THE POPULATION ECOLOGY AND FEEDING BIOLOGY OF ROCKY SHORE CRABS ON THE CAPE PENINSULA

By

Peter James Le Roux

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Supervisor: Assoc. Prof. C.L. Griffiths

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Dedicated to

Jesus, because He died and rose, my Father and Mother, because they gave all they could, Warren and my friends, because we stood shoulder to shoulder, Graham, because he pushed and to Suki, because she believed.

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DECLARATION

I hereby declare that unless otherwise stated this thesis represents my own work. I had complete responsibility for the collection and processing of samples, the analysis of data and the writing of all the chapters. Data collected by Mrs L. van Herwerden and by Mrs M.A.P. Joska was incorporated into chapters two and four with their permission. The data sets were small and were almost totally reworked for presentation. The text of chapter two is based on original notes by Mrs M.A.P. Joska. Professor G.M. Branch provided the concept and funds for the study completed in chapters two and three and edited the manuscripts. Associate Professor C.L. Griffiths provided the funds for the rest of the study and edited all the manuscripts. In all other respects, I lay claim to uncited ideas, concepts, hypotheses or conclusions contained in this thesis.

Signed by candidate

PETER JAMES LE ROUX

DATE : 1 / 2 / 91

ABSTRACT

This thesis consists of five chapters. One is a published paper, two are in paper format, and one is a thesis chapter. The thesis is preceded by a general introduction. The central theme of this work is the population ecology and feeding biology of rocky-shore crabs on the Cape Peninsula. The biology of three crabs is examined, namely, the ubiquitous brown shore-crab *Cyclograpsus punctatus* (M.Edw), the Cape rock-crab *Plagusia chabrus* (De Haan) and the invasive European shore-crab *Carcinus maenas* (L.). The possible impact of *C. maenas* upon the South African intertidal and local crabs in particular is also assessed.

Briefly the chapters are as follows :

CHAPTER 1 - A general introduction with a review of relevant literature.

CHAPTER 2 - *On the distribution, diet and possible impact of the invasive European shore crab* *<u>Carcinus maenas</u>* *(L.) along the South African coast.* This paper is co-authored by Professor G.M. Branch and Mrs M.A.P. Joska and was submitted to and published in the South African Journal of Marine Science, volume 9, 1990. The distribution and spread of *C. maenas* is followed from its discovery in 1983 to 1990. Information on the maximum size recorded at each site is also given. The diet of *C. maenas* on our shore is examined and predation experiments are used to determine which common intertidal species, if any, have a refuge from *C. maenas* predation. *C. maenas* is established and reproductively active at several sites along the South African coast, including Sea Point, Table Bay Harbour (the site of original introduction), Bloubergstrand, Melkbosstrand and Saldanha Bay. The crab has spread 117 km north and 10 km south of Table Bay Harbour since its introduction in 1983 but is restricted to sheltered waters. *C. maenas* was shown to prey on a wide

variety of South African intertidal species, in particular the slow moving isopod *Paridotea* spp., limpets and a variety of errant polychaetes associated with mussel beds. Larger animals such as the mussels *Choromytilus meridionalis*, *Aulacomya ater*, and *Mytilus galloprovincialis* and the periwinkle *Turbo sarmaticus* achieve a refuge in size from *C. maenas* predation. It is predicted that *C. maenas* will only have a significant impact in areas protected from wave action.

CHAPTER 3 - *Predator-prey interactions between the European shore-crab* Carcinus maenas *(L.) and three South African mussels*. This paper was co-authored by Professor G.M. Branch and examines the predator-prey interactions between *Carcinus maenas* and *Aulacomya ater*, *Choromytilus meridionalis* and *Mytilus galloprovincialis*. *M. galloprovincialis* is a Mediterranean invasive while *A. ater* and *C. meridionalis* are indigenous. The experiments performed were designed to test aspects of the optimal diet model of optimal foraging theory and the effect of shell ribbing and novelty on *C. maenas* predation. The predictions of the optimal diet model are supported by this study. Novelty provided the mussels with no refuge from *C. maenas* predation. Shell ribbing only provided *A. ater* with a refuge at larger prey lengths. Crabs preferred *M. galloprovincialis* to *A. ater* in selection experiments. It is predicted that *C. maenas* will affect mussel populations in sheltered areas where the crab occurs in high densities.

CHAPTER 4 - *Feeding, activity rhthym and zonation of rocky-shore crabs on the Cape Peninsula*. The zonation, habitat, diet, gut enzymology and activity rhythm of *Cyclograpsus punctatus*, *Plagusia chabrus* and *Carcinus maenas* are examined. An attempt is made to predict whether or not *C. maenas* invasion will affect *C. punctatus* or *P. chabrus*. Intertidal and subtidal observation, shore transects, seasonal gut content analysis, bioassay, measurement of chelal mechanical advantage, field observation of activity and laboratory analysis of gut content fluctuations over a 24 hour period were used to complete this study. *C. punctatus*

was found to be strictly intertidal, feeding primarily on kelp wrack and a few selected gastropods. It has an enzyme compliment which matches its diet, including high levels of algolytic enzymes such as alginase, cellulase and laminarinase. It is active and feeds primarily at night at low tide. *P. chabrus* is primarily subtidal and is usually found on wave-washed shores. The crab is omnivorous and has high levels of preoteolytic enzymes such as azocasein, chitinase and amylase in the gut along with moderate levels of cellulase and alginase. It is active throughout the day but mostly at dusk (when it feeds) and at dawn. *C. maenas* is found in the mid to low intertidal and is only found in sheltered waters. This carnivorous species has a powerful crusher-chela and a largely proteolytic enzyme compliment with very low levels of alginase, cellulase and laminarinase. It is active by day and by night moving up the shore with the incoming tide. The activity pattern, diet, enzymology and zonation of the three species studied shows very little overlap and it is felt that the impact of *C. maenas* on indigenous species will be minimal.

CHAPTER 5 - *On the morphometrics and population biology of the crabs Cyclograpsus punctatus (M. Edw.) and Plagusia chabrus (De Haan).* Seasonal morphometric and population data for these crabs is presented. Male size frequency distributions were skewed to the left and females slightly to the right. Recruitment appears to occur between July and January for *C. punctatus* and in July for *P. chabrus*, but these results are not conclusive due to the quarterly nature of the data. All morphometric parameters with the exception of abdominal width and chelae size scaled isometrically with carapace width. Abdominal width and chelae size scale allometrically. Males grew larger than females and outnumbered them in both species. Sex ratio fluctuated, following the percentage ovigerous curve. A classical, U-shaped sex ratio curve with respect to size was found in both species. *C. punctatus* breeds between May and September, *P. chabrus* between September and February. The number of eggs increases allometrically with carapace width. *C.*

CHAPTER 1

GENERAL INTRODUCTION

Decapod crustaceans, in particular, crabs and crayfish, form an integral part of many intertidal ecosystems throughout the world (Warner 1977). These animals are not simply passive components of these ecosystems but are often important links in the dynamic processes which constitute ecosystem functioning. Examples are interactions between the coral, *Pocillopora* and crabs of the genus *Trapezia*, in tropical waters (Glynn 1983, Coen 1988), the structuring of populations of the edible cockle *Cerastoderme edule* by *Carcinus maenas* predation (Jensen and Jensen 1985, Sanchez-Salazar *et al.* 1987a), and the development and evolution of gastropod shell architecture in response to crab predation (Vermeij 1976, 1982, Hughes and Elner 1979, Dudley 1980 and Bertness and Cunningham 1981). Crab galleries under mussel beds create space for other intertidal animals, ordinarily excluded from the Chilean intertidal, to settle and flourish (Castilla *et al.* 1989).

Crabs are also commercially important. They are used as bait or as food in many parts of the world and are often harvested in large quantities. The size of these industries vary. The Namibian red crab, *Geryon maritae* has been harvested since 1973. The fishery netted R16 million in 1986 with a total catch of 4.7 million kilograms (Melville Smith 1987, 1988). Figures quoted by Warner (1977) show that the blue crab, *Callinectes sapidus* , is the most important commercial crab in the U.S.A. In 1973, 61.1 million kg were harvested. *Callinectes sapidus* is followed by the king crab, *Paralithoides camtschatka* (34.4 million kg), the snow crab, *Chionoectes tanneri* (27.7 million kg) and the dungeness crab, *Cancer magister* (5.5 million kg). The red crab (*Geryon quinquedens*) and the Florida stone crab (*Menippe mercenaria*) are also harvested in the U.S.A. but on a smaller scale (Warner 1977). The pond culture of *Scylla serrata* in Japan produced 168 000 kg of crab in 1968 while a similar program in Java produces 200 crabs / ha / yr (Warner 1977). Crabs can also be vectors of disease and aquacultural or agricultural pests (Kitching *et al.* 1959, Hanks 1961, Warner 1977 and Sanchez-Salazar *et al.* 1987b).

Crabs, by virtue of their size, accessibility, influence in the community and commercial value have been the subject of a great deal of study in various parts of the world. This is clearly illustrated by work on the European shore-crab *Carcinus maenas* (Broekhuysen 1936, Naylor 1962, Crothers 1967, 1968, Ropes 1968 and Elner and Hughes 1978), the edible crabs *Cancer spp.*, the fiddler crabs *Uca spp.* and the blue crab *Callinectes sapidus* (Christy and Salmon 1984, Colby and Fonesca 1984, Warner 1987, Reilly 1987, Ryer 1987 and Eggleston 1990).

The South African coast supports a number of crab species. The most abundant of these are probably the estuarine crab *Scylla serrata*, the mud-crab *Sesarma catenata*, the swimming sand-crab *Ovalipes punctatus* , the ghost crabs *Ocypode* spp., the rock crab *Plagusia chabrus*, and the shore-crabs, *Cyclograpsus punctatus* and *Grapsus grapsus* (Day 1974). General, taxonomic information on all these species may be found in a descriptive catalogue on South African brachyurans produced by Barnard (1950). Various aspects of the biology of *Scylla serrata* including diet, feeding methods, activity pattern and the rates of gastric evacuation have been studied by Hill (1975, 1976, 1979 and 1980). Alexander and Ewer (1969) compared the general ecology of the mud crab *Sesarma catenata* with that of *C. punctatus* living in a muddy environment in the Kowie river estuary. Baird (1978) looked at the fecundity of *S. catenata*. Du Preez (1981) thoroughly examined the morphometrics, growth, reproduction, larval development, biochemistry, respiration and energy balance of *Ovalipes punctatus*. The biology of and effects of oil upon ghost crabs have been studied by Berry (1974) and Berry *et al.* (1976).

South African rocky-shore crabs have, by comparison, been neglected. *Grapsus grapsus* is only found between the Storms river mouth and Imhabane in Mozambique (Figure 1) and has not been studied. *Cyclograpsus punctatus* (Figure 2a) and *Plagusia chabrus* (Figure 2b) are the only abundant crabs that occur on the rocky shores of the Cape Peninsula and are more widespread than *G. grapsus* (Figure 1). *C. punctatus* and *P. chabrus* are both grapsid crabs belonging to the family Grapsidae (more details about these species are given in paper 3).

Montgomery (1930) examined the taxonomy of *C. punctatus* and *P. chabrus* as did Barnard (1950). Broekhuysen (1941) studied the population ecology of *C. punctatus* at a single site in the Cape. His work showed that *C. punctatus* has two breeding peaks, the principal one in winter (May to September) and the other in summer (January and February). *C. punctatus* females were also shown to extrude more than one batch of eggs in the principal breeding season and the author suggests that the crab moults mainly during spring and summer. The life histories of *C. punctatus* and *C. maenas* are compared by Broekhuysen (1941). He contends that they are "ecologically comparable forms inhabiting similar environments in different hemispheres". Heeg and Cannone (1966) examined osmoregulation in *C. punctatus* and *P. chabrus* showing that *C. punctatus* is better able to tolerate fluctuating extremes of salinity. This improved

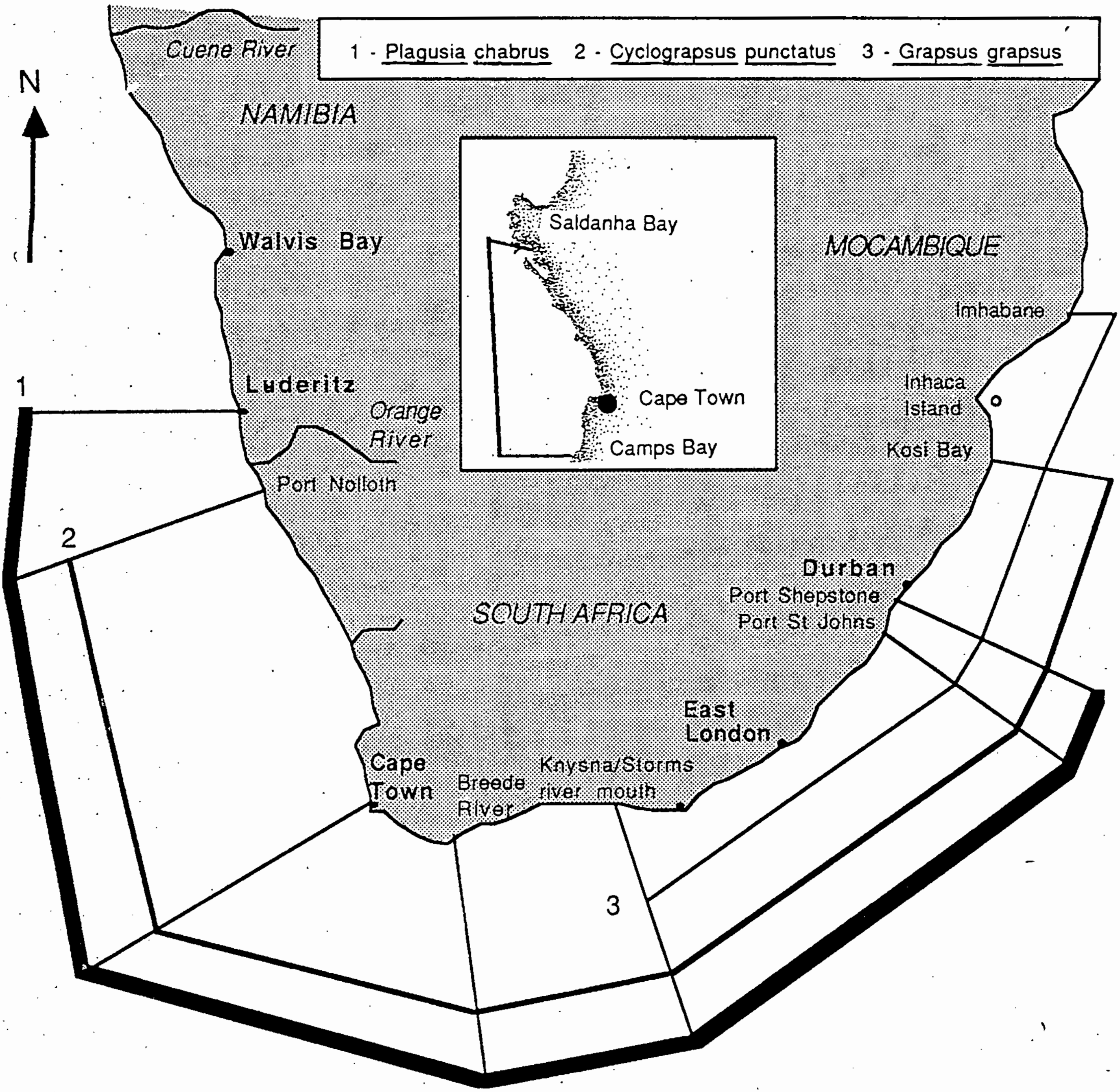

FIGURE 1. A map of Southern Africa showing the distribution of the three most abundant species of rocky-shore crab on the coast viz. Plagusia chabrus, Cyclograpsus punctatus and Grapsus grapsus. The distribution of the invasive European shore crab, Carcinus maenas is shown in the insert.

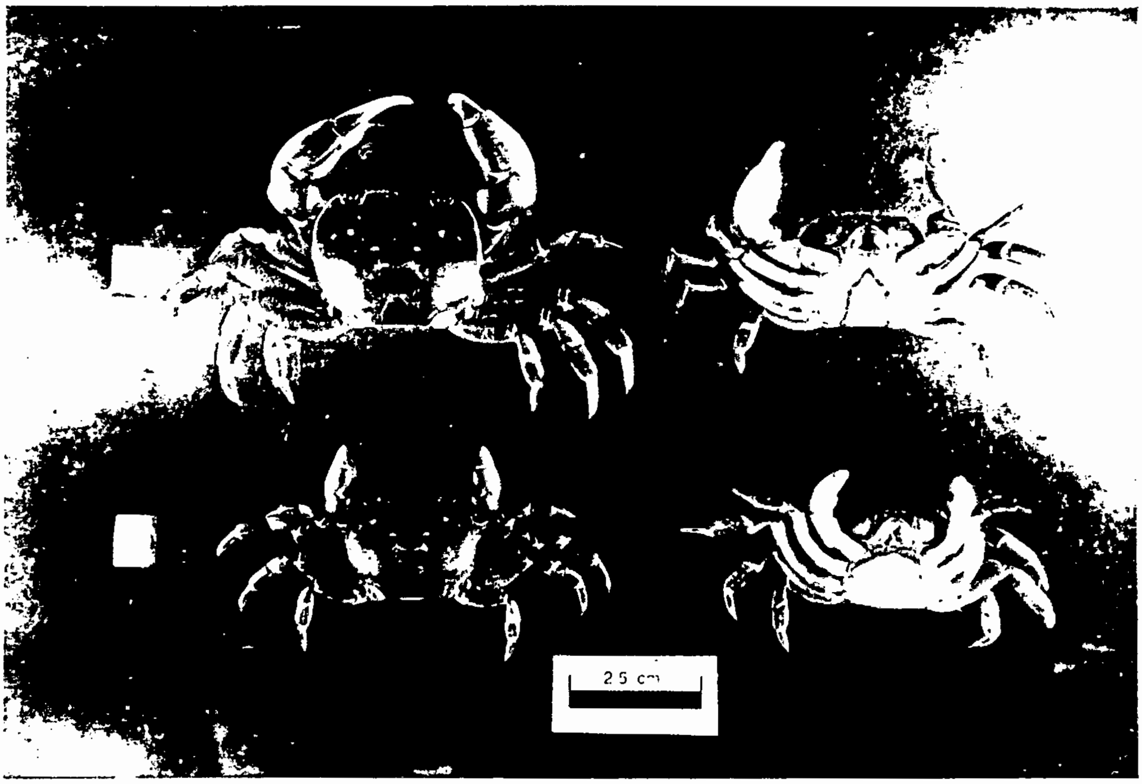

Figure 2a. The common Cape shore-crab, *Cyclograpsus punctatus*, a - male and b - female.

