smaller than that at 50-per-cent female maturity.

Some idea of the impact of commercial fishing on egg production over the last five years can be gauged from the differences in cpue over the period 1981–1986. Assuming that cpue is a rough index of crab density, then it follows from Table IX that the density of crabs on the South West African grounds has decreased by some 26 per cent over the 6 years. The decrease would undoubtedly have been much higher if cpue information had been available to permit examination of the full history of the fishery.

Table IX: Difference in catch rate between 1981 and 1986 in different areas on the South West African red-crab grounds

Grids	Catch rate (kg·trap^{-1})		Change in catch rate (%)
	1981	1986	
100–101	13,52	9,45	−30,1
103–104	12,87	10,65	−17,2
106–107	13,82	10,34	−25,2
109–110	13,53	9,97	−26,3
113–114	11,55	10,37	−10,2
118–119	11,53	10,13	−12,1
123–125	8,06	7,62	− 5,5
129–131	7,30	7,66	+ 4,7
135–137	8,67	6,50	−25,0
142–145	12,03	5,78	−52,0
151–153	9,06	4,87	−46,2
157–158	11,89	4,23	−64,4
Mean			−25,8

Reproductive studies on both *G. maritae* (Melville-Smith 1987a) and the closely related *Geryon quinquedens* (Haefner 1977) have revealed that females do not become ovigerous immediately after their maturity moult. It has been suggested by Ganz and Hermann (1975), quoted by Cassels and Krebs 1983, that the incubation period for *G. quinquedens* is about 300 days. Therefore, effective management would require that female crabs be protected from fishing gear for a considerable period prior to their spawning.

MANAGEMENT OPTIONS

The evidence suggests that the historically high rates of exploitation, combined with the present relatively small size at first capture, may have maximized the yield per recruit of females while causing recruiting crabs to be subjected to excessive rates of exploitation. On the basis of this knowledge, it is felt that one of three strategies could be employed by management to offer some protection to the breeding stock. In discussing each strategy, particular attention has been paid to the effects that the proposals would have on present and future expected yields. The most obvious means of protecting the breeding stock, i.e. the imposition of a ban on the packing of females, is not considered to be a feasible management option because it would be virtually impossible to enforce.

Increasing the age at first capture (t_c)

Yield-per-recruit models over the range of M from 0,05 to 0,15 (Fig. 9) suggest that maximum yields for males could be optimized at an age of first capture in excess of 11 years (104 mm CW). This is considerably larger than the present size at first capture (75 mm

CW) or 6–7 years old. As the data for both sexes point to a benefit if the size/age at first capture is increased, it is pertinent to examine the effects of such an increase on the current yields.

The percentage of the current catch (both sexes) lost to production in the first year were the size at first capture to be increased, for instance by the introduction of a larger mesh size or escape gaps, is shown in Table X. Such extreme losses would be temporary and yields would be expected to recover rapidly in subsequent years (Fig. 10). The specific ages at first capture modelled in Figure 10 (8 and 12 years) were selected because a t_c at that age would protect 50 and 100 per cent of the mature females from exploitation.

Table X: Percentage of the commercial catch of whole crab mass, in two areas of the South West African red-crab grounds, that would be lost to production if the minimum size was increased. Data based on commercial samples taken during 1986

Minimum size (mm)	Northern area (17–19°S)	Southern area (19–21°S)
≥ 80	19,1	13,9
≥ 85	45,0	25,1
≥ 90	67,1	36,6
≥ 95	83,2	49,6
≥ 100	91,7	62,7
≥ 105	96,9	73,2
≥ 110	98,9	81,5

Any increase in the age at first capture would result in decreased yields. The reason for this is that relatively small increases in the age at first capture would result in large proportions of the mature female population being excluded from contributing to the fishery. Some of the loss to production as a result of their exclusion could be offset by increased yield per recruit of males, but that would be insufficient to restore the fishery to its present performance. In the case of the modelled situation (Fig. 10), the ages and consequently the sizes at first capture (8 years, 84 mm CW; 12 years, 109 mm CW), would be expected to lower current yields by about 13 and 40 per cent whole mass respectively once equilibrium was attained following changes in age at first capture. It must be borne in mind that larger crabs contribute a greater percentage of their mass to production than small crabs (Melville-Smith in press a). Any increase in t_c would increase the mean size of the catch, in turn probably further decreasing the percentage disparity between present yields and those that could be expected from a change in t_c.

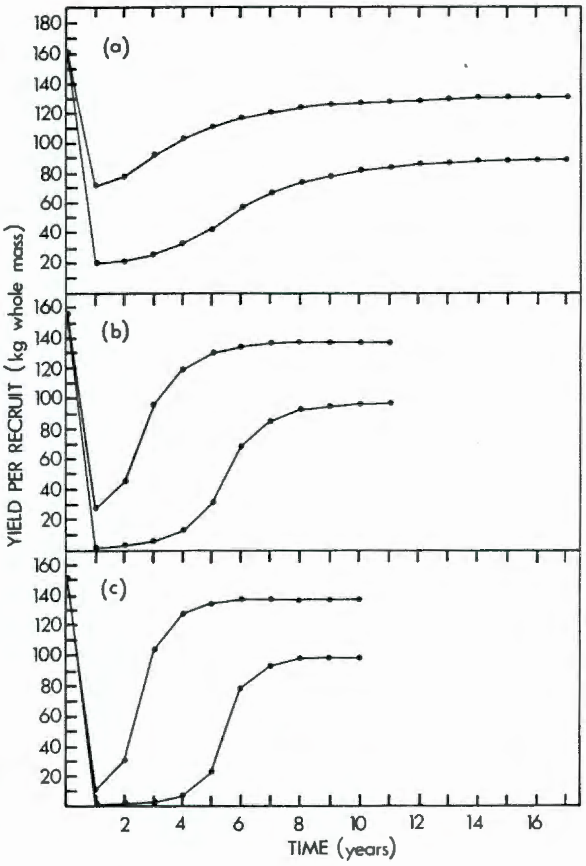

Fig. 10: Predictions of the expected changes in yield per recruit that would follow two possible changes of age at first capture. For each prediction, $M = 0{,}15$ and F is (a) 0,30, (b) 0,98 and (c) 1,25

Reducing fishing effort (F)

Reducing F would probably necessitate the withdrawal of some vessels from the fishery while maintaining a close watch on the distribution of effort over the grounds by those remaining. The two obvious benefits of such a strategy would be that not all vessels would suffer decreased yields, as would be the case if t_c were increased, and that yields per recruit would be optimized (it was shown earlier that females should be exploited for optimal fishing yields to be obtained).

The F values for the southern part of the ground fall roughly within those values considered to produce optimal yields. However, on the northern grounds F is particularly high (Table VIII). To bring these values in line with the suggested optimal F (assuming

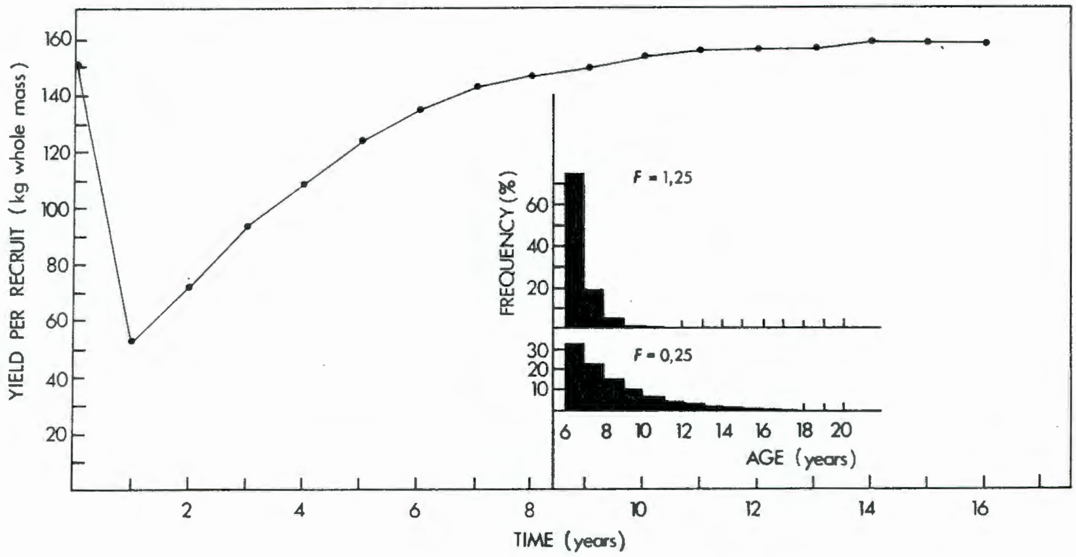

Fig. 11: Prediction of the effect on yield per recruit and (inset) population age frequency if fishing mortality is decreased from 1,25 to 0,25

the highest *M*, Fig. 9c) would require cutting the effort at present exerted in those areas by between 60 and 70 per cent (to an *F* of 0,20–0,25).

Fishing mortality is thought to be particularly high in the northern areas of the crab grounds ($F = 1,25$ and 0,83 between latitudes 17 and 18°S and 18 and 19°S respectively — Table VIII). In Figure 11, an attempt has been made to model the change in yield per recruit and population age frequency that would result if *F* was reduced from 1,25 to 0,25 (the latter being the *F* value suggested to optimize yield per recruit). Naturally, a reduction of effort would result in a proportional reduction of catch. In the modelled situation, the yield per recruit fell by ~65 per cent in the first year before climbing back to reach and even surpass the original levels after about 10 years.

For other situations with slightly different values of *M*, sex ratios and assumed ages of female maturity, the results were similar. It is unlikely that yields in a real situation would respond as favourably as suggested by the model. A reduced *F* would result in a higher standing stock, which would in turn probably result in reduced growth and higher natural mortality. Even bearing this fact in mind, it is obvious that the yield per recruit would be expected to improve substantially with much less effort. However, of more importance is the fact that a reduced fishing effort would result in a more healthy age frequency distribution (Fig. 11). Such an age distribution would permit a very much greater number of females to spawn before capture than is at present the case in the northern areas.

A strategy of reduced effort would result in the number of large (old) males in the population approximating that of the natural situation more closely than were a higher t_c to be imposed. As with most crabs, *G. maritae* males are polygamous and, furthermore, relatively small males (~80 mm CW or 7–8 years of age) have been shown to be sexually mature. The presence of large males in the population would therefore not be particularly beneficial to the stock. However, it is possible that mating by small males may result in fewer eggs being fertilized than would be by large males. Such a possibility has still to be evaluated and the outcome of such an experiment could have an important bearing on the recommended choice of management strategy.

Restricting fishing shallower than 500 m

It is widely reported in the literature that female *G. maritae* tend to be found shallower than males (Cayré and Bouchereau 1977, Le Loeuff *et al.* 1978, Beyers and Wilke 1980, Gaertner and Laloë 1985), though both sexes are found over the full depth range at which the species is caught. If crab fishing off South West Africa were to be restricted only to depths greater than 500 m, some protection would be afforded to females (Table III). However, such protection would not be as effective as that offered by a larger mesh size, because there is considerable movement by crabs between depths (Melville-Smith 1987b). The effect of a "sanctuary depth zone" on the commercial fishing fleet can be gauged by effort data submitted by the Taiyo Fishing Co. for 1986. That company's vessels reported 23 per cent of their fishing effort expended at depths shallower than 500 m.

General

Some form of stock management policy is desirable although there are several options open to this end. One of the less obvious advantages of an increase in *F* or of a decrease in t_c would be to improve the quality of the product produced. A larger mean size of the catch would result in more leg, claw and section product and less flake being produced.

ACKNOWLEDGEMENTS

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PAPER 11:

Product-whole mass conversion factors in the Namibian red crab fishery

ICSEAF 1988
Colln scient. Pap. int. Commn SE. Atl. Fish.
Pages 81-86

PRODUCT-WHOLE MASS CONVERSION FACTORS IN THE NAMIBIAN RED CRAB FISHERY

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Commercial vessels fishing for red crab off Namibia produce a variety of products from the catch. Factors are presented in this report enabling red crab product mass (as recorded in catch statistics) to be converted to whole mass.

*Il est tiré divers produits des captures des bateaux pêchant le crabe rouge (***Geryon maritae***) au large de la Namibie. Dans cette étude, l'auteur présente des facteurs permettant de convertir le poids du produit (figurant dans les statistiques de captures) en poids entier du crabe rouge.*

Los buques comerciales que pescan cangrejo rojo frente a Namibia elaboran cierta variedad de productos a partir de la captura. En este trabajo se presentan los factores que permiten convertir el producto elaborado (según figura en las estadísticas de captura) en peso vivo.

INTRODUCTION

Foreign vessels fishing for red crab **Geryon maritae** off Namibia supply this Institute with statistical information on their daily catches. These data are used for management purposes (Melville-Smith 1988). Catches made by commercial crab vessels are reported as packed product mass, but for analysis purposes, it is necessary to convert the data from product mass to whole crab mass. The object of this paper is to describe the methods used and results obtained in the establishment of product to whole mass conversion factors for **Geryon maritae**.