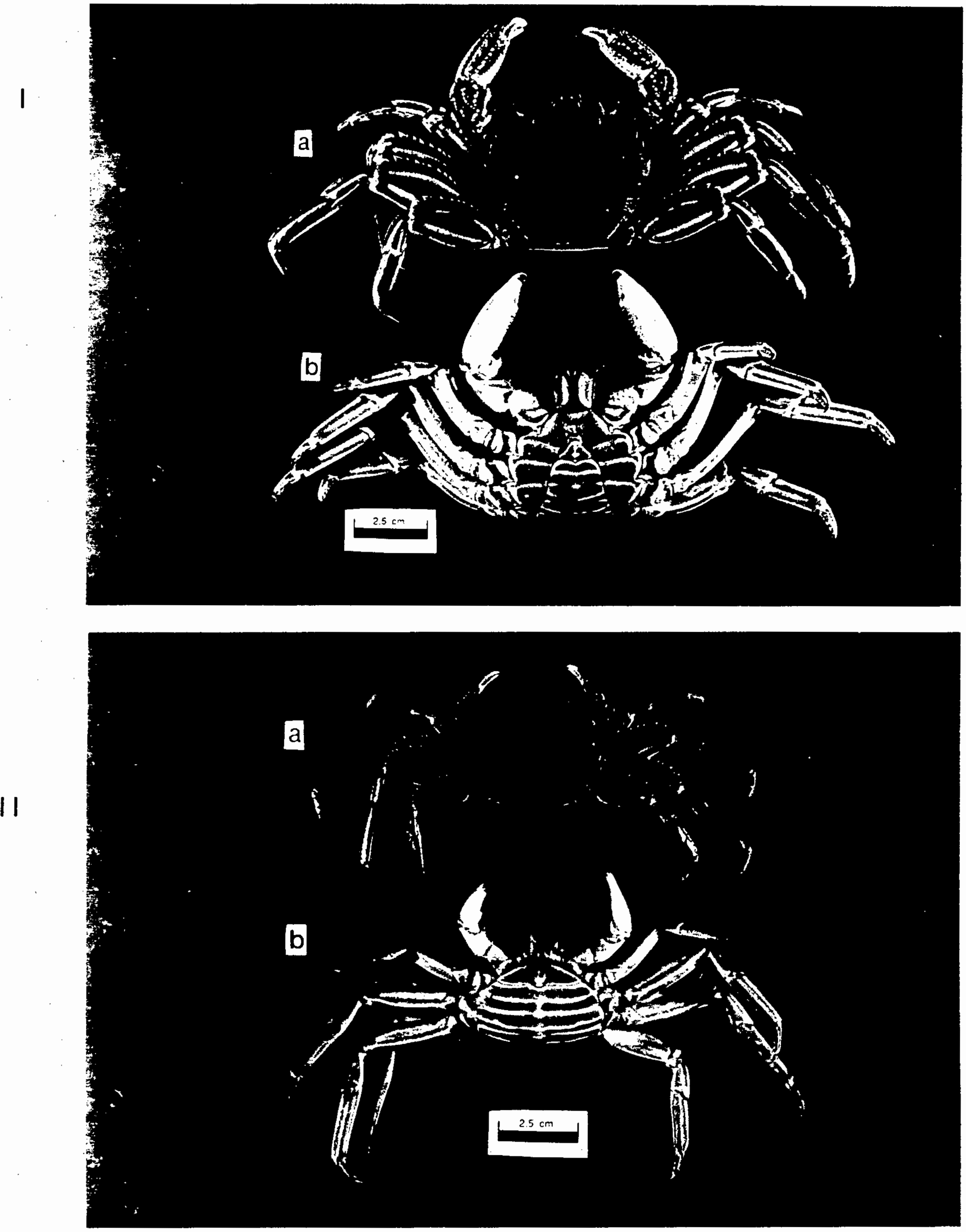

Figure 2b. The Cape rock-crab Plagusia chabrus. I - Male and II - female,

a - dorsal and b - ventral.

tolerance is attributed to the longer midgut found in *C. punctatus.* Schaefer (1970) compared the foregut morphology of *Cyclograpsus punctatus* with that of the hermit crab, *Diogenes brevirostris* and the mud-prawn, *Upogebia africana* . The author related the relatively powerful, sclerotised gastric mill found in *C. punctatus* to their preference for coarser food than that of the hermit crab and mud prawn.

The existance of dominance heirarchies within groups of*C. punctatus* was demonstrated by Caiger and Alexander (1973). They also showed that the androgenic gland was responsible for this phenomena. Muir (1974) completed a morphological study of *P. chabrus* designed to act as a dissection guide for the animal. Bevis Challinor (1984) compared the tolerance of *P. chabrus* and *C. punctatus* to fluctuating water temperature. *C. punctatus* was shown to be more tolerant of such fluctuations than the largely subtidal *P. chabrus.* The work was, however, never published.

The only other work of significance done on these species was a non quantitiative study on Australian *P. chabrus* by Shepherd (1973), who concluded that *P. chabrus* was the main predator of *Haliotis roei* and that it had a consistent dusk-dawn activity peak.

In addition to the indigenous species discussed above approximately 150 kilometers of the Cape coast is also infested with the European shore-crab, *Carcinus maenas*, which belongs to the family Portunidae (Figure 2c and Paper 1). The distribution of this species is shown in the insert to Figure 1.

Figure 2c. The invasive European shore-crab Carcinus maenas, a - male and b - female.

The introduction of a large, aggressive, predatory crab such as *Carcinus maenas* to our coast is a cause for immediate concern. It has wide, flexible dietary preferences (Ropes 1968) and can tolerate low oxygen levels (Klein Breteler 1975), protracted periods of aerial exposure (Newell et al. 1972) and wide fluctuations in salinity (Spaargen 1974). The ability to reverse its respiratory current (Arudpragasam and Naylor 1964) allows *C. maenas* to cope with excessive siltation. When present in high densities, *C. maenas* predation can fundementally alter community dynamics within an intertidal zone (Hanks 1961, Hadlock 1980, Dudley 1980, Dare et al. 1983, Jensen and Jensen 1985 and Sanchez-Salazar et al. 1987a/b). *C. maenas* presents a very real threat to the biotic integrity of the South African intertidal. Our lack of understanding of the biology of local species makes accurate assessment of the possible effects of *C. maenas* invasion on local crabs almost impossible. This study was conducted to broaden our understanding of the biology of the two species of crab with which *C. maenas* is in contact namely, *Cyclograpsus punctatus* and *Plagusia chabrus*. This study also examines the biology of *C. maenas* on our shore and attempts to predict what effect it will have on local bivalves and on *C. punctatus* and *P. chabrus* .

Paper 1 deals with the introduction of *C. maenas* to our shore, its spread, past and present distribution and its diet. Paper 2 examines the interactions between *C. maenas* and three South African bivalves, *Aulacomya ater*, *Mytilus galloprovincialis* and *Choromytilus meridionalis*. Certain aspects of optimal foraging theory are tested and the effects of prey novelty and shell ribbing on *C. maenas* predation is examined. The possible ecological impact of *C. maenas* predation on these bivalves is assessed. Paper 3 compares the feeding biology, diet, enzymology and activity patterns of *C. punctatus*, *P. chabrus* and

C. maenas. The general habitat and zonation of the three species is also compared. Paper 4 deals with aspects of the population dynamics, morphometrics and reproductive biology of *C. punctatus* and *P. chabrus*.

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CHAPTER 2

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1990

ON THE DISTRIBUTION, DIET AND POSSIBLE IMPACT OF THE INVASIVE EUROPEAN SHORE CRAB *CARCINUS MAENAS* (L.) ALONG THE SOUTH AFRICAN COAST

P. J. LE ROUX, G. M. BRANCH* and M. A. P. JOSKA**

The crab *Carcinus maenas* (L.) has an endemic distribution along the European Atlantic coastline but has been accidentally introduced into intertidal habitats in several parts of the world. Its discovery at the Cape Peninsula in South Africa is recorded here. The crab is well established in Table Bay harbour and the population is at least seven years old. From here it has spread 117 km north and 10 km south. Populations on the open coast are more recently established. The crab feeds on a wide range of intertidal animals, particularly the isopod *Paridotea ungulata*, limpets and polychaetes, but it is too early to make quantitative assessments of its impact on local intertidal communities. Initial predation experiments suggest that the barnacle *Notomegabalanus algicola* and the whelks *Oxystele variegata* and *O. tigrina* have no refuge in size or zonation from the crab. *O. sinensis*, of similar size to *O. tigrina*, is less vulnerable by virtue of its stronger shell. Its critical size (above which it is too large to be attacked) is correlated with crab size. Larger species, such as the mussels *Choromytilus meridionalis* and *Aulacomya ater* and the periwinkle *Turbo sarmaticus*, clearly achieve a refuge in size, but predation on their recruits may influence their abundance and size structure. *C. maenas* rejected only the urchin *Parechinus angulosus* as a source of food. While it is conceivable that shifts in community structure, selection for thicker shells in molluscs and localized extinction of certain species may occur at high crab densities, it is predicted that *C. maenas* will only have a significant impact in areas protected from wave action.

Die krap *Carcinus maenas* (L.) kom endemies langs die Atlantiese kuslyn van Europa voor, maar is per ongeluk in tussengetyse habitatte van etlike wêrelddele ingebring. Sy ontdekking langs die Kaapse Skiereiland in Suid-Afrika word hiermee geboekstaaf. Die krap is goed gevestig in Tafelbaai, en die bevolking is ten minste sewe jaar oud. Hiervandaan het dit 117 km noord en 10 km suid versprei. Bevolkings aan die onbeskutte kus is meer onlangs gevestig. Die krap teer op 'n wye verskeidenheid tussengetyse diere, veral die isopode *Paridotea ungulata*, klipmossels en borselwurms, maar dit is te vroeg om nou al kwantitatiewe ramings van sy invloed op plaaslike tussengetyse gemeenskappe te maak. Voorlopige voedingstoetse dui daarop dat die seepok *Notomegabalanus algicola* en die wulke *Oxystele variegata* en *O. tigrina* geen ontvlugting in òf grootte òf sonering van die krap vind nie. *O. sinensis*, van soortgelyke grootte as *O. tigrina*, is minder kwesbaar vanweë sy sterker skulp. Sy kritieke grootte (waarbo hy te groot is om aangeval te word) hou verband met krapgrootte. Groter spesies, soos die mossels *Choromytilus meridionalis* en *Aulacomya ater* en die alikreukel *Turbo sarmaticus*, verwerf wel deeglik beskerming wanneer hul groot word, maar roofbedrywighede op hul rekrute kan die talrykheid en grootteasamestelling beïnvloed. *C. maenas* het net die seekastaiing *Parechinus angulosus* as 'n voedselbron verwerp. Ofskoon dit denkbaar is dat verskuiwings in gemeenskapstruktuur, seleksie vir dikker skulpe by weekdiere en plaaslike uitwissing van sekere spesies by hoë krapdigtheid kan geskied, word verwag dat *C. maenas* net 'n beduidende uitwerking sal hê in gebiede wat beskut teen branderwerking is.

Carcinus maenas (L.), commonly known as the green or shore crab, has an endemic distribution on European Atlantic coastlines (Crothers 1968). It has, however, been introduced to several other parts of the world, including the North American east coast from Nova Scotia (Welch 1968) to Virginia (Holthuis and Gottlieb 1958), Willapa Bay, Oregon, on the North American west coast (Ricketts and Calvin 1968), Brazil, the Bay of Panama (Rathbun 1930), Hawaii and Ceylon (Crothers op. cit.). Uncertainty exists as to whether the later records for the last two localities were for *C. maenas* or *C. mediterraneus* (Crothers op. cit.). Christiansen (1969) listed Madagascar as a locality to which *C. maenas* had been introduced. *C. maenas* has also established itself in Australia (Fulton and Grant 1900, McNeil 1953) and is at present found on the coastlines of New South Wales, Victoria and South Australia (Zeidler 1978).

While trap-sampling in Table Bay Docks, Cape Town, in January 1983, Prof. J. Kittaka and co-workers from the University School of Fisheries Science, Japan, collected two crabs which we identified as the European shore crab *Carcinus maenas* (L.). A male and a female were sent to the British Museum, where Dr R. Ingle confirmed the identification. Although this is the first record of this crab in South African waters, Barnard (1950) had predicted its eventual arrival on the South African coast.

C. maenas is an active and voracious predator, especially on molluscs (Ebling *et al.* 1964, Crothers

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* Department of Zoology, University of Cape Town, Rondebosch 7700, South Africa

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1968, Welch 1968, Elner 1980, Hughes 1980), and in some cases has caused severe declines in mollusc populations (Ropes 1968) or prevented their establishment (Jensen and Jensen 1985). It also appears to have been the selective agent causing interspecific morphological variation in some mollusc species (Ebling *et al.* op. cit., Seeley 1986, Sanchez-Salazar *et al.* 1987). Dare *et al.* (1983) suggest that polychaete distributions may be controlled by *C. maenas* predation.

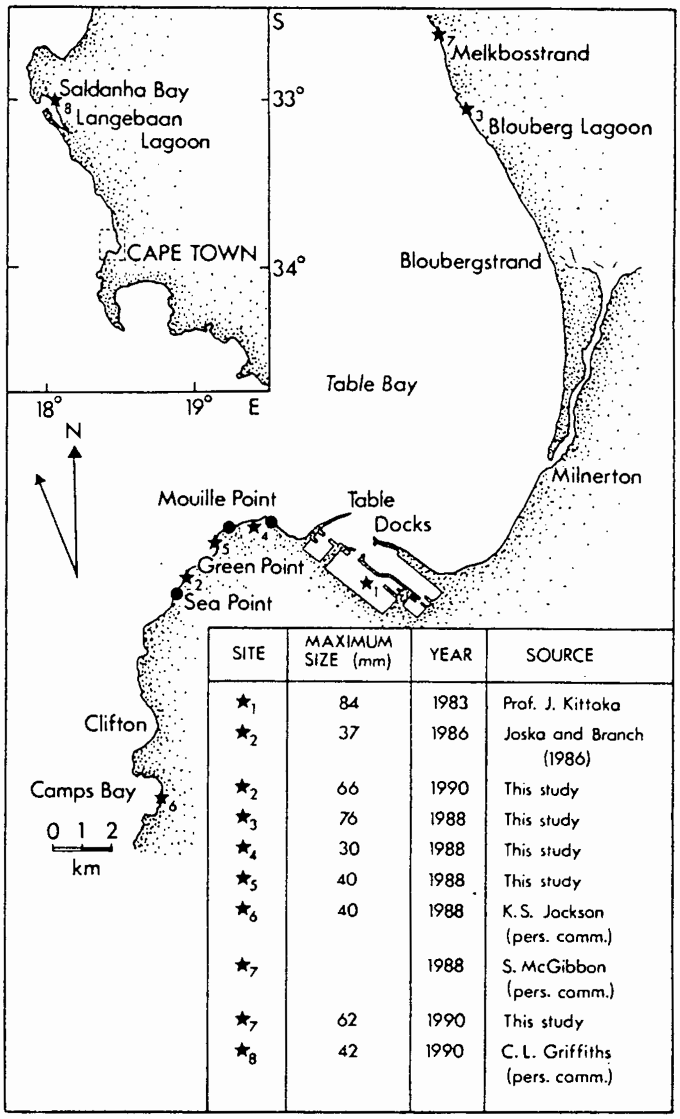
In view of the above effects, the recent discovery of *C. maenas* on the coast of South Africa is a cause for concern. In this study, the extent, number and size distribution of *C. maenas* populations along the Cape coast are documented. Gut content analyses were conducted in conjunction with laboratory studies to establish which South African intertidal animals are, or potentially may be, consumed. In the light of these findings, speculations are made on the possible impact of this crab on South African intertidal community structure.

MATERIALS AND METHODS

Crab capture

Standard crab traps with a rectangular metal box frame (60 × 40 × 20 cm), covered with 1,5 cm stretched-mesh nylon netting were used to collect the crabs from Table Bay Yacht Basin in 1984. Traps were baited with fish heads and retrieved within 48 h in order to obtain crabs for experimental purposes. Thereafter, traps were laid and retrieved at monthly intervals from February to October 1984. On three occasions divers surveyed the population and collected females in berry, seldom found in traps. Comprehensive sampling of Table Bay Yacht Basin was subsequently undertaken in 1989 by diving. Crabs were also collected by snorkeling and hand collection between March and May 1988 from a small lagoon approximately 400 metres south of Bokkom Bay at Bloubergstrand in the Cape (Fig. 1). Voucher specimens have been housed in the type collection of the University of Cape Town (No. CP 841a) and in the South African Museum (SAM - A - 39788). In 1990, areas of 50 m^2 were censused in more detail at Melkbosstrand and Sea Point by snorkeling and intertidal surveys.

Crabs were separated into size classes on the basis of carapace width *CW* (i.e. the distance between the most marginal teeth), and those used for experiments were held singly in marine aquaria with an aerated through-flow of water at temperatures ranging from 12 to 17°C.



SITE	MAXIMUM SIZE (mm)	YEAR	SOURCE
★$_1$	84	1983	Prof. J. Kittoka
★$_2$	37	1986	Joska and Branch (1986)
★$_2$	66	1990	This study
★$_3$	76	1988	This study
★$_4$	30	1988	This study
★$_5$	40	1988	This study
★$_6$	40	1988	K.S. Jackson (pers. comm.)
★$_7$		1988	S. McGibbon (pers. comm.)
★$_7$	62	1990	This study
★$_8$	42	1990	C. L. Griffiths (pers. comm.)

Fig. 1: A map of the Cape Peninsula, showing the sites at which *Carcinus maenas* has been found, the dates on which it was first found and the maximum size found at each site

Gut contents

The gut contents of 50 crabs collected at Bloubergstrand (21 males and 29 females, ranging in size from 28 to 71 mm) were analysed. Methods were adapted from Hynes (1950), Berg (1979) and Pulfrich and Griffiths (1988), and included visual estimates of percentage fullness and percentage composition, measurement of stomach volume and food volume and calculation of percentage occurrence of each prey item. Counts of the number of individuals of each prey species or taxon were also made.

redation experiments

To determine the critical size of each prey species aten by *C. maenas* of a particular size, each crab was iven a full size range of the prey species in question, ie sizes of the prey being measured and recorded beorehand. After five days the numbers and sizes of ach prey animal which remained were recorded. In ases where only the smaller representatives of a prey pecies were eaten, crabs were then left with the larger idividuals.

Both male and female crabs were used in the experiments, but not in equal ratio because fewer females vere caught in the traps. Because crabs in premoult ondition do not feed (Crothers 1967, Elner 1980), any rabs which developed this condition during the experiment were excluded from the analyses. The crabs vere starved for three days prior to the start of each xperiment in order to standardize hunger level.

The sizes and numbers of each prey species offered *C. maenas* during the experiments are summarized Table I. In addition, less extensive tests were made n a wider range of species to determine if there were ny species *C. maenas* would not eat.

hell strength

The shell strengths of *Oxystele sinensis* and *O. tigrina* were measured by means of a point-compression ad apparatus. In all, 20 individuals of each species, ranging in size from 11 to 33 mm shell width, were crushed and the kg-resistance of each recorded. These values were then converted into Newtons using the standard conversion (1 kg = 9,8 N).

RESULTS

Size frequency and distribution

The sites at which *C. maenas* has been recorded, data concerning its current distribution and the maximum size recorded at each site are shown in Figure 1.

Male crabs in Table Bay Docks ranged in carapace width from 42 to 84 mm and females between 45 and 56 mm (Fig. 2a, b). Females carried egg plugs between July and November. In Europe, Broekhuysen (1936) and Crothers (1967) also found berried females during these months, although Naylor (1962) reported that some British populations had females in berry throughout the year. Females in berry have been collected randomly from Bloubergstrand and Sea Point between July and December.

Sea Point supported only small individuals (maximum size 37 mm *CW*) in 1986, but by 1990 the population had reached $6{,}55 \cdot m^{-2}$ and maximum size had risen to 66 mm. Sampling in Blouberg Lagoon in 1988 produced 165 individuals, far more than had been captured during a preliminary study in 1984. Sampling done by Joska and Branch in 1984 and 1985 yielded

able I: Number, size range, size offered, maximum size consumed and maximum size attained in the field of each prey species fed to *Carcinus maenas* (50–70 mm *CW*) during the initial predation experiments (*after Griffiths 1981)

Species offered	Number of		Size range offered (mm)	Maximum size (mm)	
	Individuals offered per trial	Trials		Offered	Attained in the field
xystele variegata (Gastropod)	8	6	10–22 (width)	22	25*
xystele tigrina (Gastropod)	7	6	10–30 (width)	30	40
xystele sinensis (Gastropod)	7	6	10–30 (width)	30	40
otomegabalanus sp. (Barnacle)	30	6	5–10 (diameter)	10	10
horomytilus sp. (Bivalve)	14	6	10–60 (length)	55	140*
ulacomya ater (Bivalve)	14	6	10–60 (length)	45	90*
urbo sarmaticus (Gastropod)	6	1	30–40 (width)	40	90
arechinus sp. (Urchin)	8	1	20–50 (width)	–	70

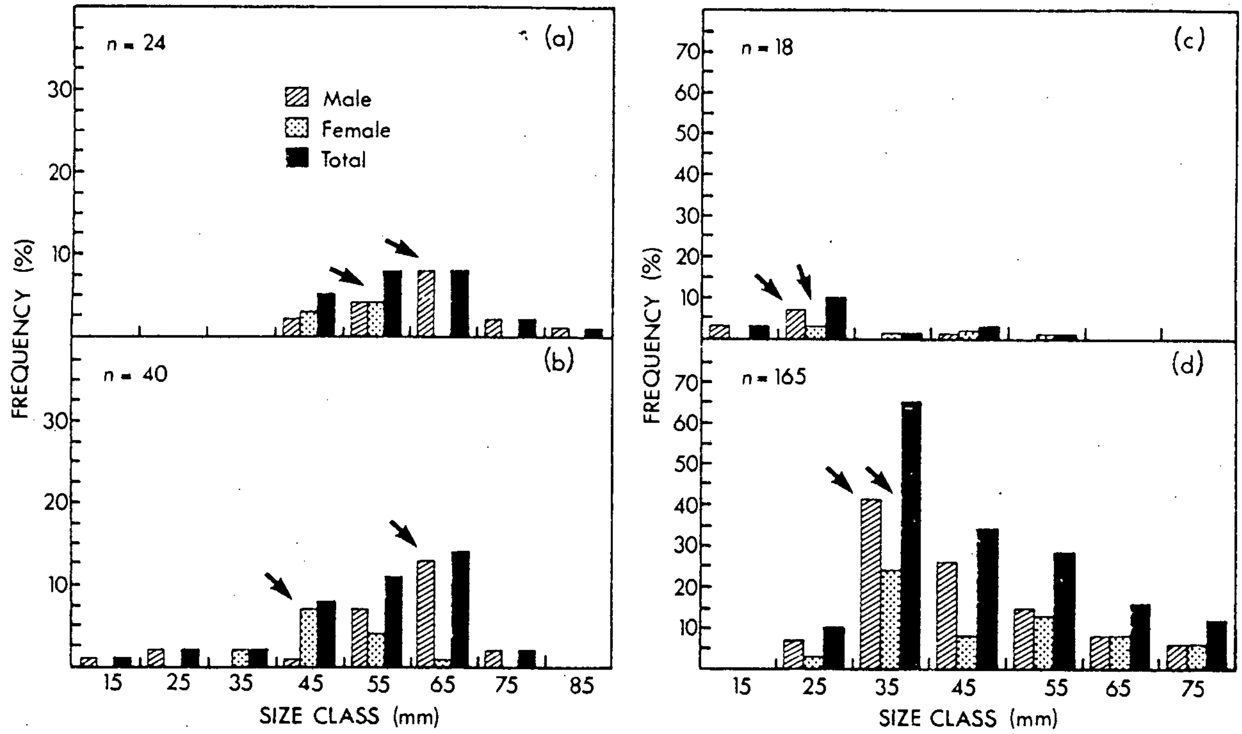


Fig. 2: Size frequency distribution of *C. maenas* populations in (a) Table Bay Docks (February–October 1984), (b) Table Bay Docks (April–May 1989), (c) Blouberg Lagoon (August 1984), and (d) Blouberg Lagoon (March–May 1988). Arrows indicate in which size class the majority of male and female crabs are found at each site. Data for (a) obtained by trapping, for (b), (c) and (d) by diving

no animals larger than 55 mm, whereas the 1988 study produced many crabs larger than that. Mean size increased from 25 to 35 mm between 1985 and 1988. In 1988, most crabs in Blouberg Lagoon had a *CW* of between 30 and 40 mm (Fig. 2c, d). The largest specimen caught during 1988 was a male with a *CW* of 76,1 mm. Females were, on average, smaller than males and dominated the 40–49 mm size class. No females of *CW* >60 mm were caught and the population was clearly dominated by males (57%; $n = 121$; t-test $p = 0{,}05$). Male dominance was also noted during shore collections conducted by Naylor (1962) at Mumbles Point, Swansea, and by Crothers (1968) at Dale Peninsula, Pembrokeshire, both sites in the United Kingdom.

A search of the Bloubergstrand rocky shore failed to find any *C. maenas* on wave-exposed sites, all specimens at this site being restricted to a wave-protected area, permanently underwater and containing numerous boulders.

In 1988, two specimens of *C. maenas* were sighted at Melkbosstrand. By March 1990 the species was well established there with a mean density of $3\cdot m^{-2}$ and a maximum size of 62 mm in the low-shore. In April 1990, a mating pair of *C. maenas* was recorded in Saldanha Bay among cultured mussels in the sheltered waters of Sea Farm Dam. This represents an extension of almost 100 km over its northernmost record.

If the growth rate of the crabs in Table Bay Docks is similar to that elsewhere (Broekhuysen 1936, Crothers 1968, Dries and Adelung 1982), then the size frequency distribution and maximum *CW* of captured crabs suggests that the population in Table Bay Docks is well established and at least seven years old, whereas that at Blouberg Lagoon is between four and five years old. Isolated records and sizes of crabs suggest that the populations at Green Point, Sea Point and Camps Bay are between three and four years old.

Diet

The southern African species now known to be consumed by *C. maenas*, on the basis of gut content analyses and laboratory observations, are listed in Table II. With the exception of *Parechinus angulosus* the crab consumed all species offered to it, provided they did not exceed the sizes the crab was capable of handling.

From analyses of gut contents the most important prey items were gastropods, isopods and polychaetes (Fig. 3). The gastropods *Aetoniella* spp., *Tricholia*

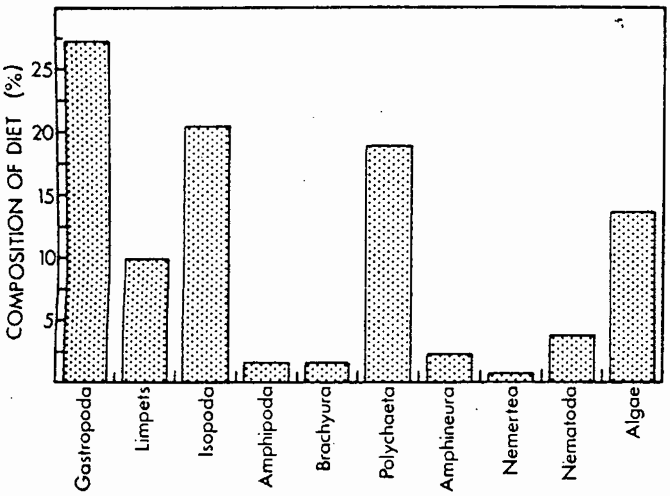


Fig. 3: Histogram showing the percentage composition of the diet of *Carcinus maenas* individuals in Blouberg Lagoon

Table III: Mean number of prey items eaten by *Carcinus maenas*, their percentage occurrence and percentage volume

Species consumed	% Occurrence	Mean number consumed per crab	% Volume
Oxystele sp.	4	1	2,18
Aetoniella sp.	42	5,5	1,71
Tricholia sp.	16	2,5	1,38
Burnupena sp.	2	1	0,03
Lasaea sp.	4	1	–
Gregariella sp.	4	1	0,13
Patella sp.	16	1	14,18
Helcion sp.	2	1	0,16
Crepidula sp.	6	1,8	0,16
Fissurella sp.	2	1	2,49
Paridotea sp.	34	1	29,39
Exosphaeroma spp.	16	1,4	1,78
Cirolana sp.	2	1	1,78
Other isopods	2	1	0,16
Amphipods	4	1,5	0,27
Marphysa sp.	6	1,3	4,60
Orbinia sp.	8	1,5	2,40
Platynereis sp.	6	3,0	0,36
Eunice spp.	12	1	9,10
Other nereids	14	1	6,65
Other polychaetes	4	1	0,05
Carcinus maenas	2	1	3,27
Cyclograpsus sp.	2	1	4,37
Zygonemertes sp.	2	1	0,10
Nematoda	10	1,8	0,17
Chiton tulipa	2	1	–
Ischnochiton sp.	4	1	0,17
Cladophora sp.	2	–	1,14
Enteromorpha sp.	16	–	5,10
Ulva sp.	6	–	1,09
Ectocarpus sp.	8	–	4,33
Other algae	4	–	1,65

capensis and *Patella* spp., isopods *Paridotea ungulata* and *Exosphaeroma* spp. and nereid polychaetes were the most frequently eaten taxa, in terms of numbers and percentage occurrence (Table III). Most of these groups were, however, less prominent in terms of percentage volume (Table III). Only *Patella*, *Paridotea* and a variety of polychaetes constituted large proportions of gut volume. Cannibalism and predation on another crab, *Cyclograpsus punctatus*, were also recorded.

Paridotea ungulata is a large (25 mm long), slow-moving isopod of variable colour (green to brown), found in close association with the green alga *Ulva capensis* (Day 1974). *C. maenas*, which also apparently associates with *U. capensis*, would find the isopod readily available and easy to catch and consume.

The polychaetes consumed by *C. maenas* were largely errant forms which often frequent mussel beds. It is possible that they are caught while the crab forages over mussels. Mussels were, surprisingly, absent from the gut contents of all the crabs analysed. Many

Table II: A list of the South African intertidal animals known to be consumed by the European shore crab *C. maenas*

Gastropoda
Oxystele sinensis
Oxystele variegata
Oxystele tigrina
Turbo sarmaticus
Burnupena cincta
Tricholia capensis
Aetoniella sp.
Patella sp.
Helcion sp..
Crepidula sp
Fissurella mutablis
Pelecypoda
Lasaea adansoni
Gregariella sp.
Choromytilus meridionalis
Aulacomya ater
Amphineura
Chiton tulipa
Ischnochiton textilis
Isopoda
Paridotea ungulata
Exosphaeroma spp.
Cirolana sp.
Polychaeta
Nereis spp.
Platynereis dumerilii
Marphysa sp.
Orbinia sp.
Eunice sp.
Cirripedia
Notomegabalanus algicola
Brachyura
Cyclograpsus punctatus
Hymenosoma orbiculare
Nemertea
Zygonemertes sp.
Algae
Cladophora capensis
Enteromorpha sp.
Ulva capensis
Ectocarpus sp.

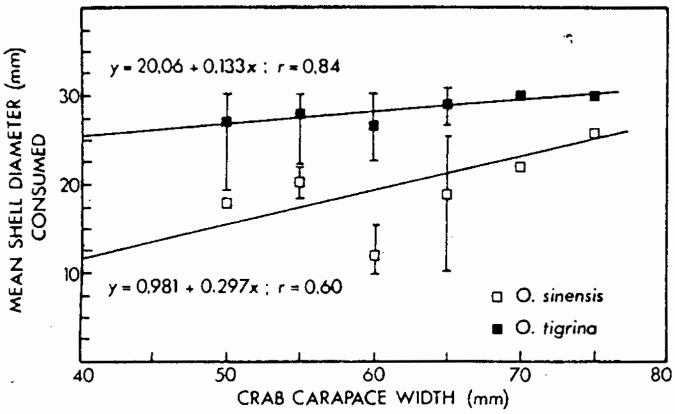


Fig. 4: The mean shell diameter (mm) of *Oxystele tigrina* and *Oxystele sinensis* consumed by *C. maenas* of increasing size. Error bars indicate ranges of data for individual crabs of a given size class

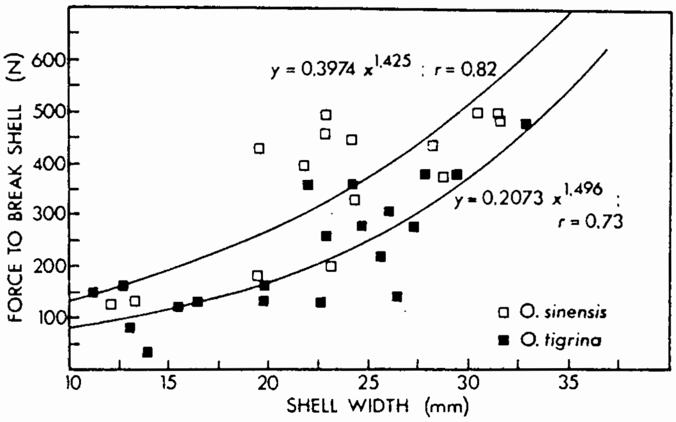


Fig. 5: The force required to break the shells of *Oxystele sinensis* and *O. tigrina*

of the large crabs (> 60 mm), which might have been expected to consume mussels, had empty cardiac stomachs.

Algae found in the gut were usually present in small quantities, possibly accidentally ingested. However, two crabs had guts filled with algae, and Ropes (1968) records *C. maenas* as eating algae.

Predation experiments

In the first set of predation experiments, in which individual crabs covering a size range of 50–75 mm were given a full size range of individual prey species, *Notomegabalanus algicola* of all sizes (5–10 mm) were crushed and eaten within 24 h. Similarly, all sizes of *Oxystele variegata* (10–22 mm) were eaten within 48 h, and *O. tigrina* of all sizes (10–30 mm) were eaten within four days.

No preference for prey of a particular size was exhibited by crabs preying on these three species. In the case of *O. sinensis*, however, the success rate of the crabs was related to crab size (Fig. 4), larger *O. sinensis* being immune to attack by smaller crabs, despite the fact that *O. tigrina* of comparable size were readily eaten. Results of the point-compressive load experiments show that *O. sinensis* has a stronger shell than *O. tigrina* (Fig. 5). Analysis of covariance between the regressions of shell strength on shell size showed a significant difference ($F = 15{,}97$; $df = 1{,}34$; $p < 0{,}001$).

Less extensive observations made on *Aulacomya ater* and *Choromytilus meridionalis* indicate that large mussels (>45 mm and >55 mm respectively) are invulnerable to attack from even the largest crabs and that, below this size, the critical size of prey is related to crab size. More detailed observations of predation on these mussels will be published separately.

Turbo sarmaticus of up to 40 mm were consumed by the largest crabs. *T. sarmaticus* commonly achieves a size of 120 mm and it is therefore likely that larger individuals will be too large for the crabs to handle. No *Parechinus angulosus* were eaten even when the crabs were starving and had no alternative food. When the same crabs were subsequently offered *O. variegata* they immediately consumed them, supporting the suggestion that *P. angulosus* is actively rejected. *C. maenas* used three handling techniques to consume *Oxystele* spp. and *Turbo sarmaticus*. Shells were either crushed as a whole (*O. variegata, O. tigrina*), crushed at the apex (*O. sinensis*) or broken slowly from the lip inwards (*T. sarmaticus*). All three techniques have been previously recorded for *C. maenas* (Sanchez-Salazar *et al.* 1987).

DISCUSSION

Establishment

Considering its effective establishment and rapid spread along the American and Australian coast, it is curious that *Carcinus maenas* has not been recorded in South Africa before. Its introduction was possibly brought about by "passenger" crab colonies, established on the feet of semi-submersible exploratory drilling vessels which have called at South African ports since 1969. Benech (1978) found that a community of *Plagusia dentipes*, endemic to Japan, had established itself on such a vessel in Los Angeles harbour. Ballast water can also be a mode of transport for marine organisms (Carlton 1985). If either of these were the means of transport to South Africa, then it is highly likely that *C. maenas* has established populations in other ports along the South African coast.

The subsequent discovery of *C. maenas* at a variety of sites along the Cape coast and the fact that the Bloubergstrand and Green Point populations are now maturing, indicates that the crab is spreading from its first site of introduction, Table Bay Docks, and is establishing itself within South African intertidal and nearshore waters. Females in berry are common in Table Bay and have been found at sites along the open coast as well. This fact, coupled with the existence of juveniles in all populations, leaves no doubt that *C. maenas* is successfully reproducing. One interesting feature is that the crab appears to be reproducing between July and November, as they do in Europe, despite the seasonal differences between northern and southern hemispheres.

At present, *C. maenas* appears to be limited to wave-protected habitats such as docks or large pools, Kitching *et al.* (1959) and Crothers (1968) have shown that strong wave action limits *C. maenas* predation and, as a result, its local abundance. The existence of many sheltered waterways along the eastern seaboard of America may explain why the crab has spread so rapidly and become such a serious pest to the shellfish industry along that coast (Hanks 1961). By contrast, the exposed wave-beaten nature of most of the coast of South Africa may inhibit the spread of the species and restrict its impact on local biota.

Diet

From laboratory experiments and analyses of gut contents it seems that *C. maenas* eats a wide variety of prey. In the field, the large majority of prey consisted of relatively small gastropods, polychaetes and isopods, but in the laboratory even shells of *Turbo sarmaticus* of up to 40 mm were broken. Only the urchin *Parechinus angulosus* was actively rejected. A preponderance of gastropods in the diet was also noted by Ropes (1968). High consumption of isopods, not recorded by Ropes (op. cit.), is a reflection of high local availability of the slow-moving isopod *Paridotea ungulata* in the lagoon at Bloubergstrand.

Many of the larger crabs examined during this study had empty cardiac stomachs. Very few crabs of any size contained bivalve remains. It is possible that the smaller crabs, although foraging over the mussel beds, were eating other more readily available prey, such as *Paridotea ungulata*, while the larger animals were eating the bivalves. Larger crabs fracture the shells of the bivalves and remove the flesh and a few shell chips. This may explain the preponderance of empty cardiac stomachs among larger crabs.

Possible impact of *C. maenas* in South Africa

Notomegabalanus algicola, *Oxystele variegata* and *O. tigrina* of all sizes appear to be highly vulnerable to predation by *C. maenas*. The vulnerability of *O. sinensis* with shell widths >18 mm increases with crab size. All three species of *Oxystele* tend to migrate up the shore with increasing size (McQuaid 1982), the largest individuals occurring in the balanoid and lower littoral zones. These gastropods therefore have no refuge in size or zonation from *C. maenas*, because the largest crabs forage at the highest tidal levels (Naylor 1962). In comparison to *O. tigrina*, large *O. sinensis* may be relatively safe from attack by virtue of their stronger shells. Both *Aulacomya ater* and *Choromytilus meridionalis* and, almost certainly, *Turbo sarmaticus* can attain sizes which render them invulnerable to attack by *C. maenas*. This does not mean that these species will be unaffected by *C. maenas*. Attacks directed at spat or juveniles may strongly influence the size structure and abundance of the populations. Jensen and Jensen (1985) have previously shown that predation of spat by *C. maenas* can even prevent the establishment of bivalve populations.

It is possible that there will be a persistent selection against weaker-shelled animals in areas where crab density and subsequently crab predation is high. Such selection has been demonstrated by Vermeij (1976), Elner and Hughes (1978) and Dudley (1980). Selection may occur for alarm behaviour, such as that exhibited by *Littorina littorea* (Hadlock 1980) in response to predation by *C. maenas*. Local reductions in gastropod populations may also occur.

It is difficult to predict whether *C. maenas* will be able to establish itself in sufficiently large numbers to pose a threat to the South African intertidal molluscan fauna. Its range in Australia is limited to a small section of coastline (Zeidler 1978), and no reports of serious effects to the intertidal fauna of that area could be found. Its establishment and spread on the American west coast was slow, but on the American east coast its effect on the soft shell clam *Mya arenaria* was so serious as to provoke drastic control measures (Hanks 1961).

Assuming that this crab does manage to establish itself in the South African rocky intertidal, it is predicted that it could have a destabilizing influence on existing intertidal community structure. Predation by *C. maenas* could cause local extinctions and alter selection pressures within certain species. Careful monitoring of the extent of *C. maenas* establishment and dispersal will be necessary if its effects on South African intertidal community structure are to be ascertained. There is clear evidence that the crab is well established and spreading.

However, it is predicted that its impact is likely to be most intense in sheltered areas such as lagoons, bays, estuaries and harbours. Indeed, since this prediction was made, *C. maenas* has been recorded in Saldanha Bay.

ACKNOWLEDGEMENTS

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CHAPTER 3

PREDATOR-PREY INTERACTIONS BETWEEN THE EUROPEAN SHORE CRAB *CARCINUS MAENAS* (L.) AND THREE SOUTH AFRICAN MUSSELS.

P.J. LE ROUX and G.M. BRANCH**

*Marine Biology Research Institute, Department of Zoology, University of Cape Town, Rondebosch, 7700, S. Africa

ABSTRACT

Predator prey interactions between the introduced European shore crab *Carcinus maenas* (L.) and three abundant South African mussels were investigated. Two of the mussels, *Choromytilus meridionalis* (Kr.) and *Aulacomya ater* (Molina) are indigenous and the third, *Mytilus galloprovincialis* (Lmk.) a Mediterranean invasive alien to Southern Africa. Experiments were designed to test certain aspects of optimal foraging theory and the effect of ribbing on the shells of prey on *C. maenas* predation. The time needed to open and consume mussels increased with increasing mussel size but decreased with increasing crab size. The preferred size of prey was smaller than the critical size in all cases. The crabs selected mussels of slightly less than the calculated optimal size in preference to other size classes. Novelty provided the mussels with no protection from *C. maenas* predation. Shell strength only provided *Aulacomya ater* with a refuge from *C. maenas* predation at larger prey lengths. Total handling times for *M. galloprovincialis*, *A. ater* and *C. meridionalis* did not differ appreciably. The crabs preferred *M. galloprovincialis* to *A. ater* in selection experiments. Total handling time and prey value are both determined by eating time. It is predicted that predation by *C. maenas* will have a pronounced effect on South African mussel populations, and particularly those of *C. meridionalis*. All mussels have refuges in size and space. Commercial mussel culture operations are threatened.