METHODS

The numerous products are described in Melville-Smith (1988) and are shown in Figure 1. The type of product packed is generally dependent on the size of the crab: large crabs are usually used for sections, medium animals for leg, claw and flake, and small crabs for flake product only (Figure 1). A product to whole live mass conversion factor varies for crabs of different sizes. To facilitate an appropiate conversion factor according to the mean size of crabs in the catch, it was necessary to establish a product to whole mass relationship for a range of crab sizes.

The whole crab to product ratios (excluding the whole mass to flake ratio) calculated in this report, are based on measurements made on over 180 male crabs varying in size from 68 to 154 mm carapace width (CW). The animals were captured using crab traps in the area 19°30' S to 20°00' S at depths of 450 to 600 m, and were kept alive in holding tanks on board ship until they could be processed in the laboratory. Only animals alive at the start of the experiment were used for the size-mass calculations.

Each crab was individually measured, sectioned, cooked and reweighed with the mass being noted at each stage. The same time duration as used by the commercial crab boats was used for each stage in the cooking process. The cooked crab sample was divided into two similar samples of approximately six animals per 5-mm size class. The samples were then processed, each according to one of the methods employed by the two Japanese crab companies currently operating vessels off Namibia.

It was particularly difficult to obtain a conversion factor for flake to whole mass. The machinery to produce the product is specialized and was only to be found on the Japanese crab vessels. However, permission was obtained by courtesy of the Taiyo Fishing Company to conduct a conversion ratio experiment on one of their crab boats.

A sample (188,5 kg) of live small-sized crabs (i.e., crabs <95 mm CW) ranging from 80 to 94 mm CW were weighed, sectioned, cooked and put through a 10-mm flake machine. The flesh and shell discarded by the 10-mm machine was then put through a 1-mm machine. In both cases the product was weighed.

A second sample (248 kg) of live medium-sized crabs (95 to 110 mm CW) was treated similarly to the small crabs above, but once in cooked section form, the leg merus was processed and packed as leg product. Claw, arm, shoulder and nail were first put through a 10-mm and then a 1-mm flake machine as described above for the small crabs.

RESULTS AND DISCUSSION

The suitability of a crab for a particular product is determined by its size. Since it is generally difficult to obtain the accurate weight of a crab at sea, these size limitations have been given as a carapace width measurement in this report. Carapace width can be converted to whole live mass by the following relationship:

Carapace width: whole live crab mass
Males: $y = 0{,}000167x^{3{,}156}$ (49-160 mm CW)
N= 203; r=0,99
Females: $y = 0{,}000218x^{3{,}056}$ (47-104 mm CW)
N=76; r=0,99

where:
y - whole live crab mass in g
x - carapace width in mm

Various product to carapace width regressions are given in Table 1. Using these regressions, a percentage relationship has been calculated between the product mass and whole crab mass for the mean size of crabs used in the manufacture of the particular product (Table 1). The regressions for each product have been restricted to crabs falling into the size range used for that product with the exception of whole mass to section mass.

The relationship between section product and whole crab mass has been calculated for crabs 68 - 154 mm CW. It has been mentioned that only crabs larger than 110 mm CW are packed for this product. Since the ratio of section product to whole crab mass for sizes of 110 to 140 mm CW varies between 58 and 59 %, a mean conversion value of 58,5% has been proposed for this product in Table 1.

Leg product is usually restricted to crabs of between 95 to 110 mm CW. Larger crabs are also used occasionally for this product and, consequently, the product to carapace width regression has been calculated using crabs over the range of 95 to 154 mm CW (Table 1). Conversion values for leg to whole mass were calculated for animals of 100 mm CW (judged to be the most commonly used size for this product) and are presented in Table 1.

The following flake product to whole crab mass values were obtained using a commercial flake machine.

(i) A sample of small live crabs 80 to 94 mm was weighed before sectioning. Their mass was 188,5 kg. The crabs were then sectioned, cooked and put through a 10-mm flake machine. A total of 62,3 kg of flake product or 33,1 % of the original whole crab mass was produced (Table 1). The "waste" from the 10-mm flake machine was then put through a 1-mm flake machine. This second machine produced a further 15,4 kg of flake product or 8,2 % of the original whole crab mass (Table 1)

(ii) A sample of medium live crabs (95 to 110 mm) was weighed before sectioning. Their mass was 248,0 kg. The crabs were then sectioned, cooked and put through a 10-mm flake machine. A total of 45,2 kg of flake product or 18,2 % of the original whole crab mass was produced (Table 1). The "waste" from the 10-mm flake machine was then put through a 1-mm flake machine. This second machine produced a further 14,0 kg of flake product or 5,6 % of the original whole crab mass (Table 1). These production values for medium-sized crabs were obtained after removal of the merus for leg product (see Melville-Smith 1988, "leg product").

(iii) The smaller the meat-separating holes of a flake machine, the lesser the flake products yielded. The Taiyo Company obtained the following yield figures for a sample of whole crab to flake product using a 5-mm flake machine. No attention was paid to the size of animals used for the experiment, but since the whole crab section was reduced to flake, it can confidently be assumed that they were all less than 95 mm CW. The mass of the whole live crabs before sectioning was 100 kg. The crabs were sectioned, cooked and put through a 5-mm flake machine. The experiment yielded 30,3 kg of flake product or 30,3 % of the original whole crab mass (Table 1)

iv) Comparing the figure of 30,3 % obtained in (iii) with that obtained in (i), the percentage difference in whole crab to flake product conversion values for the 5-mm and 10-mm machines is 8,5 %. The figure for medium crabs in (ii) can therefore be adjusted by the same percentage difference i.e., 91,5 % of 18,2 %, which gives 16,7 % (Table 1).

In the early years when catch statistics were first reported by the fishing fleet, there was only one mass figure given for flake product. No distinction was made as to what grid size had been used in the manufacture of the flake, and when both 10-mm and 1-mm machines had been used, the amount produced was a lump sum. As a result, the conversion ratio for small crabs (80-94 mm CW) during those years might have varied from 30,3 % if only 5-mm flake had been produced, up to 41,3 % if 10- and 1-mm flake had been combined. It has been mentioned that usually one third of the catch is processed as 5-mm flake with 10- plus 1-mm, flake constituting the balance. Using this ratio, conversion factors of 38,0 % and 21,0 % have been employed for small and medium crab, respectively, in cases where no distinction has been made as to the size of flake machine used in the manufacture of the products (Table 1).

The above whole mass to flake conversion factors were all calculated using flake machines belonging to one company. As mentioned earlier, the two Japanese companies currently fishing for crab off Namibia use flake machines with slightly different sized meat-separating holes (9-mm and 10-mm diameter). Taking into account that the calculated difference in yield between a 5-mm and 10-mm sized hole is small (2,8 %), the difference in yield between a flake machine with a 9-mm and 10-mm hole is considered to be negligible.

It was further assumed that there is no difference in the flake yielded by medium-sized crabs (95 to 110 mm CW) for the two fishing companies. This assumption is undoubtedly incorrect, due to the different methods employed by the companies in packing the leg product. The company which cuts the legs (see "leg product" description in Melville-Smith 1988), supplements their flake yield with the upper portion of leg which is attached to the shoulder. The amount gained by the inclusion of these pieces of merus is not known, but is assumed to be small enough to be ignored.

Use of conversion factors

Catch statistics, as recorded in log books kept by the skippers of the crab fishing vessels, have been converted into whole crab mass using the following method. Section product mass has been divided by 0,585 to give the estimated whole mass of large crabs (>110mm CW). Leg product has been divided by either 0,133 or 0,084, depending on whether the product was with or without shell, to give a whole crab mass for medium-sized crabs (95-110 mm CW). The contribution of medium-sized crabs to the flake total can be calculated by multiplying the whole mass for medium crabs (calculated above) by either 0,182, 0,167 or 0,210, depending on whether the grid size of the flake machine used was 10-mm, 5-mm or unrecorded, respectively. When this quantity is subtracted from the total amount of flake product produced, it leaves the estimated amount of flake produced from small-sized crabs (<95 mm CW). The whole mass of small crab can be estimated by dividing the quantity of flake product produced from small crabs by either 0,331, 0,303 or 0,380 depending on whether the grid size used in the production of flake was 10-mm, 5-mm or unrecorded, respectively. The above three sub-totals for small, medium and large crabs added together give the total estimated mass of whole crab caught.

Some of the carapace width: mass relationships examined in this study have been previously documented (Beyers and Wilke 1980). Comparison of those results with this study shows that although the regression slopes (and, therefore, percentage difference between whole crab mass and product mass) are similar, there is a discrepancy in the mass at carapace width relationship. It is the author's opinion that this difference is due to the fact that the crabs used by Beyers and Wilke (1980) were frozen prior to being weighed and cooked. A considerable amount of water is lost in the thawing process, leading to a consequent lower mass at carapace width result.

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TABLE 1. Regression equations describing the relationship between red crab CW and product mass and the conversion factor used to transform product value to whole crab mass

PRODUCT	Size of crabs (mm)	CW/Product regression	Numbers of crab (n)	Correlation coefficient	Product/whole mass ratio %
Section	68-154	$y=0{,}0000633x^{3{,}246}$	180	0,99	58,5
Leg (with shell)	95-151	$y=0{,}000011x^{3{,}309}$	70	0,98	13,3
Leg (without shell)	95-154	$y=0{,}0000091x^{3{,}250}$	66	0,96	8,41
Flake (10 mm)	80- 94				33,1
Flake (1 mm) residue from above	80- 94				8,2
Flake (10 mm) from shoulders	95-110				18,2
Flake (1 mm) residue from above	95-110				5,6
Flake (5 mm)	80-94				30,3
Flake (5 mm) estimated quantity from shoulders	95-110				16,7
Flake (machine size not recorded)	80-94				38,0
Flake (machine size not recorded) shoulders	95-110				21,0

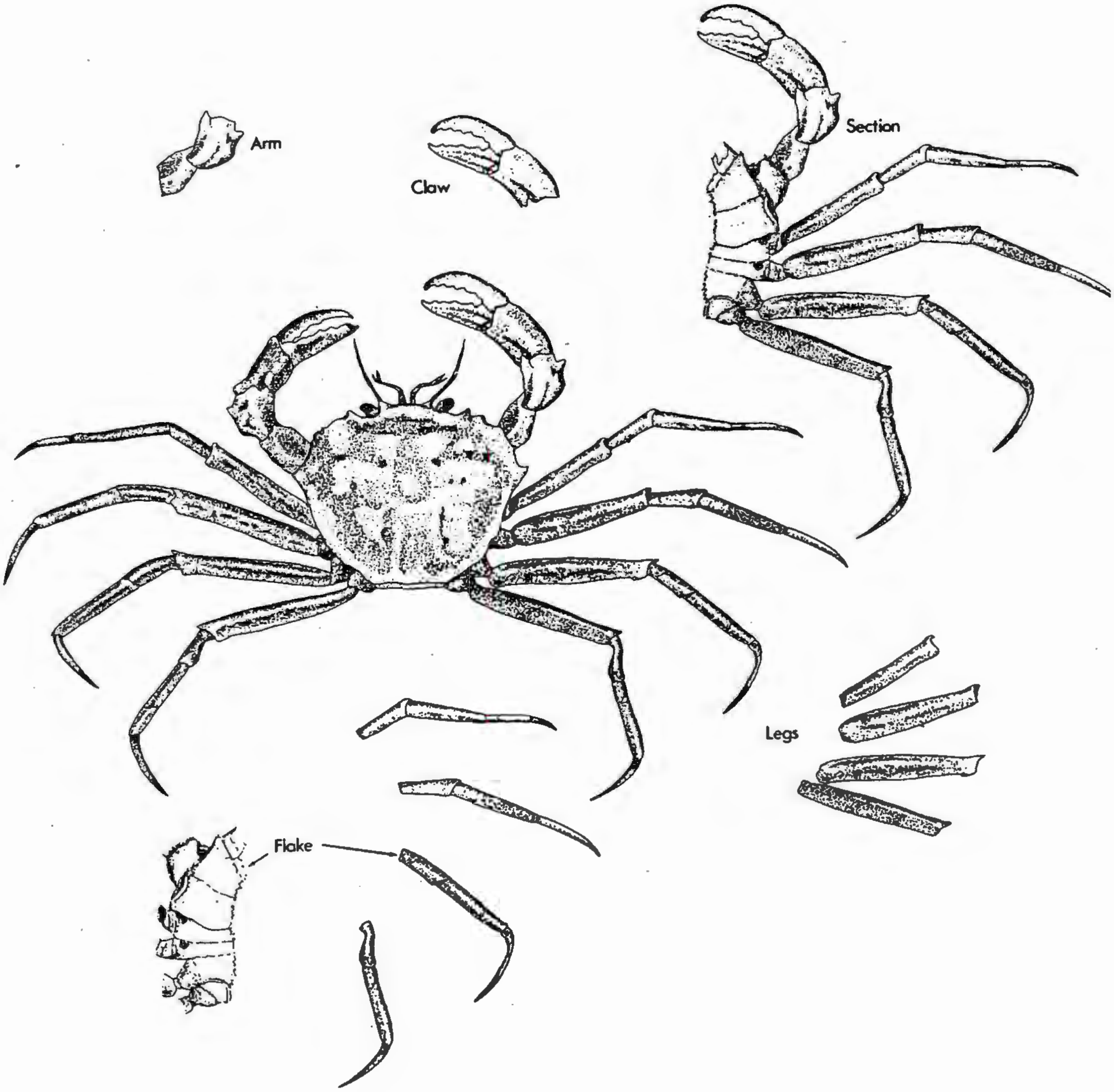

FIG. 1. Products from red crab caught off Namibia (after Melville-Smith 1988)

PAPER 12:

A brief exploitation of the stone crab *Lithodes murrayi* (Henderson) off South West Africa, 1979/80

Fish. Bull. S. Afr. 16:45–55
1982

A BRIEF EXPLOITATION OF THE STONE CRAB *LITHODES MURRAYI* (HENDERSON) OFF SOUTH WEST AFRICA, 1979/80

R. MELVILLE-SMITH

The stone crab *Lithodes murrayi* was exploited briefly off South West Africa between November 1979 and April 1980, the fishery being terminated when the catch per unit effort fell to an uneconomic level. The extent of the *L. murrayi* grounds is examined on the basis of catch-per-unit-effort data. The species is largely confined to a bathymetric corridor of 500 — 700 m off South West Africa. Prior to commercial fishing, there was a densely populated region between 24°00'S and 24°40'S, although the crabs were present in small numbers over a much larger area. Over 90 per cent of the fishing effort was applied in this area of high concentration, accounting for almost 95 per cent by mass of the total catch. Although the catch rate declined, the mean size of exploitable crabs and of undersize crabs stayed virtually constant. Some morphometric relationships and a factor for converting processed crab section mass to whole crab mass have been calculated.

Die klipkrap *Lithodes murrayi* is langs die kus van Suidwes-Afrika ontgin gedurende die kort tydperk November 1979 tot April 1980. Die vissery is gestaak toe die vangs per pogingseenheid tot 'n onekonomiese vlak gedaal het. Die omvang van die *L. murrayi*-gronde word op grond van vangs-per-pogingseenheid-data ondersoek. Die spesie word grotendeels in 'n batimetriese strook tussen 500 en 700 m langs die kus van Suidwes-Afrika aangetref. Voor die aanvang van kommersiële ontginning was daar 'n dig bevolkte streek tussen 24°00'S en 24°40'S, hoewel die krappe oor 'n veel groter gebied yl versprei was. Meer as 90 persent van die vangpoging is toegespits op hierdie gebied van hoë konsentrasie, waar meer as 95 persent van die totale massa gevang is. Al het die vangkoers gedaal, het die gemiddelde grootte van ontginbare krappe en ondermaatse krappe feitlik konstant gebly. Enkele morfometriese verhoudings is bereken, asook 'n faktor vir die omsetting van die massa van verwerkte krapseksies tot dié van heel krap.

The presence of the stone crab *Lithodes murrayi* (Fig. 1) has been reported from several parts of the Southern Hemisphere and over a wide range of depths. In the literature, areas and depths of occurrence are cited as being : Prince Edward Islands (567 m) — Henderson (1888); Macquarie Island (120m) —Hale (1941); southern New Zealand (209 m) — Yaldwyn and Dawson (1970); Crozet Islands (35 —180 m) — Arnaud and Do-Chi (1977); Chile (70 m) — Campodonico and Guzman (1972); east coast of South Africa (600 — 810 m) — Kensley (1977); west coast of southern Africa (800 m) —Kensley (1980). This report is the first record of commercial exploitation of the species.

Since 1973 there has been an active red-crab (*Geryon quinquedens*) fishery off the continental shelf of northern South West Africa/Namibia (Beyers and Wilke 1980). Small numbers of stone crab have occasionally formed an insignificant by-catch of vessels fishing for red crab, but only very infrequently have they been processed.

During August and September 1979, the Sea Fisheries Institute and a company based in South West Africa already engaged in the red-crab fishery conducted a joint survey with the aim of establishing the southern extent of the red-crab grounds. In the course of this survey, an area (Grid Area 233, Fig. 2) yielding large catches of *L. murrayi* was discovered in a depth range of 600 — 700 m.

The fishing company conducted further experimental fishing during September and October 1979 and established that *L. murrayi* occurred in high numbers over a substantial area. This led to the transferring by the company of one of their two crab-fishing vessels from the red-crab grounds in northern S.W.A. to these stone-crab grounds off central and southern S.W.A.

The F.V. *Cormorano*, of 611 g.r.t., began intensive commercial fishing for *L. murrayi* in November 1979. The fishery was short-lived, however, and it terminated in early April 1980 when the catch per unit effort (C.P.U.E.) dropped to uneconomic levels. It is the object of this report to examine the decline in C.P.U.E. and the change in the population size structure of *L. murrayi* as a result of exploitation.

METHODS

Experimental fishing

Prior to the commencement of commercial fishing, an attempt was made by the industry to gain some idea of the extent of the *L. murrayi* grounds. During September and October 1979, experimental fishing was conducted in a total of 23 different grid areas (Fig. 2). In February 1980, after commercial

Fig. 1: The stone crab *Lithodes murrayi*

fishing operations had commenced, experimental fishing was also conducted in three other grid areas.

The experimental fishing during September and October was conducted with longlines of 50 traps set at different depths, 88,4 per cent of which were set between 500 and 700 m (*L. murrayi* has seldom been caught in large quantities outside these depths off S.W.A.). The lines were set for varying periods of time, the majority being hauled after 12 — 24 hours. No line was set for longer than 28 hours. Experimental catches in February were made with standard commercial longline gear.

Commercial fishing

The method of fishing for *L. murrayi* was similar to that described for *G. quinquedens* (Beyers and Wilke 1980). The catcher vessel had several longlines, each of which usually had about 300 crab pots spaced approximately 10 fathoms (18 m) apart. The time that the pots were left in the water varied widely, but it was usually between 24 and 48 hours. On most working days three, or occasionally four, longlines were hauled, the catch was processed and the traps were reset.

The industry considered it uneconomic to process small crabs, despite the absence of an imposed minimum legal size limit. Samples of the commercial catch showed that, in general, crabs larger than 10,2 cm L_s, measured from the tip of the most anterior spine to the posterior edge of the cephalothorax (Fig. 3), were retained. The rest of the catch was returned live to the sea.

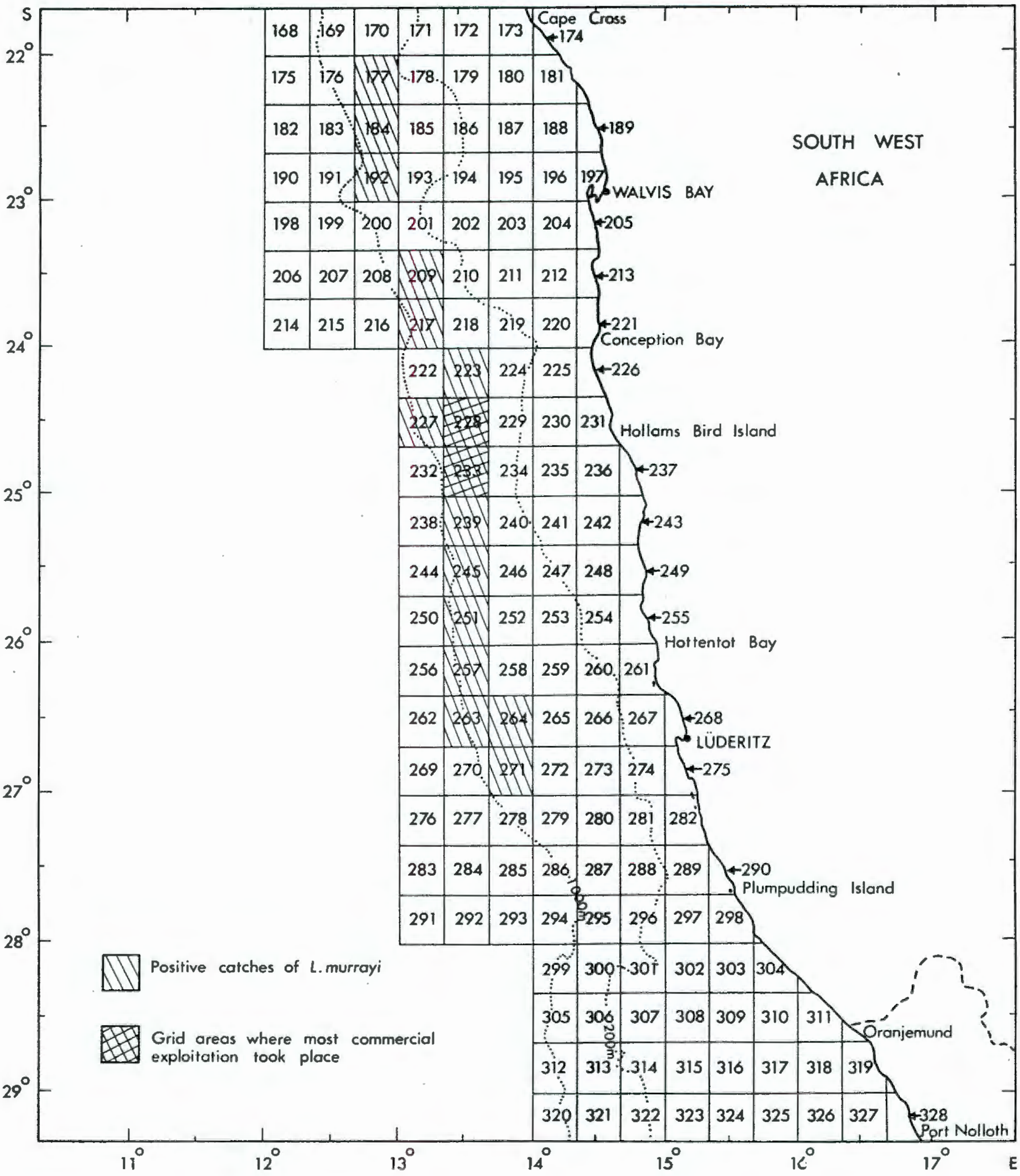

Fig. 2: Areas of positive catches of *Lithodes murrayi*, as identified on the standard trawl grid

The crabs retained were processed by removing the carapace and then splitting the body down the centre of the thoracic sternum into two halves. Each half, termed a section by the industry and referred to as such in this report, was cleaned of the gills and any attached viscera by means of rotating nylon brushes.

Analysis of statistics

The F.V. *Cormorano* was accompanied by a representative of the Sea Fisheries Institute for approximately ten days of each of the first three months of 1980. Random samples of 200 — 300 crabs per longline set were analysed on board. All the animals sampled were sexed and measured with calipers to the nearest millimetre. Measurements were initially (January and February) taken from the anterior tip of the rostrum to the posterior edge of the cephalothorax, denoted L_r (Fig. 3). From March onwards, L_s (Fig. 3) was measured instead, because the rostrum was frequently found to be broken, making it impossible to determine L_r accurately.

Commercial catch statistics were supplied to the Institute as kilogramme uncooked, sectioned crab per longline of traps. In each case the exact number of traps, the time (in hours) of submersion, the grid area (see Fig. 2) and the depth were given.

Some of the early catch statistics for experimental fishing (September and October 1979) were supplied as kilogramme whole mass per longline per hour. In order to standardize the data, all catch statistics have been converted to kilogramme whole mass per trap per 24 hours.

During commercial operations, the crab traps were usually retrieved after 24 — 48 hours. Occasionally however, they were left for much longer periods before being retrieved, and the effort was then disproportionate to the catch. For this reason, whenever the traps were left for longer than an arbitrarily chosen 60-hour period before being retrieved, the data have been disregarded unless otherwise stated.

Research fishing

During September 1979 and October 1980, two longlines of 20 and 50 traps each were set on the commercial grounds in Grid Area 233 (see Fig. 2). Although the number of crabs caught in these two settings was small ($N = 225$ and $N = 199$), they nevertheless provided an opportunity to examine the population size structure before and after commercial fishing had taken place.

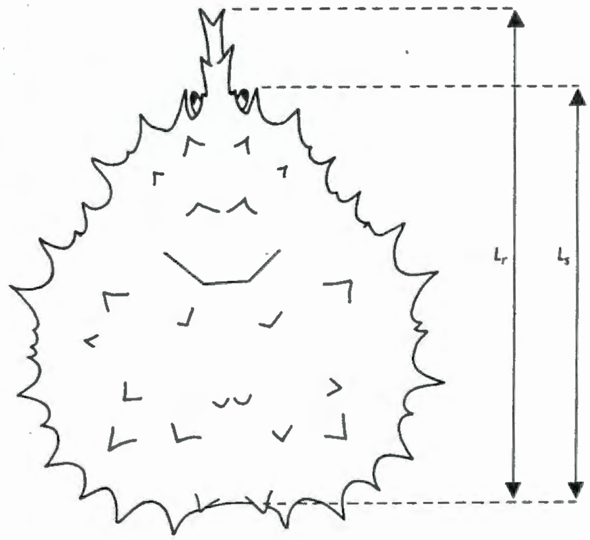

Fig. 3: A generalized *Lithodes murrayi* carapace, showing the anatomical features used for taking length measurements

RESULTS

Experimental fishing

The results of experimental fishing are given in Table I. No substantial catches were made further south than 26°20'S (Grid Areas 257 and 258). Trap C.P.U.E. values to the north showed that, although low values were recorded as far north as 22°S (Grid Area 177), no notable catches (C.P.U.E. greater than 1 kg whole mass per trap per 24 hours) were made north of 24°S, except in Grid Area 192.