INTRODUCTION

The recent introduction of the carnivorous European shore-crab, *Carcinus maenas* (L.) to South Africa is a cause for concern (Joska and Branch 1986). A detailed discussion of its diet, distribution and spread along the South African coast is presented in Le Roux, Branch and Joska (1990). *C. maenas* frequently consumes bivalve molluscs and gastropods, often causing changes in the abundance, size distribution or morphology of these organisms (Hanks 1961, Ebling *et al.* 1964, Muntz *et al.* 1965, Ropes 1968, Hughes and Elner 1979, Dudley 1980 and Sanchez-Salazar *et al.* 1987 a,b). It may even prevent the effective recruitment and establishment of bivalve spat (Jensen and Jensen 1985) in the same way as rock lobsters (Branch *et al.* 1987). *C. maenas* has become a serious pest to commercial bivalve culture operations on the New England coastline (Hanks 1961) and may pose a similar threat to the culture industry in South Africa.

The west coast of South Africa supports three dominant intertidal mussels (Field *et al.* 1980 , van Erkom Schurink and Griffiths 1990). Two of these *Choromytilus meridionalis* and *Aulacomya ater,* are indigenous while the third is a recent invasive, *Mytilus galloprovincialis*. The invasion and spread of *M. galloprovincialis* has been well documented (Grant, Lombard and Cherry 1984, Grant and Cherry 1985 and Hockey and van Erkom Schurink in press).

The three mussels differ in a number of ways which may influence their susceptibility to predation by *C. maenas*. *C. meridionalis* and *M. galloprovincialis* have comparatively thin, smooth shells, whereas *A. ater* has a stronger, thicker, and ribbed shell. Its byssal attachment is also stronger than that of *C. meridionalis* (Griffiths and Seiderer 1980) and it has a slower growth and population turnover (King 1979, Griffiths 1981). Our knowledge of the relative rates and predictability of recruitment of the three species is still incomplete, but successful large scale recruitment of *C. meridionalis* is an irregular occurrence (Griffiths 1981) so that it has a patchy distribution. Maximum sizes of the mussels also differ. *A. ater* reaches a length of 95 mm in Southern Africa whereas *C. meridionalis* and *M. galloprovincialis* are larger, reaching 150 mm and 140 mm respectively (van Erkom Schurink and Griffiths 1990).

Pyke, Pulliam and Charnov (1977) and Hughes (1980) suggest that predators forage in ways which either reduce the time spent acquiring a fixed, daily energy ration (time minimisers), or increase the amount of energy gained per unit time (energy maximisers). So, for example, *C. maenas* (an energy maximiser) selects medium sized *Mytilus edulis* (L.) in preference to all other size classes (Elner and Hughes 1978).

Jubb, Hughes and ap Rheinallt (1983) proposed two alternative mechanisms to explain observed energy maximisation in *C. maenas.* The first, based on a passive interaction between chelal strength and dexterity and mussel size and shell strength, was termed the “prey evaluation hypothesis”. Small mussels have a low flesh content and are therefore unprofitable. The crabs reject them because they are unable to effectively grasp and manipulate them. Although larger mussels yield more flesh, variability in shell strength and therefore breaking time makes them potentially unprofitable. Larger mussels are rejected on the basis of increased shell strength.The second mechanism, based on the relative strengths of stimuli received from mussels held in the chelae and those touching the pereiopods, was termed the “relative stimulus hypothesis”. The strength of pereiopod and chelal stimuli is a function of the area of contact, which increases with increasing mussel size. Equivalence of pereiopod and chelal stimuli is a function of hunger level. The chelal stimulus will override that of the pereiopod if the animal is starved, forcing the animal to persist with the first mussel grasped. With a decrease in the hunger level crabs will reject a mussel already held in the chela if the pereiopods touch a more suitable prey item. If a mussel held in the chela begins to break then all other stimuli will be overriden.

The present laboratory based study investigates the interactions between *C. maenas* and the mussels *Aulacomya ater, Mytilus galloprovincialis* and *Choromytilus meridionalis*. The experiments were designed primarily to test the following aspects of optimal foraging theory as proposed by Elner and Hughes (1978), Hughes (1980) and Judd, Hughes and ap Rheinallt (1983).

1 - The basic premise that the selection of prey species and the individual prey items consumed maximises net energy intake.
2 - That *C. maenas* selects prey actively rather than by passive mechanical means.

In addition the recent introduction of *C. maenas* to South Africa implies that both *A. ater* and *C. meridionalis* are novel prey for the crab. This presents an opportunity to test whether *C. maenas* continues to forage optimally when presented with novel prey species. The possible effects of *C. maenas* on local mussels is reviewed in the light of the differences between them, and the possibility that shell ribbing protects *A. ater* against *C. maenas* is specifically examined.

MATERIALS and METHODS

Collection sites

Crabs were collected between March and May of 1988 from a small lagoon adjacent to a long, sandy beach, approximately 400 metres south of Bokkombaai at Blouberg strand in the Cape (Figure 1). The lagoon is essentially a large sheltered rock pool about 50 metres wide. It is protected from wave action by a series of rock reefs. No crabs were caught on the exposed side of the rock reef.

Mussels were collected from rock pools adjacent to the lagoon, although smaller specimens of *Choromytilus meridionalis* were collected from sites adjacent to Clovelly station (Figure 1).

Crabs were separated into size classes on the basis of carapace width (*ie.* the distance between the most distal marginal teeth) and mussels on the basis of shell length. The crabs were transferred to aquaria (46 cm by 32 cm) and supplied with sand from the study site to a depth of approximately 5 cm. Each tank was covered with shade cloth (55 % shade) in order to prevent escape and held two crabs separated by perspex mesh. The aquaria were linked to a closed circuit circulating seawater system maintained at 15 °C. Female crabs were excluded from the experiment, to eliminate the effects of sexual differences evident in chela morphology and predatory behaviour .

Critical size

The "critical sizes" of *A. ater*, *C. meridionalis* and *M. galloprovincialis* above which they were to large to be eaten were determined for crabs with

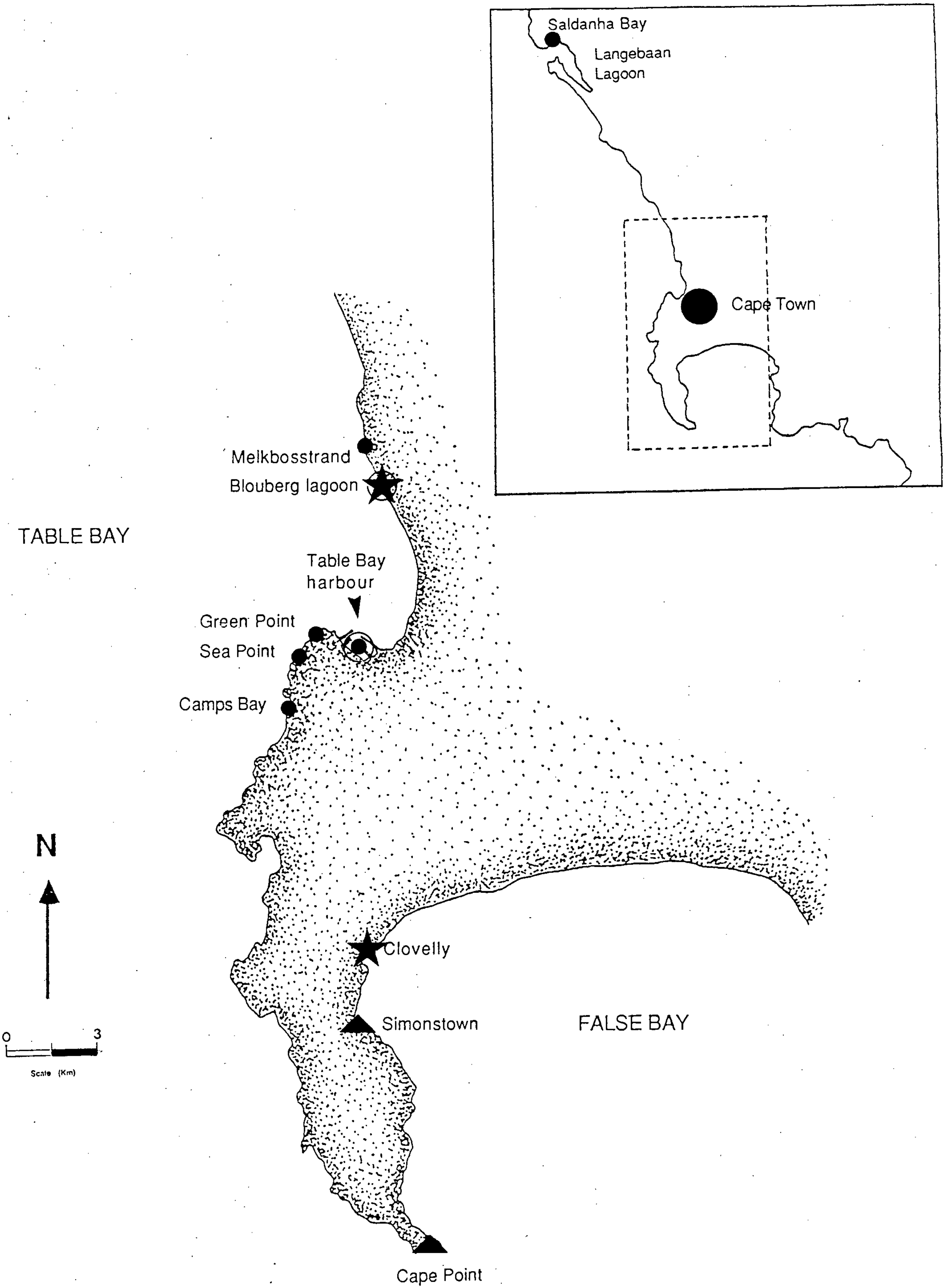


Figure 1. A map showing the sites at which the crab C. maenas (●) is known to occur [Saldanha Bay to Camps Bay] and, the sites from which crabs (○) and mussels (★) used in this study were collected.

carapace widths ranging from 30 to 75 mm. Each crab was offered mussels of increasing size. Once a size class of mussel remained uneaten for a period of > 36 hours, the largest mussel eaten prior to this period was taken to be the critical size.

Size selection and handling time

A selection of mussels of all size classes up to and including the critical size, were fed to crabs with carapace widths (CW) ranging from 30 to 75 mm. The crabs were starved for 48 hours prior to the experiment. The numbers and sizes of mussels eaten per day, were recorded for each size class of crab. As the mussels were eaten they were replaced with mussels of the same size class, and shell debris was removed.

Crabs were observed for two hours directly after food was supplied and handling times were measured. Total handling time (Th) consisted of the sum of two components: (1) Breaking time (Tb) - the time from first contact with the prey item to the first bite of exposed flesh; (2) Eating time (Te) - the period of time from the end of Tb to the final abandonment of the shell (Sanchez-Salazar *et al.* 1987a). The size class of mussel most frequently consumed by each size class of crab was considered to be the preferred size class.

Prey value

Energy content (E) was calculated for each of the size classes of *A. ater*, *C. meridionalis* and *M. galloprovincialis* using size to weight regression curves and calorific values derived from Griffiths and King (1979) and Griffiths and van Erkom Schurink (unpubl. data). The regressions are given below. The calorific values appear in brackets next to each regression.

A. ater - $y = 0.0000013 * x^{(3.276)}$; (20.85 $KJ.g^{-1}$) 1

M. galloprovincialis - $y = 0.0000017 * x^{(3.297)}$; (20.375 $KJ.g^{-1}$) 2

where x = shell length (mm) and y = dry flesh mass (g).

Prey value was calculated using the following three formulae: E/Tb, E/Te and E/Th (Elner and Hughes 1978). In cases where regression equations are not given, curves were fitted by eye, after Sanchez-Salazar *et al.* (1987a).

Selection between mussel species

Crabs of carapace widths between 60 and 80 mm were used to test whether *C. maenas* selected the optimal prey species. Each crab was offered a full size range of *A. ater* and *M. galloprovincialis*. Numbers eaten, size classes and prey species chosen were recorded on a daily basis. Handling times were also measured.

RESULTS

Handling techniques

The methods used by *C. maenas* to break the shells of *A. ater*, *M. galloprovincialis* and *C. meridionalis* did not vary appreciably and were very similar to those used to open the cockle, *Cerastoderme edule* on Welsh tidal flats (Sanchez-Salazar *et al.* 1987a). Only the smallest mussels could be crushed with one application of force, all others requiring some degree of manipulation to find weak spots. Shells were often broken across the valves near the middle of the shell after which they could be crushed (Figure 2.).

As mussel size approached the previously determined critical size for the size class of crab under examination, the crabs relied more on valve chipping or prising techniques to open their prey. Although unquantified, there was clear evidence that the crabs spent less time manipulating and rejecting a mussel if they had already handled and rejected it.

Critical size versus preferred size

Figure 3 shows the rate at which crabs of different size classes preyed on mussels of various sizes. All crabs tended to avoid small mussels, although the smallest *C. maenas* (30-40 mm) were able to consume the small mussels (< 17 mm) only eating small numbers of even these. Thus the suggestion that *C. maenas* prefers bivalves of intermediate size (Elner and Hughes 1978 and Sanchez-Salazar *et al.* 1987a) is once again confirmed. There was a progressive increase in the preferred size of mussels with an increase in the size of the crabs.

Critical sizes also increased with increasing crab size (Figure 4 a,b). There were clear differences between the critical sizes for the three mussels, *A. ater* having the smallest and *C. meridionalis* the largest critical sizes. The preferred sizes were lower than the critical sizes in all cases and did not differ appreciably between species.

Table 1 shows that as crabs grow larger the absolute number of mussels consumed and the energy intake per day increase. Very large crabs (70-80 mm) are the exception eating fewer mussels than would be expected, but

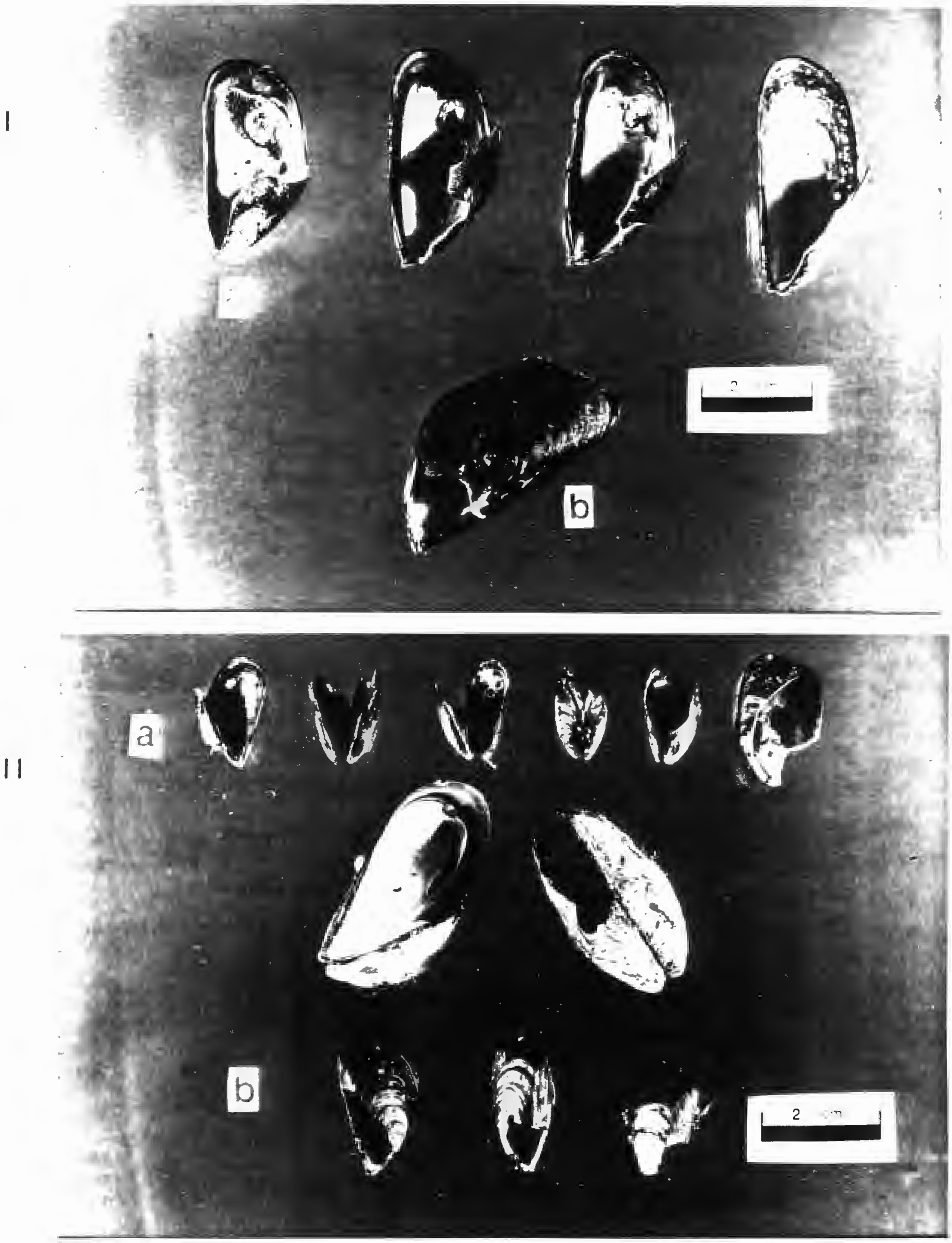


Figure 2. Photographs illustrating the various methods used by C. maenas to open bivalves. I - Choromytilus meridionalis and II - Mytilus galloprovincialis. Mussels were either broken across the valves (a) , or in the region of the umbone (b).

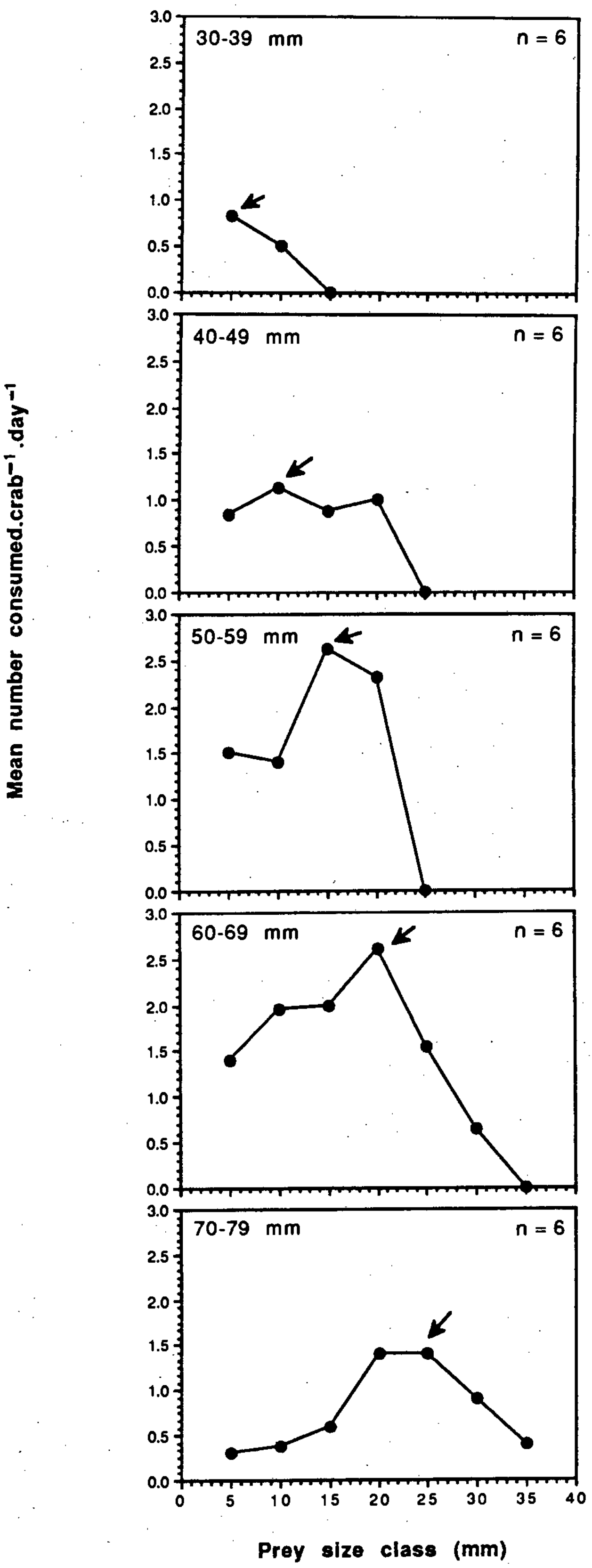


Figure 3. Mean number of Aulacomya ater of each size class (mm) consumed per day by Carcinus maenas of increasing carapace width (mm). Arrows indicate preferred size (mm).