The suggested lesser abundance of *L. murrayi* north of 24°S has been substantiated by the results of several trawling surveys (Sea Fisheries Institute, unpublished data), which have been conducted between southern latitudes 19 and 22° and in depths of 400 —800 m. These trawl surveys have never produced more than occasional single specimens of *L. murrayi* north of 21°S, though south of this latitude substantial numbers have been trawled in depths of 400 — 600 m.

Morphometrics

For the purpose of converting all data to a standard format, certain morphometric relationships

Table I: Catch per unit effort of commercial-sized *Lithodes murrayi* in various grid areas caught during experimental fishing, September/ October 1979 and February 1980

Grid area	Effort (trap-days)	Catch (kg whole mass)	C.P.U.E. (kg whole mass per trap-day)
†177	769,0	203,4	0,26
†184	1 383,0	1 016,9	0,74
192	148,9	325,6	2,19
209	160,2	128,2	0,80
217	69,8	68,8	0,99
†223	608,0	1 423,7	2,34
227	92,1	127,4	1,38
228	365,5	1 989,2	5,44
233	157,3	1 265,7	8,05
239	83,3	135,8	1,63
245	1 136,1	5 800,0	5,11
251	180,6	618,5	3,42
257	34,2	220,4	6,44
258	20,0	142,3	7,12
263	174,9	75,3	0,43
264	11,9	0	0
270	62,4	0	0
271	87,6	3,7	0,04
295	29,7	0	0
299	32,5	0	0
300	152,1	0	0
305	33,3	0	0
306	28,7	0	0
312	239,5	0	0
313	181,0	0	0
321	96,8	0	0

† Fished in February 1980 only
All other grid areas were fished in Sep./Oct. 1979 only

had to be calculated. The first of these, the conversion from L_r to L_s, was necessary because of a change in sampling technique. The second, the conversion of length to whole mass, required other regressions to be calculated before the conversion factor could be obtained.

The relationship between section mass and whole mass was calculated for male crabs 10,2 cm L_s and larger. Similar data for female *L. murrayi* (Melville-Smith unpublished data, have shown that their section to whole mass relationship differed from that of the males. However, it was considered that, because females only constitute about 9 per cent of the commercial catch by number and less than 5 per cent by weight (based on commercial samples taken in January, February and March 1980), the use of the male conversion factors on the combined data would not bias the results unduly.

The crabs used to calculate these relationships were all undamaged animals (i.e. with no appendages lost or in the process of regeneration) in the intermoult hard-shell state. They were frozen immediately after capture and were thawed in the laboratory before the measurements were made. All measurements of mass were made on an electronic balance to the nearest gramme.

Table II: Equations expressing the relationship between carapace length L_r and carapace length L_s for the sexes singly and combined

Sex	Regression equation	N	Correlation coefficient r
Male	$y = 0{,}9582\,x - 0{,}7525$	89	0,9968
Female	$y = 0{,}9850\,x - 1{,}0313$	59	0,9870
Both sexes	$y = 0{,}9630\,x - 0{,}8077$	148	0,9950

Relationship between carapace length (L_r) and carapace length (L_s) — Values of carapace length L_r were regressed against carapace length L_s in order to convert data on size composition expressed as L_r to L_s, the carapace measurement used in this report.

Females of 6,7 — 11,6 cm L_s and males between 6,1 and 14,0 cm L_s were used to calculate the regression equations presented in Table II. The equations for male and female crabs were statistically tested for significance of difference of slope and elevation (Snedecor and Cochran 1967). No significant difference was found (slope $F = 1{,}64$, $P > 0{,}1$; elevation $F = 0$, $P > 0{,}25$), and the data for the two sexes could therefore be combined (Table II).

Relationship between carapace length (L_s) and whole wet mass — The relationship between carapace length L_s and whole mass was calculated from 79 male crabs of carapace length varying between 10,2 and 16,0 cm (i.e. all of commercial size). The relationship was

$$y = 0{,}3225\,x^{3{,}0981},$$

where y = whole mass (g)
x = carapace length L_s (cm).

The correlation coefficient (r) was 0,9590.

Relationship between carapace length (L_s) and section wet mass — The same 79 crabs were processed in the laboratory to the section product in a similar manner to that used on board the commercial catcher. The relationship between carapace length and section mass was established as

$$y = 0{,}0373\,x^{3{,}7603},$$

where y = section mass (g)
x = carapace length L_s (cm).

The correlation coefficient (r) was 0,9546.

Relationship between section mass and whole mass —From the previous two relationships it was established that the wet section mass constituted a

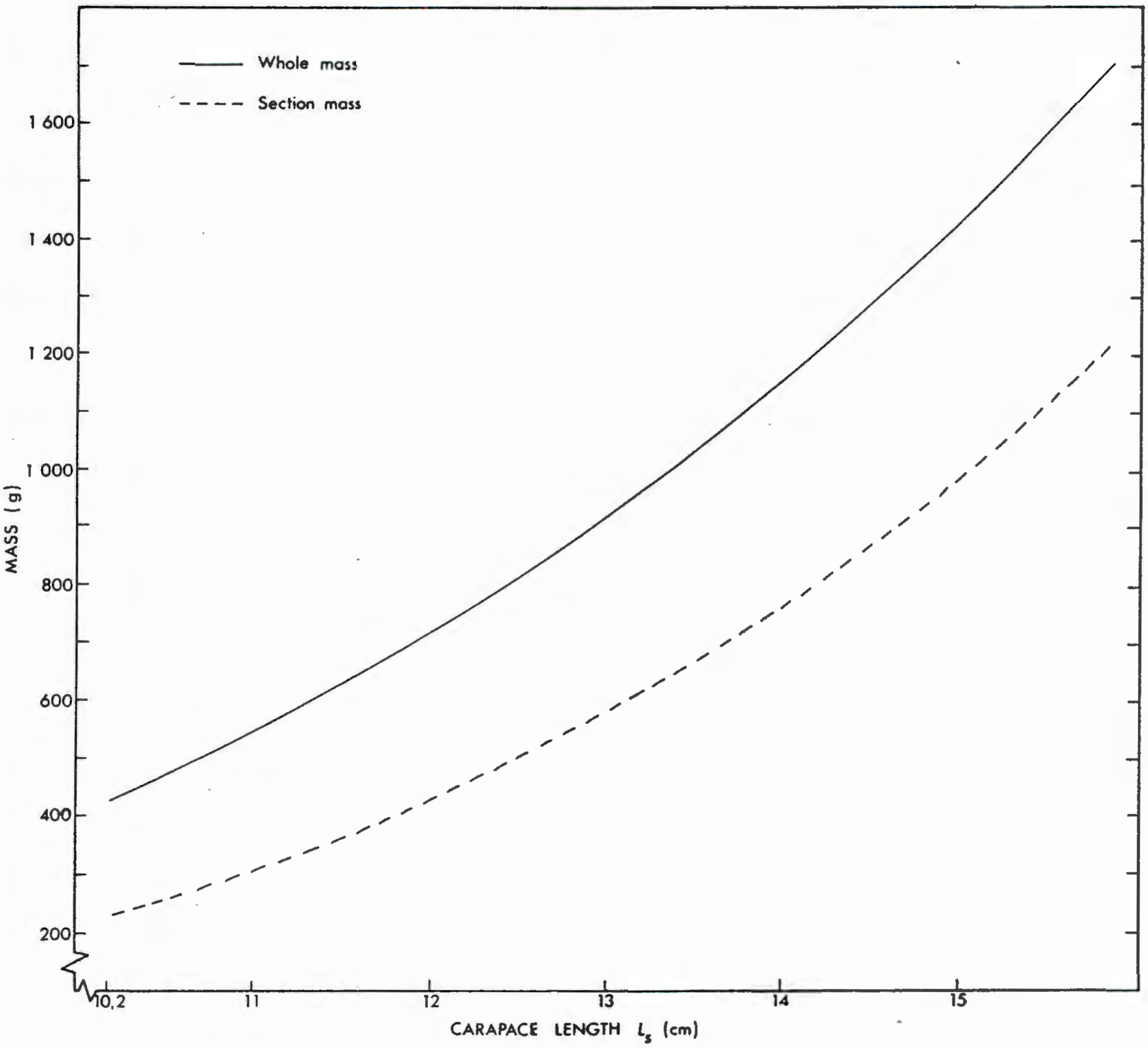

Fig. 4: Relationship between whole and sectioned crab mass and carapace length of *Lithodes murrayi* (males≥10,2 cm)

greater percentage of the whole mass in the larger commercially exploited crabs than in the smaller sizes (Fig. 4). The percentage varied from 53,8 per cent in a 10,2-cm crab to 72,5 per cent in a 16,0-cm specimen.

The mean carapace size of commercially exploited male crabs was 11,7 cm in January — April 1980, the period from which commercial catch composition data are available. For a crab of this size, the section mass constitutes 59 per cent of the whole mass, according to the equations already given. A factor of 1,6949 was therefore used to convert section mass to whole mass.

Catch per unit effort

The C.P.U.E. values per grid area, taken from commercial catch statistics for the months November 1979 — April 1980, are given in Tables III and

Table III: Total commercial effort expended and estimated quantity of stone crab processed in each grid area, November 1979 - April 1980 (excluding the data from traps set longer than 60 hours)

Grid area	Effort		Estimated whole mass	
	Trap-days	Percentage	kg	Percentage
228	43 427	66,0	96 966,0	72,9
233	15 798	24,0	30 508,5	22,9
192	2 305	3,5	2 644,1	2,0
184	1 383	2,1	1 016,9	0,8
223	1 075	1,6	1 593,2	1,2
227	1 026	1,6	84,7	0,1
177	769	1,2	203,4	0,2
Total	65 783		133 016,8	

IV. Occasions when the traps were left for longer than 60 hours have been excluded to avoid bias.

From the effort applied and the quantity of crab caught per grid area, and excluding all data from traps set longer than 60 hours (Table III), it is clear that 95,8 per cent of the catch originated from two grid areas. Grid Area 228 accounted for 72,9 per cent of the catch and Grid Area 233 for the other 22,9 per cent. Although a small amount of effort was applied in other grid areas, catches were generally poor.

The combined C.P.U.E. values and fishing effort for Grid Areas 228 and 233 are presented in Figure 5. Because these two areas accounted for over 90 per cent of the total effort (Table III), their C.P.U.E. pattern is considered to be representative of that of the stone-crab fishery as a whole.

From Figure 5, it is clear that fishing effort generally increased during the period that the stock was exploited, and by March it had virtually doubled over that of November, the month in which the fishery began. By contrast, the C.P.U.E. in March was about a third of its value at commencement and was still falling. From the start of the commercial operation in November until its termination in April, the C.P.U.E. consistently declined, and at no stage was there ever a sign of recovery in any of the grid areas (Table IV).

Table IV: Grid areas fished and the corresponding C.P.U.E. for each month of commercial fishing, November 1979 - April 1980

Month	Grid area	Effort (trap-days)	Estimated section mass (kg)	Estimated whole mass (kg)	Estimated C.P.U.E. (kg whole mass per trap-day)
Nov. '79	228	8 291	16 700	28 305,0	3,41
Dec. '79	228	5 479	10 400	17 627,1	3,22
	233	4 663	8 850	15 000,0	3,22
	Total	10 142	19 250	32 627,1	3,22
Jan. '80	228	10 792	17 610	29 847,5	2,77
	233	1 878	1 950	3 305,1	1,76
	Total	12 670	19 560	33 152,6	2,62
Feb. '80	228	924	700	1 186,4	1,28
	233	7 373	6 050	10 254,2	1,39
	192	2 305	1 560	2 644,1	1,15
	223	608	840	1 423,7	2,34
	184	1 383	600	1 016,9	0,74
	177	769	120	203,4	0,26
	Total	13 362	9 870	16 728,7	1,25
Mar. '80	228	14 303	11 000	18 644,1	1,30
	233	1 884	1 150	1 949,2	1,03
	277	1 026	50	84,7	0,08
	223	213	0	0	0
	Total	17 426	12 200	20 678,0	1,19
Apr. '80	228	3 638	800	1 355,9	0,37
	223	254	100	169,5	0,67
	Total	3 892	900	1 525,4	0,39

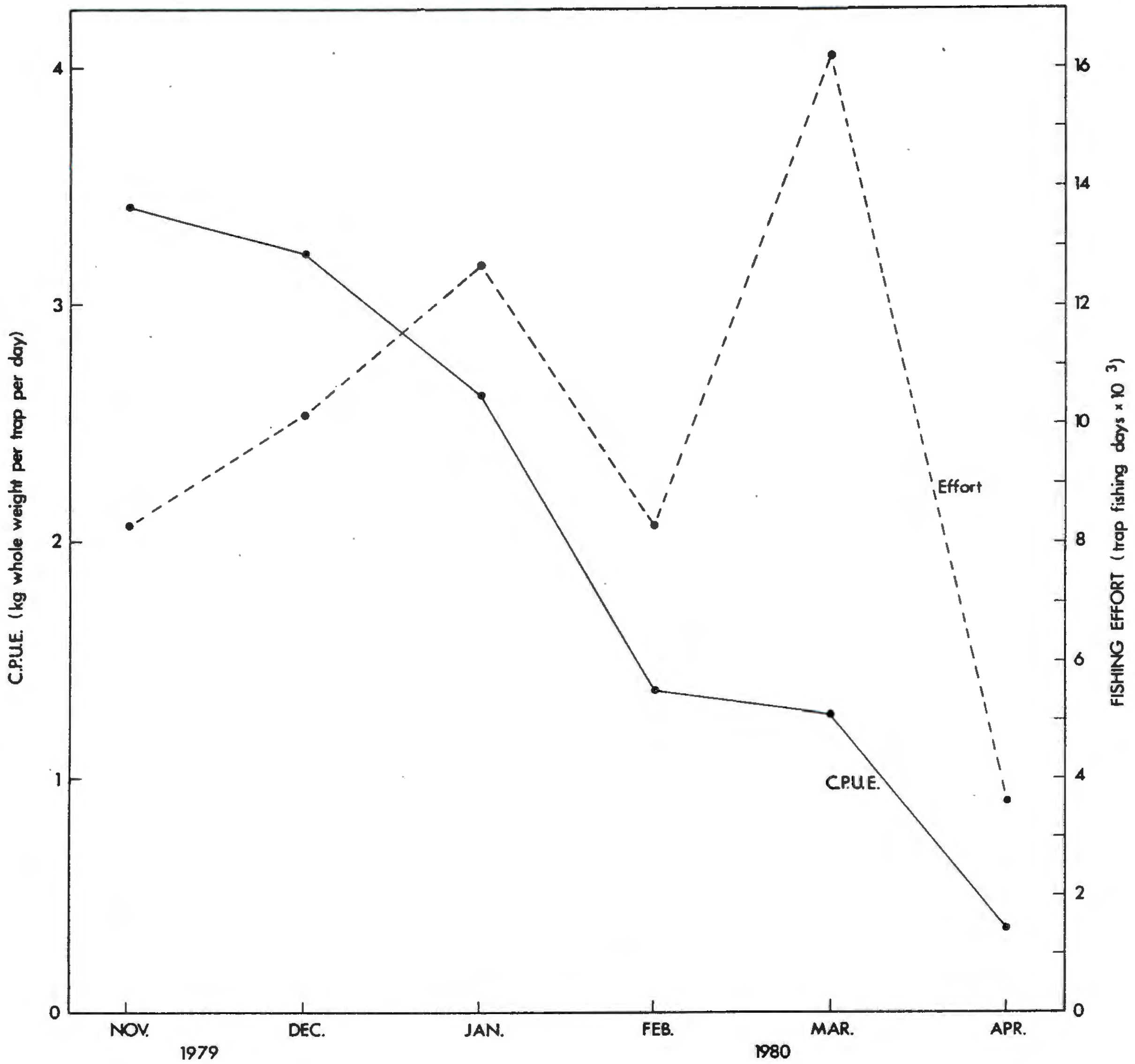

Fig. 5: Combined C.P.U.E. and fishing effort for Grid Areas 228 and 233, September 1979 — April 1980

Size composition of the catch

It was considered that, because Grid Areas 228 and 233 were regularly fished throughout the period of commercial fishing, their combined size composition data would best reflect trends.

Table V presents the size composition of the catch in five separate months. Three population mean sizes have been calculated for the sexes: that of crabs smaller than 10,2 cm, that of those larger than 10,2 cm (i.e. commercially exploited) and that of the population as a whole.

There was little change in the mean carapace length of crabs larger or smaller than 10,2 cm. The mean size in September 1979 was slightly higher than that during the other four months, but this may be

Table V: Mean carapace length of male and female stone crab of commercial size, undersize and the whole population during five months of sampling

Sex and size class (cm)	September 1979		January 1980		February 1980		March 1980		October 1980	
	Mean L_s (cm)	N	Mean L_s (cm)	N	Mean L_s (cm)	N	Mean L_s (cm)	N	Mean L_s (cm)	N
Males ⩾ 10,2	12,0	177	11,8	1 472	11,7	2 588	11,7	537	11,8	53
Females ⩾ 10,2	10,8	7	10,6	156	10,6	65	10,7	51	10,7	12
Males < 10,2	9,5	16	9,1	398	8,8	855	8,7	411	8,7	62
Females < 10,2	9,3	25	9,1	1 099	8,8	965	8,9	512	8,7	72
All males	11,8	193	11,3	1 870	10,9	3 443	10,3	948	10,2	115
All females	9,7	32	9,3	1 255	8,9	1 030	9,0	563	9,0	84

ascribed to the comparatively small sample size upon which the calculations were based. The main difference in the mean size composition of the population is apparent when all sizes are examined collectively. The mean male size declined by a total of 1,6 cm (13,6 per cent) over the fishing period, while that of females declined by 0,7 cm (7,2 per cent). The apparent excessively large decline in the mean size of females between September and January may also be attributable to the small sample size.

It appears that large male crabs (greater than 10,2 cm L_s) were being steadily fished out of the stock. Because the smaller male crabs were unaffected by fishing, their relative abundance increased proportionally. This resulted in the mean size of the population declining in sympathy with the increasing dominance of the small crabs.

The mean size of female crabs showed little decrease because the majority (about 91 per cent) were too small for commercial use and, as with small male crabs, they were returned live to the sea.

Table VI: Sex ratios per size class in Grid Area 228, January — March 1980

Size class (cm)	Sex ratio male : female	Sample size N
5,0 - 5,9	52,4 : 47,6	21
6,0 - 6,9	44,7 : 55,3	103
7,0 - 7,9	50,1 : 49,9	411
8,0 - 8,9	46,2 : 53,8	782
9,0 - 9,9	44,8 : 55,2	1 178
10,0 - 10,9	77,5 : 22,5	1 274
11,0 - 11,9	97,8 : 2,2	1 300
12,0 - 12,9	100 : 0	900
13,0 - 13,9	100 : 0	314
14,0 - 14,9	100 : 0	61
15,0 - 15,9	100 : 0	3
Total	73,9 : 26,1	6 347

Sex ratio

The sex ratios, determined for each commercial longline set, showed no consistent depth or area trends as have been observed for *L. murrayi* caught in waters off the Crozet Islands (Arnaud and Do-Chi 1977). Male : female sex ratios recorded during commercial sampling varied between 31,9 : 68,1 and 97,4 : 2,6.

Sex ratios per size class calculated from samples of commercial catches made in Grid Area 228 are presented separately for each month of the period January — March 1980 in Figure 6 and for the three months combined in Table VI.

In the smaller size classes (⩽9,0 — 9,9 cm) the sex ratio was approximately 1:1. In size classes larger than this, males became increasingly dominant and constituted 100 per cent of the sampled population for all size classes larger than 12,0 cm (Table VI).

The analysis per month (Fig. 6) shows the January catch to have had a much lower percentage of males in the small size classes than either February or March. This fact could indicate that the males were moulting, and were hence less catchable, during January. They would then have been early postmoult in February and March, and as such would have been particularly catchable having effectively starved over the moulting period. Conversely, the January sample may reflect the true sex ratio, and the relative dearth of females in February and March may have been the result of females starting to moult during those months. More data are required to substantiate either of those postulates.

DISCUSSION

The fact that male *L. murrayi* attained a larger size than females suggests that the sexes have a differential growth rate, as is the case in many decapod crusta-

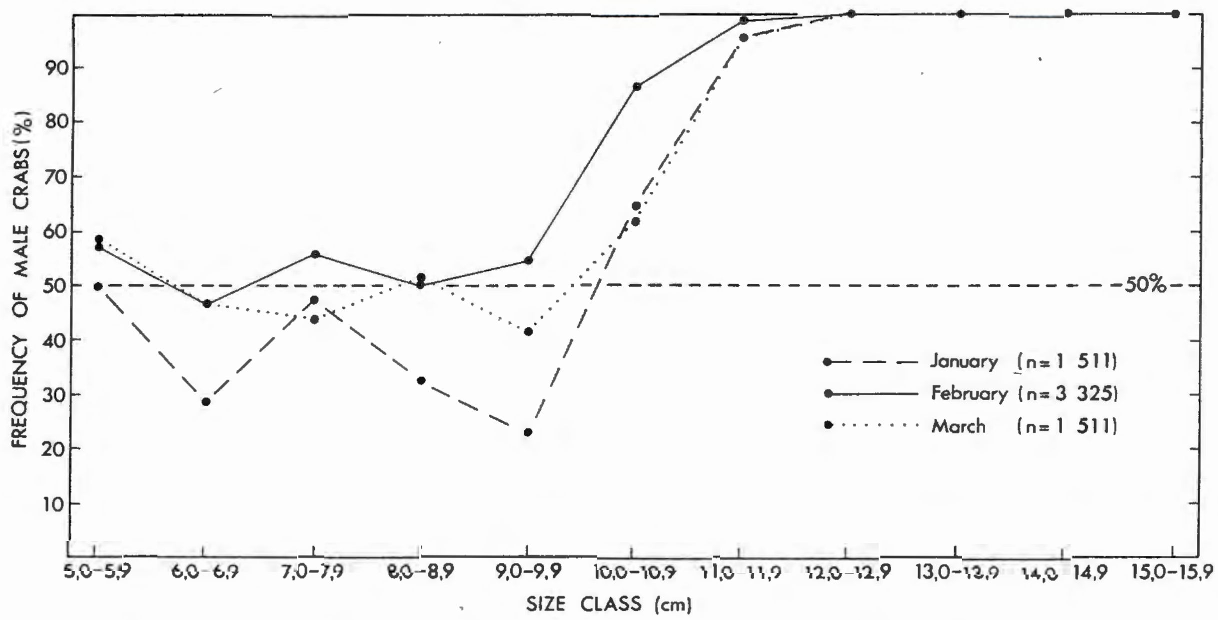

Fig. 6: Sex ratios per size class from samples of commercial catches in Area 228, January — March 1980

ceans, including the related lithodid *Paralithodes camtschatica,* the Alaskan king crab (Hoopes and Karinen 1972). This being the case, and assuming an equal sex ratio at spawning, one would expect females to have dominated the smaller size classes. However, this did not transpire during the period sampled (Table VI).

Several reasons could account for the apparent anomaly. The original assumption of a 1 : 1 sex ratio at spawning may be incorrect. Also, there may be different mortality rates for the sexes, or one of the sexes may have been at a stage in the moult cycle rendering it either particularly easy or difficult to catch. It is necessary to obtain catch composition data from a full year before a more positive assumption can be made in this regard.

C.P.U.E. can provide an indication of the changes in stock density with fishing, provided there is no natural biologically linked cycle of catchability. Such cycles can be linked to, amongst other things, seasonal environmental changes or an annual moult.

If the catchability of the *L. murrayi* stock remained relatively constant over the period of commercial fishing, then some indication of fluctuation in stock density caused by fishing can be gauged from the drop in C.P.U.E. over this period.

The C.P.U.E. in Grid Area 228 was 3,41 at the start of commercial fishing in November 1979. When fishing ceased in April 1980, the C.P.U.E. had dropped to 0,37 (Table IV). This is a nine-fold decrease, which suggests that the abundance of crabs larger than 10,2 cm in this area at the termination of fishing was only about 11 per cent of that at the start of fishing, all other factors remaining constant.

Stone crab appear to be largely confined to a hypothetical corridor between the 500- and 700-m depth contours over a distance of approximately 300 nautical miles. The densities of the crabs, based on C.P.U.E., were moderately high over most of the corridor (Table I), but not sufficiently high for a fishery to be commercially viable. Densities were apparently extremely high over the 40-mile length across Areas 228 and 233. Of the estimated 185 400 kg, being the total whole mass of *L. murrayi* landed between November 1979 and April 1980, 94,6 per cent came from these two grid areas.

It is possible that the apparent collapse of this short-lived fishery could have been avoided, and that the small *L. murrayi* stock could have been managed on a sound basis. From an economic point of view, however, the exploitation of a small continental-shelf stock such as this one poses complex problems. The fishing craft have to be of substantial size for safe operation far out at sea, and the fishing equipment is costly because of the working depth. It is therefore obvious that there is no means of avoiding the type of large-scale effort which ships of this size need to generate in order to make them an economic proposition.

Depending on the rate of growth, this stock may again become profitably exploitable in the future. Should this be the case, the solution to its healthy exploitation would be to manage it in conjunction with the *G. quinquedens* stock, which is at present fished on the continental shelf north of 21°S (Beyers and Wilke 1980). Because the same equipment is used to fish for both species of crab, it may be possible to restrict the level of exploitation of *L. murrayi* by diverting the bulk of effort towards the *G. quinquedens* fishery. The latter species, being more widespread and abundant, has proved to be better able to withstand exploitation.