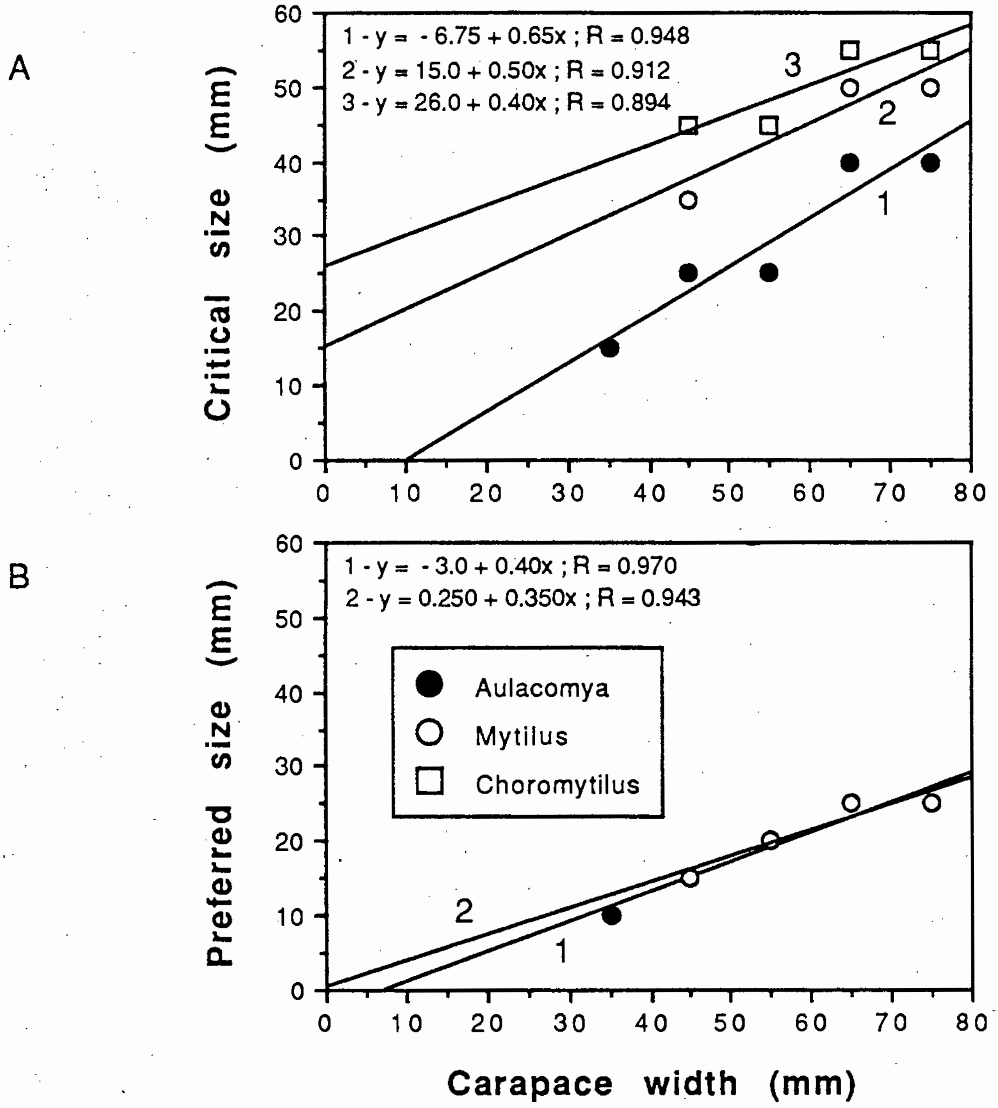


Figure 4. A comparison of, A - critical sizes for *Aulacomya ater*, *Mytilus galloprovincialis* and *Choromytilus meridionalis*, and, B - preferred sizes for *A. ater* and *M. galloprovincialis*. Regression equations are as indicated.

Table I. Maximum number of mussels Aulacomya ater consumed per day and total energy intake (J.day^{-1}) for C. maenas of increasing size (mm).

SIZE CLASS OF CRAB (MM)	MEAN TOTAL NUMBER CONSUMED	STANDARD DEVIATION	TOTAL ENERGY INTAKE. CRAB^{-1}.DAY^{-1} (J)
30-40	1.41	1.72	78.3
40-50	3.63	3.40	1342.9
50-60	7.86	2.40	3167.2
60-70	10.13	2.64	7702.7
70-80	5.50	2.80	8345.2

Table II. The mean number of mussels consumed by two size classes of crab during selection experiments (+ S.E.).

CRAB SIZE CLASS (MM)	SPECIES EATEN	MEAN NUMBER EATEN PER DAY	
60-70	Aulacomya ater	4.3	(3.0)
	Mytilus sp.	6.5	(2.7)
70-80	Aulacomya ater	3.2	(1.9)
	Mytilus sp.	5.0	(1.9)

because they are feeding on larger mussels their energy intake remains higher than for any other size class examined. Total energy intake was linearly related to crab size ($r = 0.76$).

Handling times

Breaking times, eating times and total handling times for three size classes of *C. maenas* are compared in Figure 5 a,b and c. The crabs were only offered *A. ater* during these experiments. Linear relationships were found to exist between breaking time (Tb) and prey size (mm) in all cases. Exponential curves could, however, be fitted to the eating and total handling times. Correlations were, in all cases, highly significant, despite the fact that differences in crab hunger level, strength, chelal morphology and degree of learning, as well as variations in prey fracture resistance could have contributed to variability in handling times.

Large crabs ignored smaller mussels (see Figure 5a) which appeared to be difficult for them to handle with their large chela and would as a result have been unprofitable. Large crabs have higher metabolic requirements, will not be satiated easily and are strong. As a result, their breaking, eating and absolute handling times for larger mussels are shorter than those of smaller crab size classes. At smaller prey lengths, ribbed mussels were manipulated for shorter periods of time than the smoother black mussels. The smooth shells of *Mytilus galloprovincialis* and *Choromytilus meridionalis* apparently made it more difficult for the crabs to hold the mussels steady. Note how small crabs are, however, best at handling small mussels.

Selection between prey species

When simultaneously offered the choice, *C. maenas* clearly preferred *M. galloprovincialis* to *A. ater* (Table II). This pattern was most obvious at medium to large prey lengths, disappearing at smaller prey lengths (Figure 6). Possibly differences between the shell morphology of the two species are so slight in small mussels that handling time is the same for both species.

Comparisons drawn between breaking times, eating times and total handling times for both *A. ater* and *M. galloprovincialis* for one size class of crab (60-70 mm) are presented in Figure 7. At least over the larger size classes, *M. galloprovincialis* takes longer to break than *A. ater*. This comes as a suprise, in view of the fact that *Aulacomya ater* has a stronger shell than *Choromytilus meridionalis* . Evidently *A. ater* is easier to manipulate and position correctly so that it is more readily crushed. Eating times were almost identical for the two mussels and were much longer than breaking times. As a result of this, total handling times for *A. ater* were approximately the same as those for *M. galloprovincialis* (Figure 7).

Energy intake and prey value

The theoretical energy intake per unit time derived by feeding on *Aulacomya ater* of various sizes was calculated for *C. maenas* of two size classes [60-70 mm and 70-80 mm (Figure 8)]. Optimal yields appear to be obtained from mussels of 25-30 mm and 30-35 mm respectively - values which coincide closely with the sizes of mussels preferred by *C. maenas* (20-25 mm and 25-30 mm) of equivalent sizes when they had free choice (Figure 3). The decrease in the optimal size for 70-80 mm crabs may be a result of experimental error.

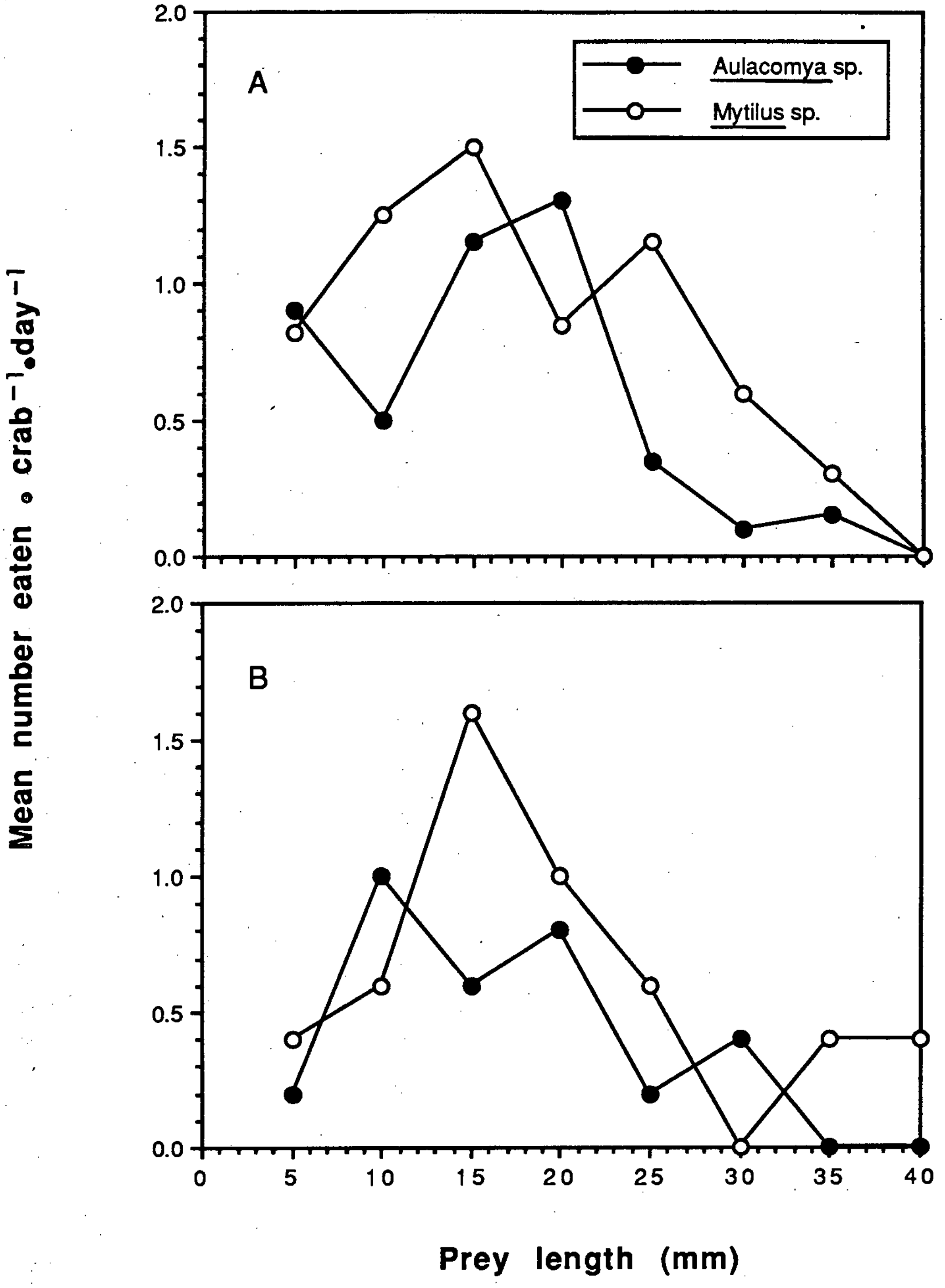
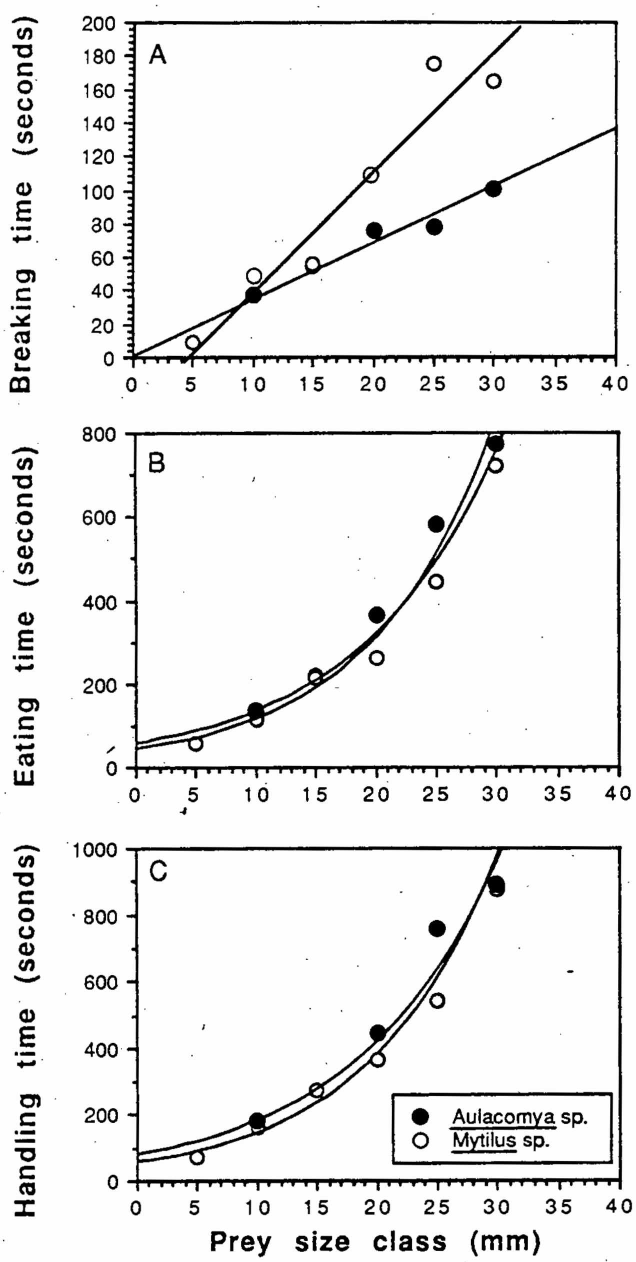


Figure 6. Mean numbers of Aulacomya ater and Mytilus galloprovincialis eaten per day by C. maenas.(A) 60-70 mm and, (B) 70-80 mm carapace width. Crabs were provided with equal numbers of both species of bivalve simultaneously.



	REGRESSION EQUATIONS
A	(●) $y = -0.0867 + 3.4123$; R = 0.980 (○) $y = -30.260 + 7.0460$; R = 0.942
B	(●) $y = 45.58 * 10^{(0.043x)}$; R = 0.988 (○) $y = 56.30 * 10^{(0.038x)}$; R = 0.980
C	(●) $y = 55.58 * 10^{(0.042)}$; R = 0.980 (○) $y = 78.83 * 10^{(0.036)}$; R = 0.984

Figure 7. A comparison of, breaking time (Tb), eating time (Te) and, total handling time (Th=Tb+Te) for C. maenas (60-70 mm carapace width) feeding on Aulacomya ater and Mytilus galloprovincialis.

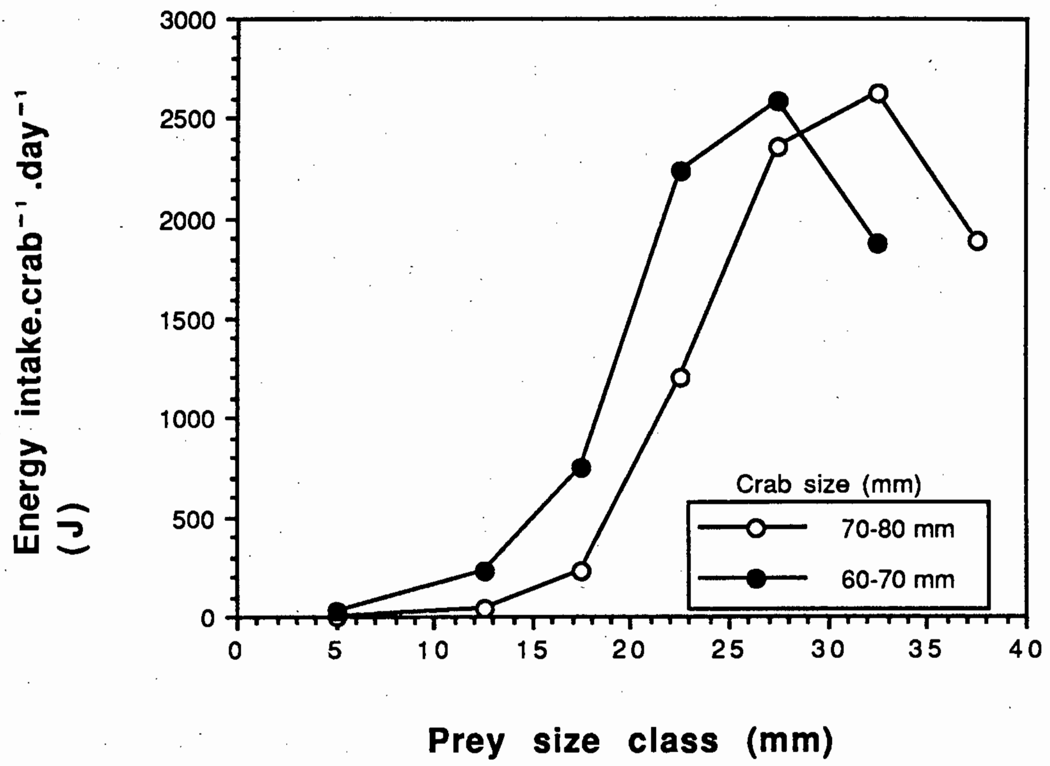


Figure 8. A plot of energy intake (J.day^{-1}) versus prey size class (mm) for two size classes of C. maenas feeding on Aulacomya ater.

Prey value curves for *A. ater* of increasing size preyed on by *C. maenas* of increasing size are presented in Figure 9. The theoretical optimal prey size increases with increasing crab size. For large crabs (70-80 mm) it decreases. The individual prey items, however, yield more energy per unit time than do prey of equivalent length preyed on by smaller crabs. Larger crabs obtain more energy per unit time than smaller ones, since they have shorter handling times. This is a function of shorter handling times for large crabs. The decrease in optimal size for 70-80 mm crabs may be a result of experimental error.

Comparisons of prey values for *A. ater* and *M. galloprovincialis* of increasing size - with respect to breaking, eating and total handling time - are presented in Figure 10 a,b and c. In terms of breaking time, prey value ($J.sec^{-1}$) increased exponentially with prey size for both species of mussel (Figure 10a). The value of *A. ater* was greater than that of *M. galloprovincialis* even although its flesh mass is lower (for any given shell length) because its breaking time is shorter (Figure 7a). When eating times and total handling times are considered, parabolic relationships exist between prey value and size (Figure 10 b,c). Overall prey values are largely dictated by eating time. Eating time increases exponentially with shell size (Figure 5b) at a faster rate than flesh mass (derived from equations 1 and 2). Consequently the yield per unit time follows a parabolic curve, declining in large mussels because the greater flesh mass obtainable from them is more than offset by the longer handling time involved. Total handling time is affected primarily by eating time and consequently follows a similar parabolic curve (Figure 10c).