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PAPER 13:

An association between a liparid fish species and the stone crab *Lithodes tropicalis* (Decapoda, Anomura)

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An association between a liparid fish species and the stone crab *Lithodes tropicalis* (Decapoda, Anomura)

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Fish eggs, thought to be those of the liparid fish, *Careproctus griseldea*, were found in the gill chambers of several specimens of the stone crab, *Lithodes tropicalis*, caught in deep-water (~600 m) off the South West African/Namibian coast (~24°46′S/13°28′E). The size class and quantity of crabs involved in this symbiotic relationship are discussed and some observations are made as to the diameter, number and maturity of the fish eggs removed from the crabs.

Viseiers, vermoedelik van die liparidvis *Careproctus griseldea*, is gevind in die kieuholtes van verskeie eksemplare van die klipkrap *Lithodes tropicalis*, gevang in diep water (~600 m) teenoor die kus van Suidwes-Afrika/Namibië (~24°46′S/13°28′O). Die grootteklas van die krappe en die hoeveelheid wat by hierdie simbiotiese verhouding betrokke is, word bespreek, en daar volg enkele opmerkings oor die deursnee, aantal en rypheid van die viseiers wat van die krappe verwyder is.

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Clusters of fish eggs were inadvertently discovered in the gill cavity of a stone crab *Lithodes tropicalis* A. Milne Edwards, 1883, captured off South West Africa/Namibia during October 1980. This phenomenon was observed during sampling of stone crabs undertaken to monitor populations of *L. tropicalis*, since the fishery based on this species had suffered a collapse owing to heavy commercial exploitation that had taken place between November 1979 and April 1980 (Melville-Smith 1982). The fishery had been aimed at large-sized crabs, with those smaller than approximately 102 mm being returned live to the sea. This stock of *L. tropicalis* was previously documented by Kensley (1980), Melville-Smith (1982) and MacPherson (1983) as *Lithodes murrayi* Henderson, 1888, but has since been reidentified as *L. tropicalis* (Abello & MacPherson 1986; E. Dawson, D.S.I.R., Wellington, New Zealand, pers. comm.) The crabs containing fish eggs were caught using beehive traps at approximately 24°46′S/13°28′E, at depths of between 600 and 620 m.

Further crabs were then examined for fish eggs in their gill cavities during October 1980 and September 1981, to determine what portion of the crab population was involved in this relationship.

Of the 152 crabs examined, ranging in size from 76 to 160 mm carapace length (measured from the tip of the most anterior spine to the posterior edge of the cephalothorax), only males of 110 mm and larger were found to have fish eggs present in the gill chamber (Table 1, Figures 1 and 2). The mean size of the six crabs containing eggs was 126 mm, compared with a combined population sample mean for the two cruises of 98 mm. It would therefore appear that the fish responsible for depositing its eggs in the crab's peribranchial cavity selectively choose the larger sized crabs, and since females seldom exceed 105 mm carapace length, it may be assumed that under normal conditions they seldom, if ever, carry these fish eggs.

The number of crabs found to be carrying fish eggs (Table 1) may have been higher than in a crab population that had not been subjected to fishing pressures. The fishery had resulted in an imbalance in the size structure of the population (Melville-Smith 1982), thus leaving fewer large sized male crabs available to the spawning fish. The crab fishery could thus also have had an indirect effect on the successful breeding of this liparid fish.

In all cases in which crabs carried these fish eggs, only one gill chamber was occupied by the egg masses. It is thus unlikely

Table 1 Numbers of male and female stone crab examined for a presence of fish eggs during October 1980 and September 1981

	October 1980		September 1981	
Sex and size	Total	Number with eggs	Total	Number with eggs
Males ⩾ 110 mm	25	5	45	1
Females ⩾ 110 mm	–	–	–	–
Males < 110 mm	27	–	–	–
Females < 110 mm	8	–	–	–

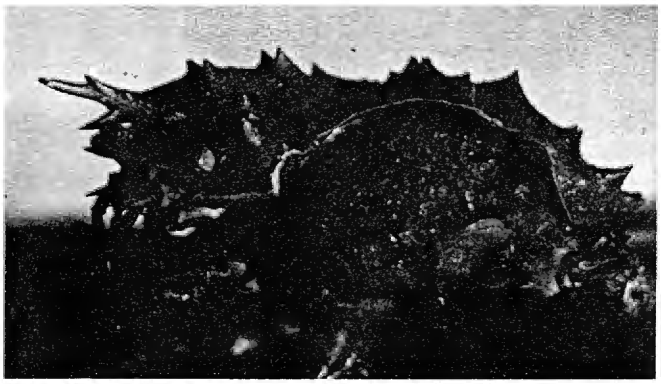

Figure 1 Lateral view of the peribranchial cavity of *L. tropicalis* dissected, showing the position and size of the fish egg mass in relation to the size of the cavity.

Figure 2 Anterior view of *L. tropicalis* with most of the carapace removed. Note the egg mass occupies the space normally taken by the gills, and the gills are displaced.

that the eggs are drawn into the crab's gill cavity by means of its respiratory current, as the eggs would then surely enter both cavities. Similarly, the eggs would not be cemented together into a compact mass. This points to the probability of direct spawning by the fish into the gill cavity — presumably by means of an ovipositor. Unfortunately no record was kept as to whether the gill chamber of one side was favoured over the other. It would appear, however, that a mechanism may exist that prevents the fish from spawning eggs in both gill chambers of the crab. Such a mechanism would serve to prevent undue stress being placed on the respiratory system of the crab, a problem that might result if both gill chambers were occupied by fish eggs.

The egg masses removed from the gill chambers of the crabs occupied a considerable volume (up to approximately 92 cm^3) and contained an estimated 200 to 1 500 eggs. The individual eggs were large (0,42 to 0,45 mm diameter), almost spherical and were cemented together. Figures 1 and 2 show the crab carapace cut back to expose the peribranchial cavity. The greater portion of the cavity is occupied by fish eggs and the gills can be seen to be compressed and misshapen by the mass of eggs displacing them.

The fish eggs were at different stages of maturity even within a single cluster. Later stage embryos with pigmented eyes were removed from one cluster and were identified as belonging to the family Liparidae.

The occurrence of clusters of fish eggs of a liparid fish (*Careproctus* sp.) in the peribranchial cavity of male king crab (*Paralithodes camtschatica*) has been reported from the North Pacific by Rass (1950), Vinogradov (1950) and Hunter (1969). This type of relationship has subsequently been recorded between several species of *Careproctus* and other members of the crab family Lithodidae. These include the reports of Parrish (1972) (*Careproctus melanurus* and *Lopholithodes foraminatus* from California), Peden & Corbett (1973) (*Careproctus* sp. and *Lopholithodes foraminatus* from British Columbia) and Balbontin, Campodonico & Guzman (1979) (*Careproctus falklandica* and *Lithodes antarctica*, and *Careproctus* sp. and *Paralomis granulosa* from Chile).

According to Stein (1986), there are three liparids which have been recorded from South West Africa/Namibian waters, namely *Careproctus griseldea* Lloris, 1982, *Paraliparis australis* Gilchrist, 1904 and *Paraliparis wilsoni* Richards, 1966. Of these species, *C. griseldea* (which may prove to be a junior synonym of *C. albescens* Barnard, 1927) appears most likely to be responsible for the egg masses in *L. tropicalis*, as it has been recorded from the same area and depths as those in which *L. tropicalis* is most abundant and where the crab specimens carrying the fish eggs were sampled (Lloris 1982; Melville-Smith 1982). *Paraliparis wilsoni* and *P. australis* are recorded from further north, the former in deeper water than where *L. tropicalis* is abundant. It should be noted, however, that relatively little is known about the liparids and their distribution off South West Africa/Namibia.

There are obvious advantages to the fish in depositing its eggs in the peribranchial cavity of the crab, as the eggs are protected from predators and at the same time are well aerated. Although the gills of the crab are compressed, this compression is slight and the 'host' individuals show no other signs of being placed at a disadvantage. Until such time as further sampling and study of this phenomenon show definite disadvantages to the crab, we choose to refer to the association between these two species as a symbiotic (*sensu lato*) relationship.

Acknowledgements

We thank Dr B.B. Collette (Smithsonian Institution, Washington) for drawing our attention to the literature documenting the *Paralithodes camtschatica – Careproctus* sp. relationship. We also thank Dr E. MacPherson (Instituto de Investigaciones Pesqueras de Barcelona) and Dr E. Dawson (D.S.I.R., Wellington) for discussions regarding the misidentification of *Lithodes tropicalis* in the literature. Finally we thank Dr P.A. Hulley for his constructive criticism of the manuscript.

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PAPER 14:

By-catches of stone crab (Lithodidae) on the Namibian red crab grounds (1981 - 1986)

ICSEAF 1988
Colln scient. Pap. int. Commn SE. Atl. Fish.
Pages 71-79

BY-CATCHES OF STONE CRAB (LITHODIDAE) ON THE NAMIBIAN RED CRAB GROUNDS (1981-1986)

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Stone crab by-catches reported by the Namibian red crab fishing fleet comprised ***Lithodes tropicalis*** *(99,5 %) and* ***Neolithodes asperrimus*** *(0,5 %), these two species forming only 0,2 % of the total crab catch. Data on their depth and latitudinal distribution are provided and discussed in relation to that of red crab (****Geryon maritae****).*

Les captures secondaires de ***Lithodidae*** *signalées par la flotte namibienne de pêche au crabe rouge (****Geryon maritae****) comprennent* ***Lithodes tropicalis*** *(99,5 %) et* ***Neolithodes asperrimus*** *(0,5 %), ces deux espèces ne constituant que 2 % du total des prises de crabes. L'auteur fournit des données sur leur répartition en fonction de la profondeur et de la latitude et les compare à celles concernant le crabe rouge.*

Las capturas secundarias de ***Lithotidae*** *comunicadas por la flota de Namibia que pesca cangrejo rojo se componían de:* ***Lithodes tropicalis*** *(99,5 %) y* ***Neolithodes asperrimus*** *(0,5 %), constituyendo estas dos especies solamente el 0,2 % de la captura total de cangrejo. Se proporcionan datos sobre su distribución latitudinal y en profundidad, y se comparan con los datos relativos a* ***Geryon maritae****.*

INTRODUCTION

A commercial crab fishery has existed off Namibia since 1976, directed mostly at deep-sea red crab **Geryon maritae** (Manning and Holthuis) and confined to areas north of Walvis Bay. During a short period between 1979/80, some effort was diverted to more southerly areas where stone crab **Lithodes tropicalis** (A. Milne Edwards) formed the target species. The history and methods of the crab fishery are already covered in the literature (Beyers and Wilke 1980, Melville-Smith 1982 and 1988).

Several species of crab, namely **Bathynecetes piperitus** (Manning and Holthuis), **Paralomis africana** (Macpherson), **Lithodes tropicalis** and **Neolithodes asperrimus** (Barnard), are caught incidentally by traps set on the commercial red crab grounds (grids 100 to 185, Figure 1), but only the latter two are large enough to be suitable for processing as by-catch.

Data on the quantity of stone crab product packed, provided by fishermen since 1981, have been used in this study to estimate the annual stone crab catch and its contribution to the total Namibian commercial crab catch.

A second objective of this paper has been to examine stone crab distribution (both depth and latitudinal) in the study area, as inferred from catch statistics.

Lithodes tropicalis is a large crab which has been recorded off the west African coast from Senegal in the north to around latitude 23° S (or even slightly south thereof) in the south (Abelló and Macpherson 1986). The species was mistaken for **Lithodes murrayi** (Henderson) in earlier work dealing with its taxonomy and fishery off the Namibian coast (see Melville-Smith and Louw, 1987, for a detailed explanation).

Abelló and Macpherson (1986) examined the distribution (and some biological aspects) of **Lithodes tropicalis** south of Walvis Bay. Their conclusions from trawl research data were similar to those presented by Melville-Smith (1982) from experimental trap fishing in the same area, namely, that greatest densities of the species are to be found between latitudes 23 and 26° S.

Very little has been published on **Neolithodes asperrimus**, although the species is known to occur off Natal (Kensley 1978), the Cape (Barnard 1950) and Namibia between 18° 11' S and 28°16' S (Macpherson 1983).

METHODS

The methods used to catch, clean and cook stone crabs, as well as the recording of commercial crab catch statistics, are the same as those for the red crab fishery (Melville-Smith 1988). As noted by the said author, catch statistics supplied by the Taiyo Fishing Company were deemed more reliable than those supplied by other vessels. Only catch information supplied by that company has been used in this report.

As the Japanese crab vessels fishing off Namibia report their catches as processed product, conversion factors were established to convert product mass to whole live mass. These factors were calculated for **Lithodes tropicalis** and all reportings were assumed to be for this species, an assumption which is not entirely justified, but which is discussed more fully later (see "Discussion").

Catch figures are shown in metric tonnes throughout this report.

RESULTS

All grids where stone crab catches have been reported between 1981 and 1986 are shown in Figure 1. Catches have consistently been reported from northern (17° S) and central (south of 21° S) Namibia, and only infrequently in the area between these positions. Vessels have not fished commercially south of about 22°30' S.