The data reveal clear optimal prey lengths at which energy intake per unit time is maximised. In *M. galloprovincialis* the optimal size (c. 40 mm) is

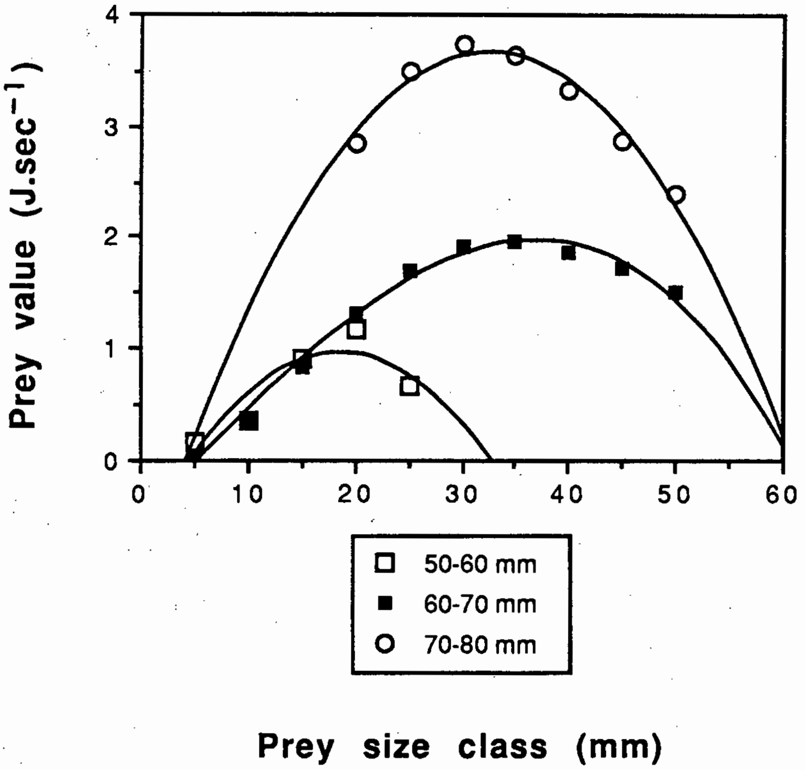


Figure 9. Prey value (J.sec^{-1}) plotted against prey size class (mm) for A. ater consumed by C. maenas of increasing size (mm) expressed with respect to total handling time (seconds).

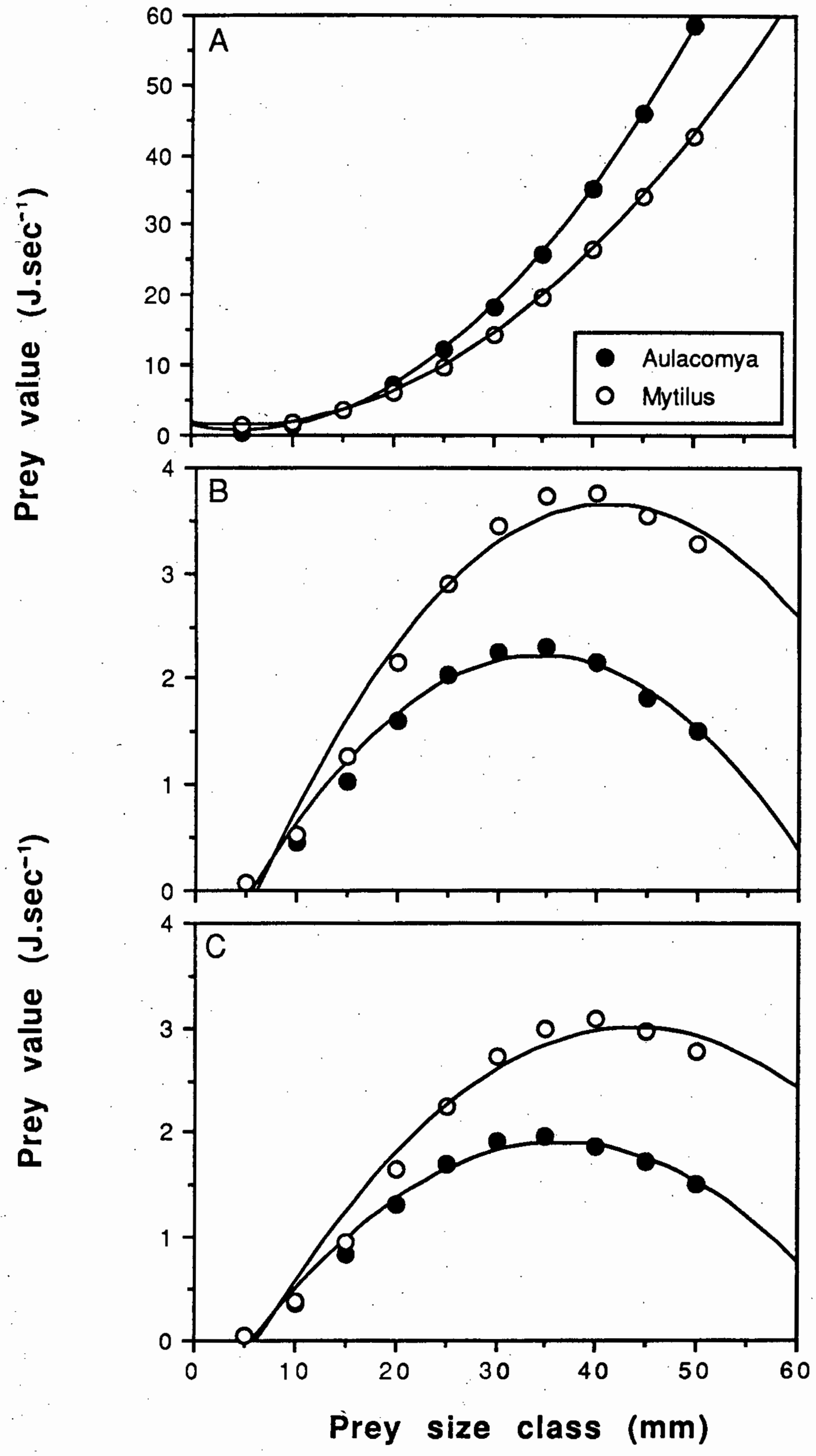


Figure 10. Prey value (J.sec^{-1}) plotted against prey size class (mm) for A. ater and M. galloprovincialis consumed by C. maenas (60-70 mm CW) expressed with respect to (A) breaking time, (B) eating time and (C) total handling time.

larger than that of *A. ater* (c. 35 mm). Over the size range 5 to 50 mm it is more profitable for *C. maenas* to consume *M. galloprovincialis* than *A. ater.*

DISCUSSION

The optimal diet model (ODM) is simplistic and makes assumptions which reduce it's overall value (see Hughes 1980 p. 441). These include the assumptions that energy yield is in fact the currency by which an animal evaluates prey, that hunger plays no role in prey selection, and the exclusion of predation and interference as valid modifiers of the selection process. The model has nevertheless provided us with a useful tool to begin to quantify and understand animal foraging technique.

The ODM predicts that organisms will select prey species and individual prey items so as to maximise their net rate of energy intake, or reduce the time spent foraging (Charnov 1976, Hughes 1980). This selection will involve a finite recognition time and may be active (using some form of analogue of the prey value curve) or passive (based on the mechanical limitations of the predator). Whichever "strategy" is adopted should also minimise the time an animal spends exposed to predators and maximise the time spent in other survivial functions such as, growth, territorial defence, courtship and reproduction (Hughes 1980). This study tests whether *C. maenas* does select the optimal prey species, the optimal prey size and whether or not the process is active or passive.

Size selection and handling time

Larger crabs ate higher numbers of prey than small crabs (Table I), opened larger individuals and took less time to do so (Figure 3 and 5). Preferred sizes were in all cases smaller than the critical sizes. Prey handling times and energy yields for *Aulacomya ater* and *Mytilus galloprovincialis* were similar to those recorded for *C. maenas* preying on *Mytilus edulis* (Elner and Hughes 1978) and *Cerastoderma edule* (Sanchez-Salazar *et al.* 1987a).

Handling times presented in this study are best described by exponential functions as are those presented for *C. maenas* preying on *Mytilus edulis* and *Thias lapillus* (Elner and Hughes 1978, Hughes and Elner 1979) and for *Cancer pagurus* feeding on *Littorina littorea* and *Nucella lapillus* (Lawton and Hughes 1985). Data presented by Hughes and Seed (1981) for the North American blue crab, *Callinectes sapidus*, feeding on the ribbed mussel *Geukensia demissa* (Dillwyn) also reveal an exponential trend.

Comparison of prey value (E/Th, Figure 9, 10c) and size selection data for standard size *C. maenas* of 60-70 mm consuming *A. ater* (Figure 3) suggests that *C. maenas* selects prey slightly smaller than the optimal size. A number of studies have revealed a similar trend (Elner and Hughes 1978, Hill 1979, Elner 1980, Griffiths and Seiderer 1980, Hughes and Dunkin 1984, Lawton and Hughes 1985 and Sanchez-Salazar *et al.* 1987a). Several explanations have been advanced (Elner 1980, Hughes 1980, Hughes and Seed 1981, Hughes and Dunkin 1984 and Creswell and Mclay 1990). Amongst the most compelling, are the ideas that either food shortage, adverse environmental conditions or risks associated with feeding may force predators to feed on prey that is more rapidly accessible, but slightly less than optimal in energetic terms.

The parabolic prey value curves obtained for *A. ater* (Figure 9) are similar to those obtained for *C. maenas* feeding on *Mytilus edulis* and *Nucella lapillus* (Elner and Hughes 1978, Hughes and Elner 1979). *Callinectes sapidus* , however, was shown to exhibit a monotonically decreasing prey value curve when feeding on *Geukensia demissa* (Hughes and Seed 1981). This appears to contradict the results presented here. The difference can, however, be related to differences in chelal morphology. *C. sapidus* has thinner, more delicate chelae, allowing it to efficiently clean small mussels, thereby raising their prey value. The larger, blunt chelae of *C. maenas* prevent it from achieving the same success reducing the prey value of small mussels.

Species selection

These experiments revealed few significant differences between *C. maenas* foraging patterns on *M. galloprovincialis* and *A. ater.* Over the size range 5-50 mm, *Mytilus galloprovincialis* yeilded a higher energetic return per unit time than *A. ater* (Figure 10). When *C. maenas* was provided with a choice between the prey species, *M. galloprovincialis* was eaten more frequently than *A. ater* (Figure 6 and Table II). The crabs therefore do select the optimal prey species as well as the optimal prey size.

Total handling times for *A. ater* were slightly shorter than those for *M. galloprovincialis* (Figure 7), but the differences were not significant. Figure 7 shows that it is not so much the breaking time that determines total handling time but the eating time. In fact, *Aulacomya ater* individuals were broken slightly faster than *Mytilus galloprovincialis* individuals of the same size (Figure 7). This difference is probably because *C. maenas* can manipulate the ribbed shells of *A. ater* more easily. Ribbing may increase mechanical advantage due to increased traction. Once broken the thicker more robust valves of *A. ater* are difficult to tear apart and eating time is therefore increased. *Mytilus galloprovincialis* has a smoother shell, which appears more difficult to manipulate and break, increasing the breaking time. Once broken, however, the valves are easily torn apart and the flesh quickly consumed reducing the eating time.

Mechanisms of selection

It is difficult to draw a distinction between passive selection of prey based purely on mechanical factors (eg. chelal dexterity and prey size) and active selection (based on preferential choice) of optimally sized prey. The majority of case studies suggest that the predominant means of selection is passive, based on the mechanical limitations of the predator [see Hughes 1980 pp. 446-452]. Consistent increase in the optimal prey size with increasing crab size (Figure 9), and, the similarity between prey value and prey selection curves (Figure 10 and 3), suggest that *C. maenas* selects optimally sized *A. ater* and *M. galloprovincialis* by passive mechanical means. The rejection of very small mussels (c. < 15 mm) by large crabs (70-80 mm) occurred simply because the crabs were incapable of efficiently manipulating the prey items provided. Large mussels were rejected after successive applications of force failed to break the valves.

Novelty and refuges

Novelty appears to provide *A. ater* and *C. meridionalis* with no refuge from *C. maenas* predation. Novelty does not seem to impair the ability of *C. maenas* to optimally forage. Cunningham and Hughes (1983) have shown that handling times for naive *C. maenas* feeding on a novel prey species decline by as much as 70 percent after the crabs have been fed just six individuals of a novel species.

All three species of mussel have size refuges. *C. maenas* cannot consume *A. ater, M. galloprovincialis* and *C. meridionalis* larger than 40, 50 and 55 mm respectively. *A. ater* has the largest refuge in size. These differences are a function of shell strength and shell shape. A. ater has the strongest shell, the strongest byssal attachment and the most robust shape. Shell ribbing in *A. ater* increases the traction of crab chelae upon the valves allowing them to be broken quicker. Ribbing therefore does not provide the mussel with a refuge from *C. maenas* predation.

Spatial refuges also exist. *A. ater, M. galloprovincialis* and limited numbers of *C. meridionalis* are found in rocky, often wave washed subtidal environments. Such environments exclude *C. maenas* because of a well documented preference for sheltered water (Kitching *et al.* 1964, Muntz *et al.* 1965, Crothers 1968 and Le Roux *et al.* 1990). It is predicted that this spatial refuge, although not total will reduce the impact of *C. maenas* on mussels.

C. meridionalis prefers sandy substrata or the sand/rock interface, is adapted to handle the higher siltation rates associated with these areas (Barkai and Branch 1989). The mussel thrives subtidally and intertidally in sheltered areas (Hockey and van Erkom Schurink in press) similar to those preferred by *C. maenas.* The calorific value, handling times and prey value of *C. meridionalis* approximates those of *M. galloprovincialis* and *C. maenas* could open larger individuals. This, combined with a patchy distribution and recruitment and genotypic uniformity suggests than *C. meridionalis* may be the most severely affected by *C. maenas* invasion.

More work is required to effectively assess the overall impact of this invasive on the invertebrate fauna of the South African intertidal zone. The spread of *C. maenas* must be monitored and if possible contained. The planktonic nature of crab larvae and interoceanic transport of adults and larvae on semi-submersible vessels and in ballast water (Benech 1978, Carlton 1985) may make this task impossible. It is possible, however, to shield commercial mussel farms from the adults using chemical poisons without unduly damaging the attendant intertidal community (Hanks 1961). Relatively inexpensive and possibly labour-intensive hand removal programs could be used to keep *C. maenas* numbers down within the mussel culture dam.

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CHAPTER 4

FEEDING, ACTIVITY RHYTHM AND ZONATION OF ROCKY-SHORE CRABS ON THE CAPE PENINSULA

P.J. LE ROUX and C.L. GRIFFITHS

Marine Biology Research Institute, Department of Zoology, University of Cape Town, Rondebosch, 7700.

ABSTRACT

The zonation, habitat, diet, gut enzymology and activity rhythms of *Cyclograpsus punctatus*, *Plagusia chabrus* and *Carcinus maenas* are examined, to broaden our understanding of indigenous crab biology and assess what impact the invasive European shore-crab, *C. maenas*, will have on local species. Zonation and habitat were studied by intertidal and subtidal observation and shore transects. Seasonal gut content analyses at four sites and bioassay were used to study diet and enzymology. *C. punctatus* and *P. chabrus* activity rhythms were observed in the field. Simultaneous gut analysis tracked daily feeding cycles. Mechanical advantages of the chelae were also measured. *C. punctatus* is strictly intertidal, feeding on kelp wrack and selected intertidal molluscs. It has high levels of alginase, cellulase, laminarinase and amylase but very little azocasein and chitinase in the gut. It is active primarily at night on the low tide, and feeds twice a day, mainly at low tide. *P. chabrus* is subtidal occuring primarily on wave-washed shores. It is omnivorous with high levels of amylase, chitinase and azocasein, low levels of laminarinase and moderate levels of alginase and cellulase in the gut. It is active all through the day but mainly at dusk and dawn. It feeds at dusk. *C. maenas* is found in the mid to low intertidal and is restricted to sheltered water. It is carnivorous and has the "strongest" chela of all three species. It has moderate to high protease concentrations and low levels of alginase, cellulase and laminarinase in the gut. It is active, feeding day and night at high tide. There is very little overlap between the three species and *C. maenas* impact upon *C. punctatus* and *P. chabrus* is likely to be localised and minimal.

INTRODUCTION

Crabs have been the subject of numerous dietary, zonation and activity rhythm studies. Ropes (1968) showed that *C. maenas* was a generalist, feeding on a wide variety of organisms and altering its diet with temporal or spatial variation in prey availability. Hill (1979), showed that the large estuarine crab*Scylla serrata* consumed molluscs and grapsid crabs both in South Africa and in Australia. Du Preez (1981) proved that the three spot swimming crab *Ovalipes punctatus* was a carnivore feeding almost exclusively on sandy beach bivalves, *Donax* spp. and whelks, *Bullia* spp.. *Pachygrapsus transversus* was shown to consume algae and smaller amounts of coiled gastropods (Robles 1985), while the diets of *Liocarcinus puber* and *L. holsatus* were dominated by algae, bivalves and barnacles (Choy 1986). Wear and Haddon (1987), recorded that the New Zealand swimming crab, *Ovalipes catharus* consumed the commercially important bivalve *Paphies* sp. Depledge (1989) discovered that the grapsid *Gaetice depressus* was a suspension feeder while Vannini *et al.* (1990) noted that the East African crab, *Eriphia smithi* grazed on algae by day, consuming crustaceans and molluscs at night. The diets of four species of blue crab, *Callinectes* spp. were found to differ depending on species and size of the individual (Stoner and Buchanan 1990).

Zonation in crabs and its possible causes has been specifically examined by Warner (1977), Shumway (1983) and Pellegrino (1984). Zonation may be related to differing tolerances to salinity, temperature or dessication (Shumway 1983 and Pellegrino 1984). Activity pattern has been examined in *C. maenas* by Naylor (1962, 1982) who showed that the species has complex daily and tidal activity rhythms. Activity in the fiddler crab *Uca* spp. has also been studied and is reviewed by Palmer (1974). The activity pattern of *Scylla serrata* has also been studied (Hill 1979).

Cyclograpsus punctatus (Milne Edwards) and *Plagusia chabrus* (Linne') are grapsid shore crabs. *C. punctatus*, the ubiqiutous brown shore-crab is found on shores from Port Nolloth to Kosi Bay. *P. chabrus*, the red Cape rock-crab, is found from Luderitz to Port Shepstone (Barnard 1950, Day 1974, Branch and Branch 1981). They are the dominant rocky shore crabs on the Cape Peninsula.

Cyclograpsus punctatus has also been recorded from Chile and China (Broekhuysen 1941). Several authors (Broekhuysen 1941) are of the opinion that *Cyclograpsus caudouinii*, found on the shores of New Zealand, Australia and New Guinea is in fact *C. punctatus*, or at least a very close relative of it . *Plagusia chabrus* is also recorded from South-west and South-east Australia, New Zealand, Tonga and Juan Fernandez in Chile (Montgomery 1930).

Despite their wide distribution, large population sizes, visibility and in the case of *P. chabrus*, their edibility, very little attention has been paid to these species in the literature. Broekhuysen (1941) looked at the life history of *C. punctatus* at Strandfontein in the Cape (Figure 1). He showed that *C. punctatus* has two breeding seasons, a principal one in winter (May to September) and a subsidiary in summer (December to January). Broekhuysen (1941) also showed that *C. punctatus* females may extrude more than one batch of eggs, that they moult in spring and summer and, that the life histories of *C. punctatus* and *C. maenas* are similar. Alexander and Ewer (1969) investigated the ecology of *C. punctatus* in the Kowie river estuary in the Eastern Cape. They demonstrated that *C. punctatus* could not tolerate elevated or depressed salinities for as long as *Sesarma catenata* and consequently, *C. punctatus* was unable to extend as far up the estuary. Alexander and Ewer (1969) state that *C. punctatus* is nocturnal, feeds on vegetation high on the shore and may share burrows with *S. catenata*. The androgenic control of dominance heirarchies within aggregations of *C. punctatus* has been studied by Caiger and Alexander (1973). Bevis-Challinor (1983) showed that *C. punctatus* is more tolerant of fluctuating temperature than *Plagusia chabrus* or the discoid, detrital feeding crab, *Hymenosoma orbiculare*. Other general ecological studies have also been conducted. Jackson (1988) found a correlation between the distribution of *C. punctatus* at an intertidal site and the distribution of the coiled gastropod, *Oxystele variegata*.

Very little work has been done on *Plagusia chabrus* apart from that done by Bevis-Challinor (1983). Shepherd (1973) working on the biology of five species of Australian abalone, considers *P. chabrus* to be the most important predator of juvenile *Haliotis roei*. Shepherd's work also contains a rather inconclusive and non-quantitative study of the activity of this species which suggests that *P. chabrus* has a dusk-dawn activity rhythm. An osmoregulatory study of the mid-gut diverticula of *P. chabrus* and *C. punctatus* showed that *P. chabrus* was much more sensitive to fluctuating salinities than *C. punctatus* (Heeg and Cannone 1966). Virtually all other references to this species in the Zoological Record are of a taxonomic nature (Montgomery 1930, Barnard 1950).

There are several reasons why it is important to broaden our knowledge of these species. Adequate conservation of any ecosystem necessitates a full understanding of its mechanics and dynamics. Our understanding of Cape brachyuran biology is clearly inadequate. Given the densities at which these animals are often found, they must exert an important influence on local intertidal food-webs.

This lack of knowledge may prove harmful in view of the recent invasion of our coastline by the European shore-crab *Carcinus maenas* (Le Roux, Branch and Joska 1990). *C. maenas* is a large and agressive species which although once restricted to the Mediterranean, now has a cosmopolitan distribution as a result of accidental introductions (Joska and Branch 1986, Le Roux et al. 1990). The impact of invasion by *C. maenas* is well documented (Hanks 1961, Ropes 1968) as is the role that the species can play as an agent of change within intertidal communities (Muntz *et al.* 1965, Hughes and Elner 1979, Dudley 1980, Hadlock 1980 and Jensen and Jensen 1985). The presence of this species within the Cape rocky-intertidal will undoubtedly have an effect on local species. These effects could include the disruption of natural zonation patterns, the displacement of indigenous species from favoured habitats, direct carnivory and competition for food. The impact of *C. maenas* on local crabs will be difficult to predict or assess without an adequate understanding of the biology of the local species. The possibility that *P. chabrus* may be an important predator of the local abalone, *Haliotis midae* may have implications for the proposed abalone aquaculture industry in South Africa.

In this paper, the zonation, preferred habitat, diet, enzymology and activity rhythms of *Cyclograpsus punctatus*, *Plagusia chabrus* and *Carcinus maenas* are studied and compared with a view to broadening our understanding of the biology of each species and, establishing whether invasion of the intertidal by *C. maenas* is likely to have a deleterious impact on *C. punctatus* or *P. chabrus* .

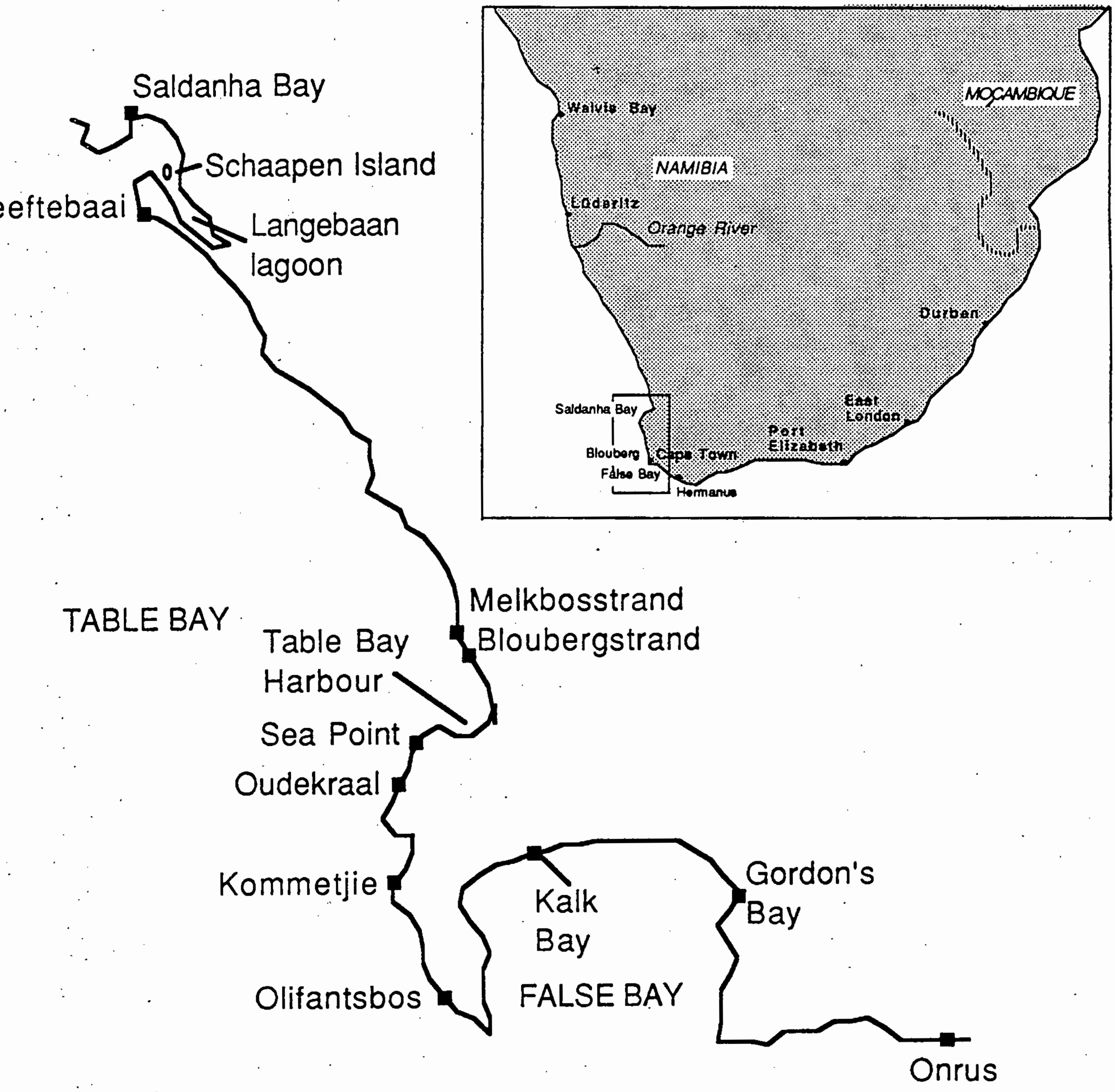


Figure 1. A map showing all the sites from which crabs were captured or at which sampling was done. The use to which each site was put can be found in the text.

macrobomb calorimeter and burnt. The mean energy value of *P. chabrus* was then calculated as the product of mean mass and calorific value g^{-1}.

This energy value was then used to calculate the number of *P. chabrus* at each station by using the formula :

$$\frac{\text{KJ. m}^{-2}\text{ at the n th station}}{\text{KJ value of the mean crab}} = \text{the number of crabs. m}^{2}$$

Distance downshore was converted to height above LWS and depth below LWS using the transect diagrams presented in Field *et al.* (1980). This derived data was then combined with that gathered during the shore transects.

During June 1989 a single field trip was conducted at Davies pool in Onrus (Figure 1) to assess whether crab size or crab number correlated with boulder size.The length and width of fifty high-shore and fifty low-shore boulders were measured and their cross sectional areas calculated as an index of size. Each rock was then turned and all crabs underneath were caught, sexed and their carapace widths measured to 0.01 mm using Vernier calipers. Unpublished data collected by L. van Herwerden during intertidal experiments at Schaapen Island (Figure 1) was reworked and added to this data set. Simple correlations were then drawn between boulder cross sectional area, crab number and mean crab size for both the high and low-shore environments.

Diet

Gut contents

Thirty individuals of *C. punctatus* were collected from Onrus every three months between April 1989 and January 1990. Thirty animals were also taken every three months from Wooley's Pool in False Bay (Figure 1). This site proved unable to sustain the sampling pressure and was substituted for in October 1989 with a similar site at Gordon's bay (Figure 1). The data from the latter two sites was then pooled and presented as a False Bay site. Thirty individuals of *P. chabrus* were caught every three months from Oudekraal on the western seaboard and from Kalk Bay on the eastern seaboard of the Cape Peninsula (Figure 1).

Analyses were the same in all cases. Methods used were adapted from several sources (Hynes 1950, Berg 1979 and Pulfrich and Griffiths 1988). The methods included: visual estimates of percentage fullness, measurements of stomach length (mm) and stomach volume and the calculation of percentage occurrence and percentage volume of each prey species.

The data for all the different sites and times was pooled and lists of all the prey species consumed by *C. punctatus* and *P. chabrus* were drawn up. These data were then compared to see if there were significant differences in diet between species, between sites within species, or between seasons.

Dietary data collected for the invasive*C. maenas* drawn from Le Roux *et al.* (1990) was processed into a form which allowed for an interspecific dietary comparison to be made between *C. maenas*, *C. punctatus* and *P. chabrus.*

Enzymology

Carcinus maenas and *Cyclograpsus punctatus* individuals were caught at Melkbosstrand on the Cape Peninsula during June 1990. *Plagusia chabrus* were caught in Kalk Bay harbour. Crabs were kept in 36 x 42 cm aquaria with rocks (*C. punctatus* / *P. chabrus*) and sand (*C. maenas*) to a depth of 10 cm until the day the assays were performed. Aquaria were linked to a through-flow water system at a temperature of 15-17 °C. The delay between crab capture and use in the assay was minimised.

Crabs were anaesthetised at -16 °C for 10-20 minutes and then held on frozen sponge blocks while the hepatopancreas was removed. Hepatopancreatic material was then homogenised in 67 mM phosphate buffer (PB) using a glass rod. The product was centrifuged at 1100 rpm for 2 minutes. The supernatant was discarded and the extract centrifuged again to improve its purity. Where necessary this process was repeated until a suitably purified extract was obtained.

Protein content was assayed using the method proposed by Lowry *et al.* (1951). Exact protein content was not determined because samples were not frozen, thus not preventing denaturing. Enzyme activity is expressed as µg substrate equivalent.h^{-1}.mg $protein^{-1}$.

- Assays

Laminarinase, cellulase and amylase.

The Nelson Somogyi assay (Nelson 1952) for reducing sugars was used. The enzyme extract was diluted 1/10, 1/50 and 1/100 in phosphate buffer and incubated with 0.125 ml of substrate (0.1 % laminarin in PB), forming the assay mix. The mixtures were held at 22 °C for 15, 30, 45 and 60 minutes. Somogyi reagent (0.25 ml) was added to the assay mix, the mixture boiled for 10 minutes then cooled. Nelson reagent (0.5 ml) and water (1.5ml) were added to the warm assay mix, mixed well and left for 20 minutes before being read at 660 nm on a Beckman spectrophotometer.

A standard curve was prepared using a 200 μg ml^{-1} glucose solution. Glucose concentrations of 0-200 μg ml^{-1} were used. Three replicate assays were performed.

The Nelson Somoygi method was also used for cellulase and amaylase. The cellulase substrate was 1 % carboxy-methyl cellulase (CMC). The substrate for the amylase assay was 1 % starch solution which was made up on the day.

Alginase

Activity was assayed using the thiobarbituric acid (TBA) method (Jacober *et al.* 1980). Thiobarbituric acid reacts with guluronic and mannuronic acid aldehyde derivatives. Aliquots (0.1 ml) of 1/10, 1/50 and 1/100 dilutions of enzyme extract were added to 0.1ml substrate (0.4 % w/v sodium alginate) and incubated for 0, 15, 30, 45 and 60 minutes. KIO_4 (0.25 ml) was added and the mixture allowed to stand for 20 mins at 22 °C. The periodate oxidation was halted using 0.5 ml of

$NaSO_4$ and two minutes later 2 ml of TBA was added. These samples were heated to 100 ° C for ten minutes, cooled and read at 500 nm.

A standard curve using malondealdehyde was plotted using a method proposed by Jacober *et al.* (1980) and adapted by Seiderer (1983).

Chitinase

The standard curve for chitinase was obtained using N-Acetyl glucosamine over a range of concentrations between 0 and 22.4 μg ml^{-1}. The 4-dimethylaminobenzaldehyde method was used to perform this assay (Monreal and Reese 1969).

A 1/10 dilution in PB of chitin served as the substrate. The enzyme extract was also diluted in PB (1/10, 1/50 and 1/100). Equal volumes of enzyme extract (0.125 ml) and substrate, were mixed and incubated at 22 ° C for 0, 30, 60 and 90 minutes. Tetraborate was added and the assay mix boiled for three minutes, cooled and left at room temperature for 45 minutes. The samples were then read at 500 nm.

Azocasein

The method used is described by Lang *et al.* (1981). The substrate (0.5 % azocasein in trys HCl) was added in aliquots of 0.4 ml to 0.2 ml of enzyme extract diluted 1/2, 1/5 and 1/10 times. The mixture was incubated at 22 °C for 0, 10, 20 and 30 minutes. Cold TCA (0.4 ml at 4 °C) was added and the samples held at 4 °C for 30 minutes. The samples were then centrifuged at 11000 rpm for 2 min. One ml of supernatant from each sample was added to 1 ml of NaOH and activity read on the spectrophotometer at 440 nm.

Mechanical advantage

Mechanical advantage is defined as the factor by which the magnitude of the force exerted by the chelal lever system is altered by that system (Warner and Jones 1976). Mechanical advantage (MA) was calculated for *C. punctatus, P. chabrus* and *C. maenas* using varying numbers of intermoult specimens with uninjured chelae. MA is calculated as the ratio of lever length 1 (L1) to lever length 2 (L2). The length of L2 depends upon at what point, along the biting surface of the chelae, force is applied. L1 varies slightly depending on the precise position of the dactylus insertion. For this study, all lever lengths are taken to be maximal. L2 is measured from the pivot to the tip of the dactylus and L1 as the distance between the pivot and the point of insertion on the dactylus of the closer muscle apodeme. The mean lengths of lever 1 and 2, as well as diagrams showing chelal shape are also presented.

Activity rhythm

Activity rhythm (AR) was measured in the field by observation. Activity rhythm in *C. punctatus* was studied seasonally at two sites, Davies Pool at Onrus and Wooley's Pool at Kalk Bay (Figure 1). The Kalk Bay site could not sustain the sampling pressure and was substituted for with a similar site at Gordons Bay in October 1989.

Two transects, approximately 10 m apart, were laid down perpendicular to the shore from high water spring (HWS) to low water spring (LWS). The transects were shifted each quarter to prevent samples being taken from the same place twice. Marked rocks were placed at 4 m intervals along the transect marking the observation stations. Every second hour for 24 hours an observer moved down the length of each transect spending three minutes at each station counting the number of crabs moving or visible within 1 m^2. The observers swopped transects every other observation to reduce individual error. Directly after each observation period 10 crabs were caught, from an area well away from the transect, killed instantly and fixed in 10 % formalin and seawater. These crabs were taken back to the laboratory for further analysis.

At the end of the observation period an area of one m^2 at each station was torn up. All the crabs in this area were caught, measured and sexed. Boulder sizes were measured and the percentage cover (algal, kelp, boulder, pebble and sand) of the area estimated. The number of *Ligia* spp., *Oxystele* spp., *Littorina* sp. and *Acanthochiton garnoti* were counted as accurately as possible.

During October 1990 three similar trips were conducted to gather data on the AR of *Plagusia chabrus*. Two were done during spring tide and one during neap tide. Every second hour for 24 hours, crabs were counted while skin-diving along a 60 m length of Kalk Bay Harbour wall. This procedure was continued throughout the night using underwater diving lamps. After each period of observation seven crabs were removed from an adjacent 40 m of wall, killed instantly and fixed in 10 % formalin. These animals were then taken back to the laboratory for further analysis.

C. punctatus and *P. chabrus* returned to the laboratory were processed in the same manner. Crabs were measured, sexed and weighed wet. Their cardiac stomachs were removed by dissection. The contents of each stomach was then washed out into a tap-fitted, Venturi vacuum filter and filtered onto predried (24 hrs at 80 °C), preweighed (to 0.0001g), GFF filter paper (2.5 cm in diameter). Filter papers and the attached gut contents were dried (24 hrs at 80 °C) and weighed again to 0.0001g. Crab dry weight was calculated using the equations shown below.

C. punctatus - $DWC = WWC - 0.232 / 2.55$

P. chabrus - $DWC = -0.418 + 0.31.WWC$

Where WWC = the wet weight of the crab (g) and DWC = the dry weight of the crab (g).

Dry weight of gut contents was then expressed as a percentage of dry body weight for each crab and averaged for each sample. This was then plotted against time and compared to the observed AR. An attempt was made to correlate observed activity peaks with feeding peaks and to see whether these peaks correlated with diurnal or tidal cycles.

RESULTS

Zonation and habitat

Figure 2 shows the distribution with depth below LWS and height above LWS of *Cyclograpsus punctatus*, *Plagusia chabrus* and *Carcinus maenas* at five different shores on the western seaboard of the Cape Peninsula. *C. punctatus* and *C. maenas* are restricted to the intertidal. Figure 2 must be interpreted with caution with respect to the distribution of *C. maenas*, since the study conducted

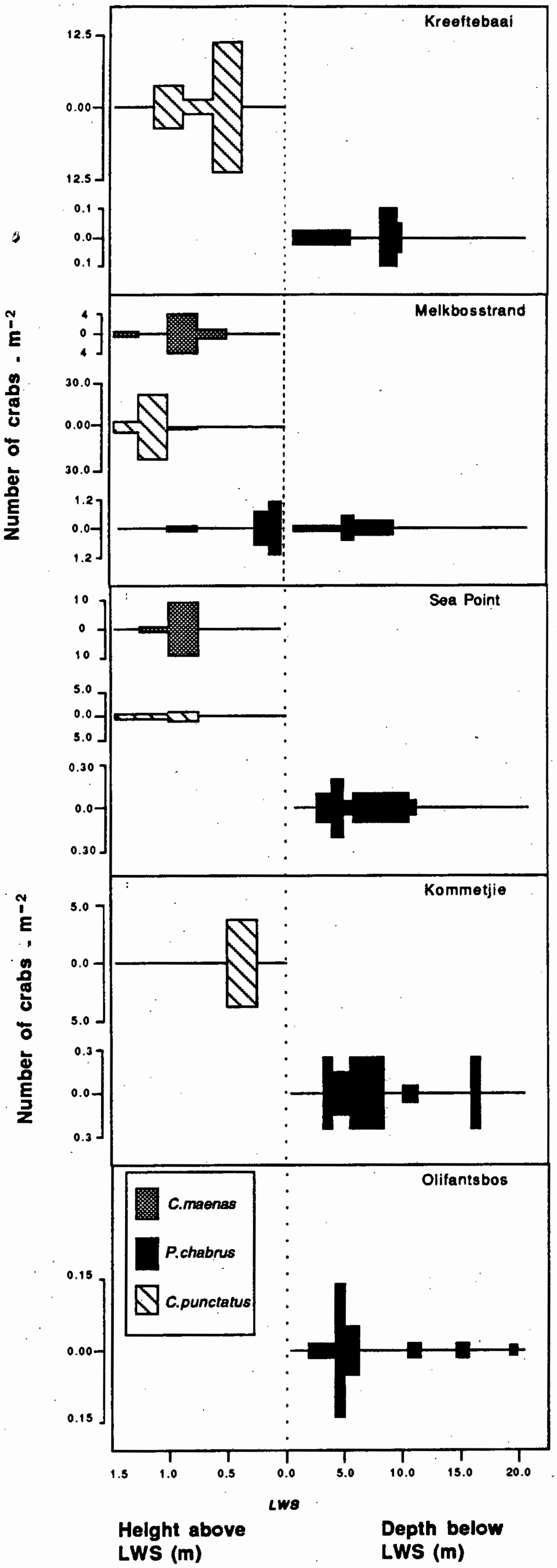


Figure 2. The intertidal distribution and density of Cyclograpsus punctatus, Plagusia chabrus and Carcinus maenas on five shores in the Cape Peninsula.

by Field *et al.* (1980) was done before the *C. maenas* began to spread along the coast. Informal diving at these sites indicates that *C. maenas* may still not have penetrated subtidal environments on these shores. This may be as a result of their preference for sheltered water. Both Sea Point and Melkbosstrand have shallow intertidal flats, sheltered by subtidal rock reefs which will limit the extension of *C. maenas* into the sublittoral. *Plagusia chabrus*, while capable of penetrating into the intertidal, is primarily a subtidal species (Figure 2). Where *P. chabrus* does penetrate the intertidal it is restricted to permanently submerged gullies and rock pools.