The relative abundance of stone crabs compared to red crabs is shown in Table 1, the former only constituting an insignificant portion of the red crab catch over most of the grounds. South of 20° S (grid row 129-131) the ratio of stone crab in red crab catches begins to increase, reaching significant levels (1 %) around 21° S (grid 151-158). In the extreme southern portion of the red crab grounds, south of 22° S (grid row 169-170) stone crabs constitute approximately 20 % of the reported crab catch.

The reported annual tonnage of stone crab caught by Taiyo Company vessels from 1981 to 1986 is shown in Table 2. The highest catches were made in 1982 and only amounted to 33,5 tonnes (whole mass) or 0,59 % of the red crab catch. Over the same period, this company contributed approximately half (52,9 %) of the total effort on the crab grounds. If other vessels had similar stone crab by-catches to those reported by the Taiyo Fishing Company, the total catch of stone crab between 1981-1986 could be assumed to have been roughly double that presented in Table 2, i.e., 150 tonnes whole mass, or 25 tonnes per annum.

The effort and resulting stone crab catches made by Taiyo Company vessels fishing at various depth intervals are shown in Table 3. The largest catches were between 400 and 499 metres. When the catch is weighted by effort (last column Table 2), a distinct double peak appears in the data, suggesting that the relative abundance of stone crabs is greatest at the extreme depths at which red crabs are commercially fished off Namibia.

DISCUSSION

There are two reasons for believing that the annual and regional quantities of stone crab caught are considerably greater than the estimates made in Tables 1 to 3: firstly, all the catches reported by this study were aimed at red crab, and although they are considered reliable, it is believed that small by-catches of stone crab were not always reported. This conclusion is based on the fact that certain skippers consistently failed to report stone crab by-catches in areas from which positive reports were made by others (see Figure 1, grids 145-169 for 1981, 176 for 1983 and 158--184 for 1985). Naturally it was not possible to eliminate these data without biasing the result. Secondly, when stone crab catches only amount to a few animals per longline, it is not worth packing them separately and instead they are processed with red crab. Quite obviuosly, in the long term this can amount to a considerable quantity of crab.

No distinction is made in catch report forms as to whether the product packed is **Lithodes tropicalis** or **Neolithodes asperrimus**. However, based on research fishing and commercial sampling information (Melville-Smith unpub. data), it can be confidently assumed that apart from odd **Neolithodes asperrimus** individuals, all the catches of stone crab made in less than 800 m would have been **Lithodes tropicalis**. These catches comprised 99,5 % of the total stone crab mass reported (Table 3).

Two stone crab catches have been reported from deeper than 800 m despite any published or research evidence for this species occuring at this depth. Closer examination of these catches has revealed both to have been pure stone crab catches, one at 930 m (grid 113 in 1981, Figure 1) and the other at 860 m (grid 118 in 1985, Figure 1). It may further be noted from the above figure, that both these catches fall outside grids in which positive catches of stone crab have been reported in other years.

Catches made during research fishing in the area 18°00' to 18°30' S, have on several occasions made quite large pure catches of **Neolithodes asperrimus** at depths outside those fished commercially (i.e; 900-1 000 m). It is therefore assumed that the two catches referred to above were of this latter species.

Longshore distribution results (Figure 1, Table 1), show that areas south of Walvis Bay which have previously been recognised as regions of high **Lithodes tropicalis** density (Melville-Smith 1982, Abelló and Macpherson 1986), do not extend much further north of 21° S. This is thought to be related to the fact that the sea bed changes in this area from being soft in the north to rough in the south (Melville-Simith unpub. data), and **Lithodes tropicalis** are most abundant on rock and coral grounds (Abelló and Macpherson 1986). The reason for the presence of stone crab off the north of Namibia remains unexplained, because the ground is not particularly rough in that area.

Only a limited depth range was fished by commercial crab vessels during 1981-1986 (Table 3). The highest densities of **Lithodes tropicalis** catches were taken between 350-600 m, which substantiates observations by Abelló and Macpherson (1986) that the highest densities in the southern area are between 400-500 m.

From the above analysis of the red crab by-catch, it can be concluded firstly, that stone crab form an insignificant proportion of the annual Namibian crab catch, and secondly, that the contribution of stone crab to the red crab fishery can be ignored in areas north of 21°20' S (grid 162). Though their importance increases south of 21°20' S (grid 162), this area only contributed 2,2 % of the effort and 1,2 % of the catch recorded between 1981 and 1986 (Table 2).

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TABLE 1. Red and stone crab catches and effort expended by Grid row for Taiyo Fishing Company vessels, for Grids 100-185 (1981-1986), with the percentage composition of stone crab in the total catch.

Grids	Effort (Traps set)	Red crab (tonnes)	Stone crab (tonnes)	Percentage composition
100-101	167 739	2 057,2	1,0	0,05
103-104	288 926	3 516,8	0,3	0,01
106-107	328 862	3 778,3	0,1	0,01
109-110	387 082	4 198,2	0,1	0,01
113-114	495 483	5 072,1	0,1	0,01
118-119	492 547	4 821,7	0,3	0,01
123-125	473 844	4 131,1		
129-131	315 415	2 818,3	0,2	0,01
135-137	214 169	1 884,1	2,5	0,13
142-145	133 756	1 008,1	7,6	0,75
151-153	106 390	844,8	9,6	1,12
157-158	71 386	565,4	5,5	0,96
162-164	36 246	210,1	9,7	4,41
169-170	27 925	147,5	22,3	13,13
176-177	15 182	71,0	14,8	17,20
183-185	550	2,7	0,7	20,60

TABLE 2. Annual red and stone crab catches for Taiyo Fishing Company vessels 1981-1986, with the percentage composition formed by stone crab.

Year	Crab catch Red crab	Tonnes whole mass Stone crab	Percentage composition
1981	5 390,0	7,7	0,14
1982	5 681,4	33,5	0,59
1983	6 277,5	7,5	0,12
1984	6 251,3	18,5	0,30
1985	5 483,7	3,5	0,06
1986	6 066,7	4,2	0,07
TOTAL	35 150,6	74,9	0,21

TABLE 3. (1981-1986) Effort and stone crab catches at depth intervals

Depth (m)	Effort (E) (Trap set)	Catch (c) (Tonnes whole mass)	Weighted catch ($\frac{E}{\Sigma E}$ c) (tonnes whole mass)
<300	...	...	...
300-349	497		
350-399	25 941	2,3	91,3
400-499	694 883	36,1	53,5
500-599	1 029 663	33,3	33,2
600-699	893 076	2,7	3,1
700-799	626 401		
800-899	287 867	0,3	1,1
900-950	1 698	0,1	60,6
>950	...	...	...

...= no data

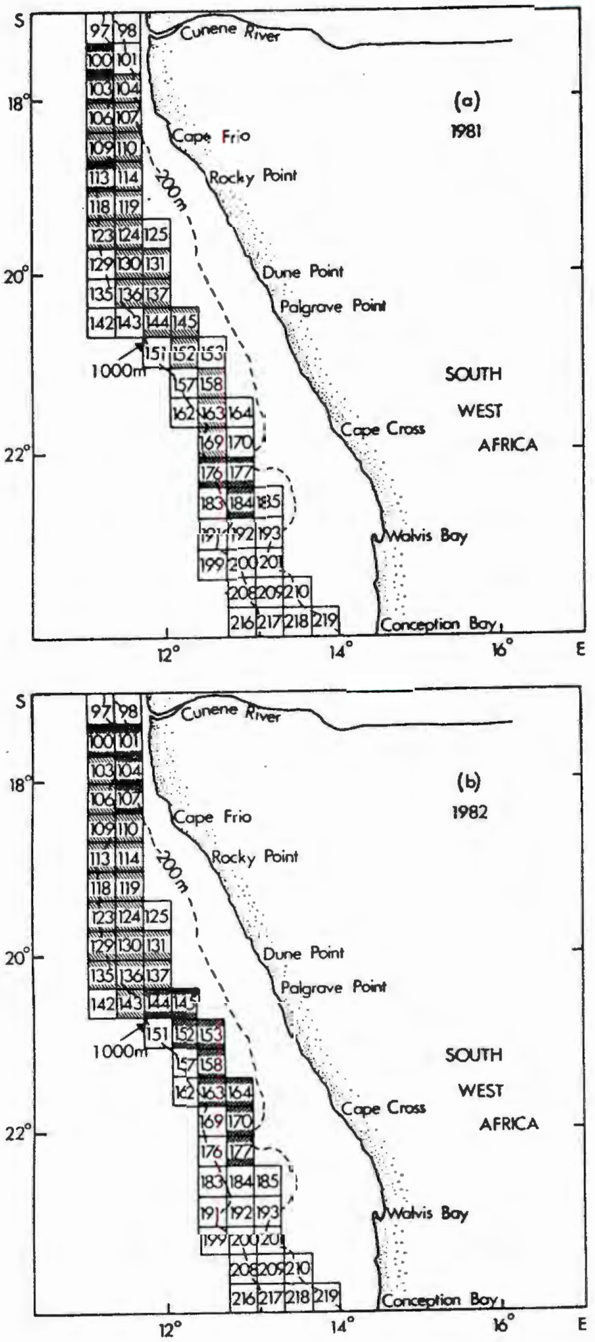

Fig. 1. (a-b): Data for Taiyo Company vessels (1981-1986), showing grids used to report commercial crab catches off Namibia. Hatched grids indicate those fished. Grids with double hatching are those from which stone crab catches we reported.

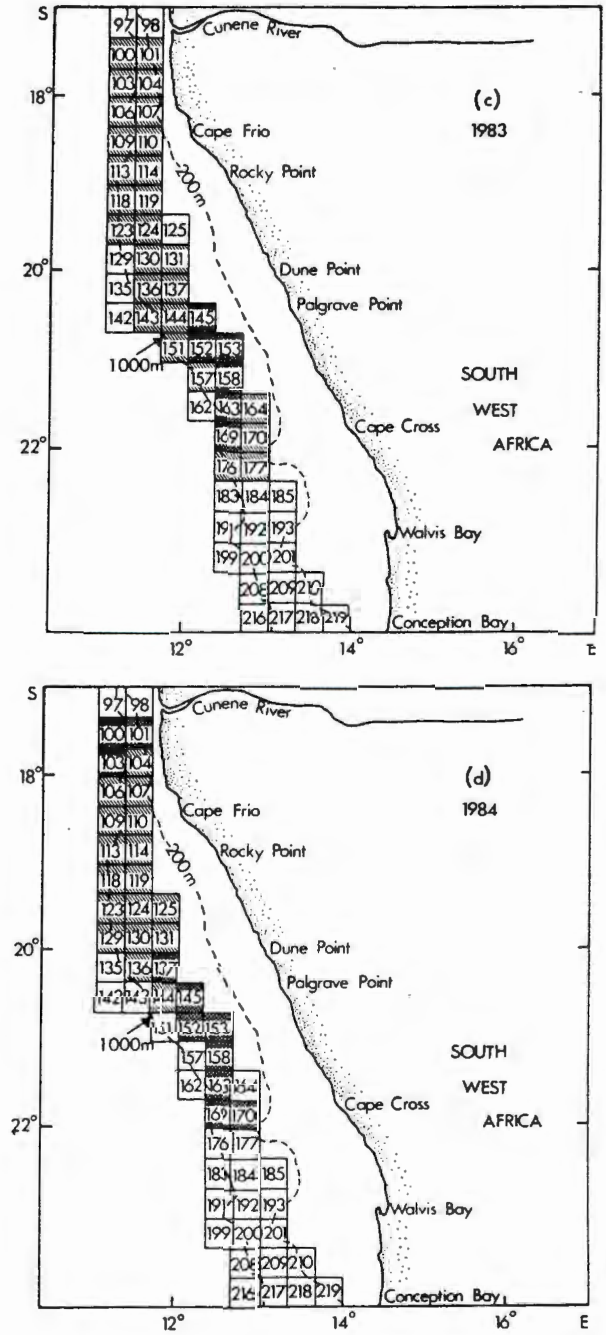

Fig. 1. (c-d): Data for Taiyo Company vessels (1981-1986), showing grids used to report commercial crab catches off Namibia. Hatched grids indicate those fished. Grids with double hatching are those from which stone crab catches we reported.

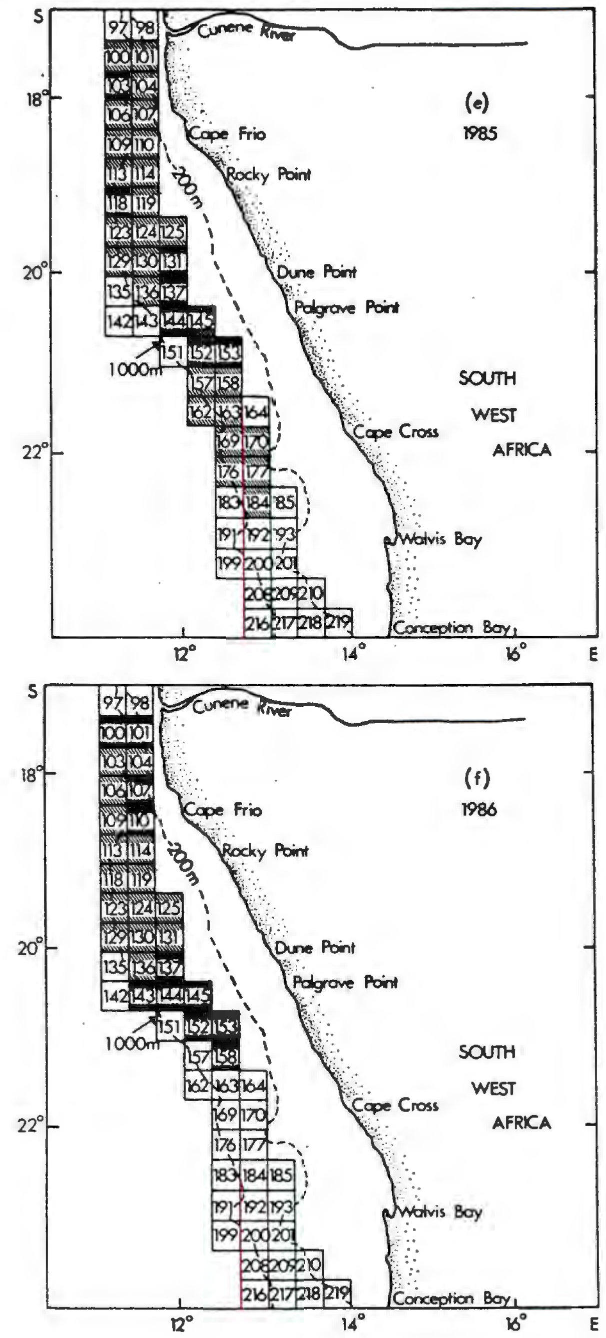

Fig. 1. (e-f): Data for Taiyo Company vessels (1981-1986), showing grids used to report commercial crab catches off Namibia. Hatched grids indicate those fished. Grids with double hatching are those from which stone crab catches we reported.

CONCLUSION

CONCLUSION

Although this thesis has provided a broad understanding of the deep-sea crab (in particular red crab) biology and fishery, there are several research aspects which have not been covered due to a lack of supporting data. This concluding chapter has been used to examine some of these omissions in more detail.

The subject of recruitment, for example, has not been broached, because the available data on this topic (eg. fecundity, presence of juveniles) has been difficult to interpret.

In Paper 1 it was noted that comparatively few ovigerous *Geryon maritae* (0,1-0,2 per cent of the female catch) have been sampled on the Namibian commercial red crab grounds. Limited information from other sources, suggested that this was also the case elsewhere on the west African coast and the discussion (Paper 1) concluded that the low numbers might be normal for the stock, or due to incorrect sampling methods.

New information on related species, suggests that the low numbers of ovigerous animals sampled were not due to sampling methods. Large numbers of berried *Geryon chuni* have been captured in South African waters by trawling (up to 60 individuals or 81 per cent of all the mature females in a single catch) (Melville-Smith unpub. data) and trap fishing has apparently yielded high numbers of ovigerous *Geryon erytheia* on the Walvis Ridge (crab vessel

Fishing Masters, Taiyo Fishing Company).

. Since sampling methods do not appear to have been the reason for the low numbers of ovigerous animals, one is tempted to speculate that such results might be due to exploitation of the stock. One could suggest for example, that heavy exploitation (such as in the northern areas of the Namibian grounds) does not allow the females sufficient time to become ovigerous, between attaining maturity and being caught. This argument, would however not hold for the southern areas, where fishing mortality is very much lighter (Paper 10).

Based on the limited discussion dealing with this subject in Paper 10 and also above, it would appear that the suggestion proffered in Paper 1, namely that the low numbers of ovigerous animals may be normal for the stock, is the only logical answer. However, this solution has biological short-comings, in that it infers both an inexplicable waste of energy in the production of large numbers of non-breeding individuals, and unrealistic natural mortality rates. Data (both sampling and published), which has become available since writing Paper 1, has led to the development of another hypothesis (outlined below).

There are several examples of non-breeding decapod crustacean populations (*Jasus verreauxi*, in Australia and New Zealand and *Palinurus elephas* in northwestern Europe (Williamson 1965), also several Palinurids off the east coast of southern Africa (Heydorn *et al.* 1978)). These non-breeding populations are considered to be extensions to the normal range of a species, caused by the dispersal of larvae out of the breeding areas. In most cases non-breeding populations are extensions (often latitudinal) to breeding populations, though this is not necessarily the case as is evident from the example of *Palinurus longipes femoristriga* off northern New South Wales, Australia (George and Holthuis, quoted by Phillips and McWilliam 1986).

Non-breeding populations fall into two categories; (i) those that live their life out without reproducing, such as must clearly be the case for the *P. longipes femoristriga* population off northern New South Wales and (ii) those that reproduce, but that migrate to breeding areas for this purpose, for example *J. verreauxi* in New Zealand (Booth 1986). Circumstantial evidence would suggest that *G. maritae* off Namibia may fit into this second category.

It was noted in Paper 10 that *G. maritae* extend over a large area of the West African coastline. It is not known whether this distribution is continuous, though available evidence (Dias and Seito Machado 1973 and Cayré and Bouchereau 1977) would certainly suggest that the population has an uninterrupted distribution between latitude 4°S off Gabon and 22°S off central Namibia. What this means is that the Namibian red crab population may be a latitudinal non-breeding extension of a breeding population situated further north.

Very little is known about *G. maritae* larvae, but Kelly *et al.* (1982) have shown that larvae of the closely related species *Geryon quinquedens* respond to deep-sea conditions simulated in the laboratory, in such a way as to suggest that they swim towards the surface and presumably develop in these waters prior to settling as megalopae.

It was shown in Papers 3 and 4, that mature *G. maritae* females are capable of moving over vast distances and that they generally move northwards. The possibility exists that these movements may be linked to reproduction and that the apparent northward movement may be a migration pattern.

A migratory pattern such as the one mentioned above was considered in Paper 4, but was rejected "because mating and ovigerous red crabs have been captured in both the northern and southern regions of the grounds." This may, however, not be sufficient reason to reject the possibility of a mature female migration. *P. elephas* for example, has been shown from numerous records to only breed south of 55°N, yet one ovigerous animal has been recorded as far north as 53°N (Fig. 1, Willamson 1965), proving that exceptions to this rule do exist. The small numbers of ovigerous *G. maritae* in Namibian waters could conceivably be such exceptions.

A more general pattern may be that females moult to maturity and mate on the Namibian grounds and then migrate to a northerly area (possibly well into Angolan waters) prior to becoming ovigerous. Such migrations would be well within the capabilities of *G. maritae*, as has been shown in Paper 4 and would help to account for the biased sex ratio (85 per cent males:15 per cent females) which has been calculated for a part of the Namibian grounds (Paper 9).

Tagging evidence does not suggest that females leave the grounds permanently once they have reached maturity; a mature female recently reported had been at large for 4,5 years, and several others have been recaptured after shorter periods at large. These recaptures may be animals that have returned to the Namibian grounds after breeding elsewhere.

Assuming that females migrate north to spawn and that the larvae of *G. maritae* and *G. quinquedens* behave similarly, one would expect the larvae to migrate into surface waters influenced by the Angolan Current. The latter current is a warm southward flowing current, detectable down to 200 m and with its western boundary between 10° 30'E and 11°E off Angola (Dias 1983). Data dealing with velocities of the Angolan Current are scarce. Based on limited data, Dias (1983) found the current to have maximum geostrophic speeds in surface to 100 m water of 70-88 $cm.sec^{-1}$ in

March 1971 and minimum speeds of 33-42 cm.sec^{-1} in July 1971.

If the pelagic development time of *G. maritae* larvae is similar to that of *G. quinquedens* (Kelly et al. 1982), they would be expected to take 23-33 days to develop in 20-25°C water (such temperatures would be reasonably typical for Angolan Current surface water (Dias 1983)). Based on the current velocities above, one might assume larvae to drift between 1 100 and 1 700 km (ie. from as far north as northern Angola to Namibian waters). Larvae would not be able to drift further south than 22°S because this is the southern limit of influence of Angolan surface waters (Shannon and Agenbag 1987). It is noteworthy that *G. maritae* do not occur in quantity further south than 22°S (Paper 10) - a fact which lends weight to the 'larval drift' theory above.

One fact that does not substantiate the above hypothesis, is that C. Alfonso Dias (Instituto Nacional de Investigacao das pescas, pers. comm.) found the percentage of egg bearing crabs caught off Angola (with traps) to be low. It is not known however how extensively, or how frequently he sampled the crabs.

Further work will obviously be necessary in order to verify the above hypothesis, though with the present political situation as it is, this would appear to be an unlikely possibility for some time to come.

Still on the subject of recruitment, it is noteworthy that few small crabs (<50 mm CW) have been observed in deep-water photographs. Wigley et al. (1975), obtained a pronounced size frequency trend with depth for *G. quinquedens* and hypothesized that juvenile crabs recruited at depth and migrated up-slope to the adult population. The same depth-size trend has been observed for *G. maritae* off Namibia (Beyers and Wilke 1980), but based on the results obtained in Paper 4, this distribution does not appear to have been due to recruitment. That Chapter suggested that red crabs of all sizes move up and down the slope (within well-defined depths), but that small crabs occur preferentially in the deeper depths of the crabs distribution.

The above does not explain why crabs <50 mm CW were not seen in large numbers at deep-depths. Though future work will be necessary to verify their whereabouts, evidence from two sources point to them possibly living beneath the sediment in disused prawn holes and other similar burrows.

The most direct evidence in this regard is from a study done by Van Heukelem et al. (1983) on juvenile growth rates of *G. quinquedens*. Juveniles of this species (which as explained earlier is a species apparently closely related to *G. maritae*) were kept individually in aquaria in the laboratory. The authors placed small pieces of plastic tubing in the aquaria and found that the young crabs generally took up residence in the tubes.

Geryon crabs live on muddy bottoms in the natural situation and under such conditions the only similar available cover would be empty burrows. Since they apparently exhibit such a ready tendency to conceal themselves in piping in the laboratory, one might deduce that they do likewise in their natural surroundings.

Another source of evidence is from an examination of the feeding ecology of deep-water fish in the area of the commercial crab grounds. MacPherson (1983, 1986) conducted such a study and found only four out of 48 deep-water fish, shark and ray species (over 11 000 stomachs examined) to have *G. maritae* remains in their gut contents. Of these fish, *Ebinania costaecanariae* (identified incorrectly as *Cottuncoloides macrocephalus* in MacPherson (1983)) was by far the most important red crab predator, with *G. maritae* constituting roughly 25 per cent by mass of the species consumed. Red crabs found in the gut of *E. costaecanariae* were generally between 20 and 40 mm CW. None exceeded 56 mm CW (MacPherson pers. comm., Melville-Smith unpub. data).

E. costaecanariae is a short (total length generally <500 mm) rotund fish, with small teeth, thick lips and a rounded protrudeable mouth - adaptations which would suggest that it might find its food by using a 'blowing action', a feeding method common to fish with such mouthparts. If this were the case and if as suggested, juvenile *G. maritae* inhabit small burrows, the high proportion of *G. maritae* in the gut contents of *E. costaecanariae* would be consistent with a 'blowing' method of feeding.

In Paper 2 it was mentioned that though trap fishing and trawling have frequently caught females in a moulting condition, males in such a shell state have been sampled on very few occasions. The small numbers of moulting males which have been sampled, have always been found to be in a post moult condition. Based on their brittle, clean exoskeletons, it can be assumed that these recently moulted males were weeks, rather than days postmoult. Premoult females are easily distinguished by their exoskeleton being soft, often partially torn along the episuture line and by the new well-formed exoskeleton developing underneath. Male animals in such an advanced premoult stage have never been captured. From the above it is obvious that red crabs do not feed during the moult cycle (premoult females are assumed to be carried into the traps by coupling males, see Paper 2), but this does not explain why they have not been caught by trawling.

One possible explanation is that they may indulge in communal moulting behaviour as has been described for numerous crabs (Warner 1977). This type of behaviour involves crabs coming together to form heaps. The purpose of these aggregations is generally considered to be for the protection of moulting and in some species mating animals.

The adaption of such behaviour would be logical in an environment that offers little protection to moulting animals. Such behaviour would also help to explain the absence of moulting males in trawl catches, because non random clumps of moulting animals would be unlikely to be caught without a large amount of sampling.

It is obvious that much work is still necessary in order to obtain a through understanding of the Namibian crab fishery. However, this investigation has achieved its stated aim in that sufficient ground work has been carried out to have enabled a management policy to be proposed for the Namibian red crab fishery. These proposals (based on those in Paper 10), are due to be submitted to the International Commission for the Southeast Atlantic Fisheries (ICSEAF) in December 1987.

The stone crab has been shown by this thesis to occur in generally low densities over a wide area, with the result that the commercial importance of the species is unlikely to increase beyond what it is at the moment. Weighing this up against the high cost of deep-water research, it is unlikely that this species will receive much scientific attention in the near future.

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