As one moves from north to south the densities of *P. chabrus* remain consistently low, never exceeding 2.5 m^{-2}. The highest density (2.3 m^{-2}) is found at Melkbosstrand. The southern-most site (Olifantsbos) is dominated by *P. chabrus* (Figure 2). This species may be caught a considerable distance off-shore. At Olifantsbos they were caught ± 1900 m beyond LWS (Field *et al.* 1980). Their distribution is, however, depth limited with very few animals ever being caught at a depth greater than 10 m. The sand-rock interface on most of the shores studied falls between 20 and 30 m and this must represent the lower limit of *P. chabrus* distribution on the shore.

Cyclograpsus punctatus densities fluctuate quite considerably from north to south, the highest density (42 m^{-2}) being found at Melkbosstrand. The lowest densities (4 m^{-2}, 8 m^{-2}) were found at Sea Point and Kommetjie respectively.

The distributions of *C. punctatus* and *Carcinus maenas* correspond quite closely at Melkbosstrand and at Sea Point, the only two shores at which both species occurred. The maximum density of *C. maenas* at Sea Point (18 m^{-2}) is significantly higher than its density at Melkbosstrand (8 m^{-2}). Frequent observation of the Sea Point site throughout 1988, 1989 and 1990 led the authors to believe that the invasion of the Sea Point intertidal by *C. maenas* may lead to a decline in *Cyclograpsus punctatus* density.

General intertidal and subtidal observation suggests that all three species have different habitat preferences, although *Cyclograpsus punctatus* and *Carcinus maenas* do overlap to some degree. *C. punctatus* makes shallow burrows in sediments underneath flat rocks or lives in the interstitial spaces created by aggregations of boulders. Although unquantified, it appears that crab densities are slightly higher underneath boulders upon or near which, kelp wrack has been deposited.

Figure 3 shows clearly that there is no relationship between *C. punctatus* number and boulder size in either high or low shore environments at Onrus or Schaapen Island. There are, however, more crabs per boulder at Onrus than there are at Schaapen Island ($x \pm s_d$; 7.86 ± 6.18 ; 1.92 ± 2.02). The data collected by van Herwerden and reworked in this study did not lend itself to a high and low-shore analysis. Data from Onrus (Figure 3) also shows no significant difference between the number of crabs per boulder in the high and low intertidal ($\bar{x} \pm s_d$, 1.83 ± 1.22 ; 1.98 ±2.02). Figure 4 a,b show that there is no correlation between mean crab size and boulder size in the high and low shore environments. The data show that there is no real difference between the size of *C. punctatus* individuals the high shore environment and those in the low shore environment.

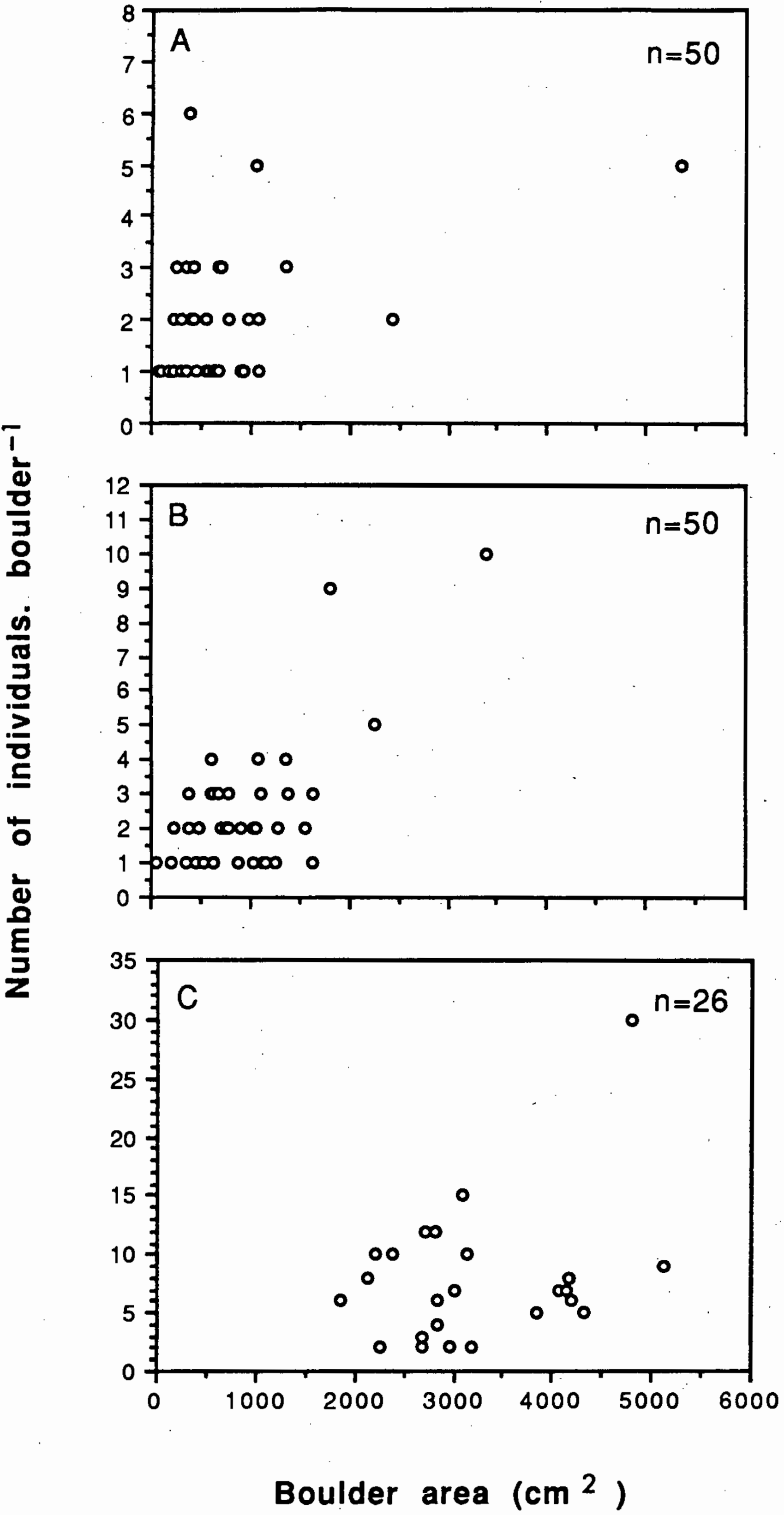


Figure 3. The mean number of Cyclograpsus punctatus found under boulders of increasing size (cm^2). A - High shore, B - low shore at Davies Pool, Onrus and, C - at Schaapen Island in Langebaan lagoon .

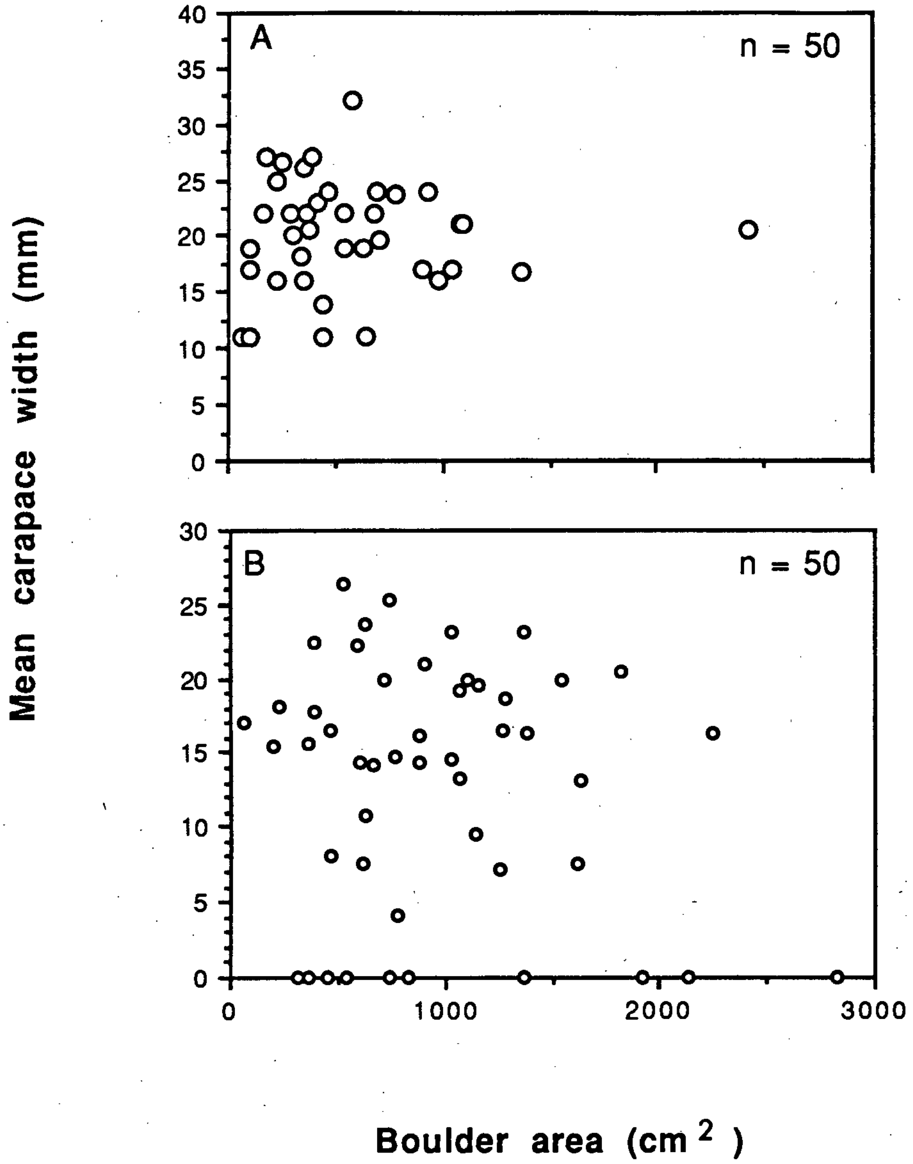


Figure 4. The mean carapace width (mm) of Cyclograpsus punctatus found under boulders of increasing size (cm^2). A - High shore and, B - low shore at Davies Pool, Onrus.

Carcinus maenas may also be found under flat rocks but usually in the mid to low intertidal. It may often be found co-occuring with *C. punctatus* at Melkbosstrand but is usually found at low tide, under very large boulders, near to or in weedy pools, or other suitably "wet" areas of the intertidal. *C. maenas* may also be found buried shallowly under the sand in sheltered weedy pools but it is never found on shores that are exposed to wave action. The subtidal distribution of *C. maenas* in South Africa is poorly known. These authors have not seen this species below LWS except within the sheltered docks of Table Bay Harbour (Figure 1).

Plagusia chabrus is found clinging to the surfaces and undersides of rocks in subtidal locations and can be seen sheltering within crevices between large offshore boulders. They are often caught within dense beds of the tunicate *Pyura stolonifera*. *P. chabrus* is a very mobile species relative to *C. punctatus* and *C. maenas* and can be suprisingly aggressive. When foraging they can be seen patrolling over subtidal rock surfaces or moving on the walls of rock pools near LWS.

Diet

Gut contents

Cyclograpsus punctatus has a much more limited diet than *Plagusia chabrus* or *Carcinus maenas* (Table I). The diet consists of kelp wrack, green and brown algae, the chiton, *Acanthochiton garnoti*, four common intertidal gastropods and the most common beach isopod and amphipod, *Ligia dilatata* and *Talorchestia* sp.. It also includes the common isopod genus *Exosphaeroma* spp., and the

Table I. A list of the common intertidal animals consumed by the Cape shore-crab, Cyclograpsus punctatus, the Cape rock-crab, Plagusia chabrus and the invasive European shore-crab, Carcinus maenas. The relative significance of each prey typre is as indicated. ( ) = not present, (+) = present, (++) = occasionally abundant, (+++) = often abundant and (++++) = a dominant constituent of the diet.

CATEGORY	Relative significance			CATEGORY	Relative significance		
	C. punctatus	*P. chabrus*	*C. maenas*		*C. punctatus*	*P. chabrus*	*C. maenas*
Algae				**Amphipods**			
Kelp wrack	++++	+		Caprella equilibria		+	
Sargassum sp.	++			Paramoera capensis		+	
Gelidium sp.		++++		Amaryllis sp.		+	
Ectocarpus sp.			++	Jassa falcata		++	
Ulva capensis	+	+++	+	Talorchestia sp.	+		
Enteromorpha capensis		+	++	Hyale sp.		++	
Codium spp.		++		Ischyrocerus carinatus		++	
Cladophora spp.		+++	+	Stenothoe sp.		+	
Bryopsis caespitosa		++		**Tanaids**			
Polysiphonia sp.		+		Leptochelia barnardi		+	
Ceramium sp.		+		**Crabs**			
Corallina spp.		++++		Plagusia chabrus	+	++	+
Sponges		+		Cyclograpsus punctatus	++	++	++
Hydrozoans				Hymenosoma orbiculare			+
Octocorallia sp.		+		Ovalipes punctatus			+
Aglaophenia pluma		++		**Molluscs**			
Bryozoans	+	+		Acanthochiton garnoti	+++	+++	
Nemertea				Chiton sp.		+	+
Zygonemertes sp.			+	Ischnochiton sp.			+
Polychaetes				Choromytilus meridionalis		++++	++++
Platynereis sp.		+	++	Mytilus galloprovincialis		++++	++++
Nereis spp.		++	++++	Aulacomya ater		++++	++
Spirorbis sp.		+++		Kellia rubra		+	
Orbinia sp.			++	Gregariella sp.			+
Eunice sp.			++	Tellina macoma		+	
Marphysa sp.			++	Petricola bicolor		+	
Cirripeds				Tricolia capensis		+	+
Notomegabalanus sp.		++++	+++	Tricolia neritina		+	
Isopods				Burnupena cincta			++
Cirolana sp.			+	Aetonaliella sp.		+	+
Paridotea ungulata		+	++++	Littorina africana	++		
Ligia dilatata	+++			Oxystele spp.	+++	+++	++
Paranthura punctata		+		Fissurella mutabilis			++
Exosphaeroma spp.	+	++	+	Patella sp.		+++	++++
Dynamanella huttoni		+		**Formicidae**	+		

crabs *C. punctatus* and *P. chabrus*. Figures 5 and 6 show quite convincingly that kelp wrack is the most important component in the diet both in terms of percentage occurrence and percentage volume at Onrus and at False Bay. At Onrus this is followed by *Oxystele* spp. and *Acanthochiton garnoti*. At False Bay sites the diets are a little more variable with the strong kelp wrack component being followed by *Acanthochiton garnoti*, *Oxystele* spp., brown and green algae and the littoral periwinkle, *Littorina africana*.

The diet of *C. punctatus* seems to fluctuate seasonally (Figures 5 and 6). Individuals at Onrus seem to include more animal material in their diet as the year progresses, the most being included in October (Figure 5). At False Bay sites we see a similar trend from April to July (Figure 6) but the substitution of the Gordon's Bay site in October seems to disturb the trend somewhat. Kelp wrack dominates the diet in October at False Bay, the animal component dominating the January sample. The diet of *C. punctatus* is narrow but stable, the "other" component being small in every season and on occasion non-existent.

Figures 7 and 8 show that green, brown and coralline algae are the most important constituents of the diet of *P. chabrus*. Algae occurs in most of the guts and makes up most of the volume. Very few guts were filled exclusively with algae most containing numbers of small amphipods, various shell chips and other material. At Kalk Bay the barnacle *Notomegabalanus algicola* was the second most important constituent of the diet of *P. chabrus*. At Oudekraal the diet was more variable with bivalves and polychaetes especially *Spirorbis* sp. being next most important (Figure 8). Guts were often found almost totally filled with any number of other prey species. As a result several other organisms

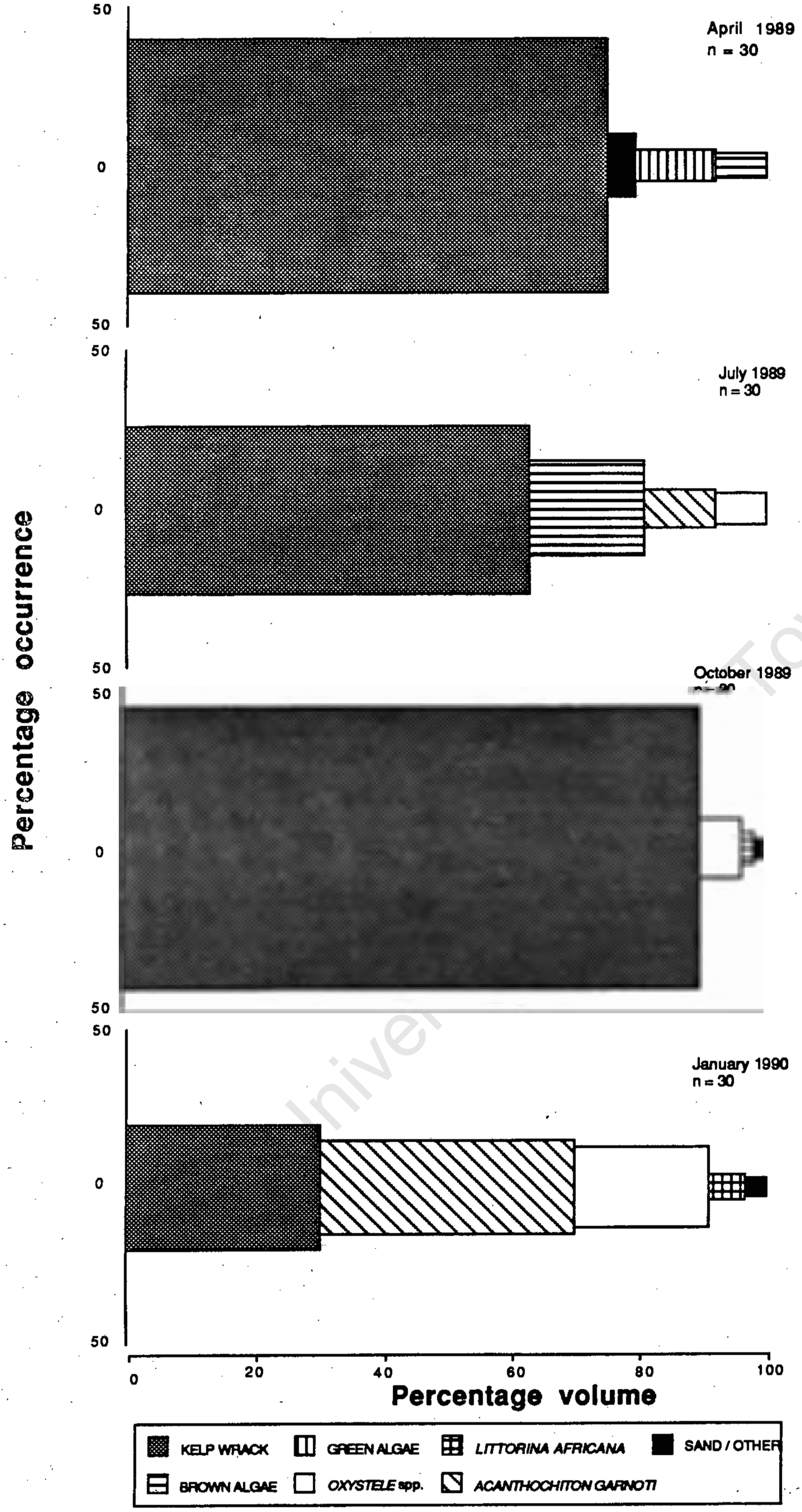


Figure 6. Percentage occurrence plotted against percentage volume of the cardiac stomachs of Cyclograpsus punctatus taken from False Bay in the Cape. Seasonal fluctuations in diet are shown

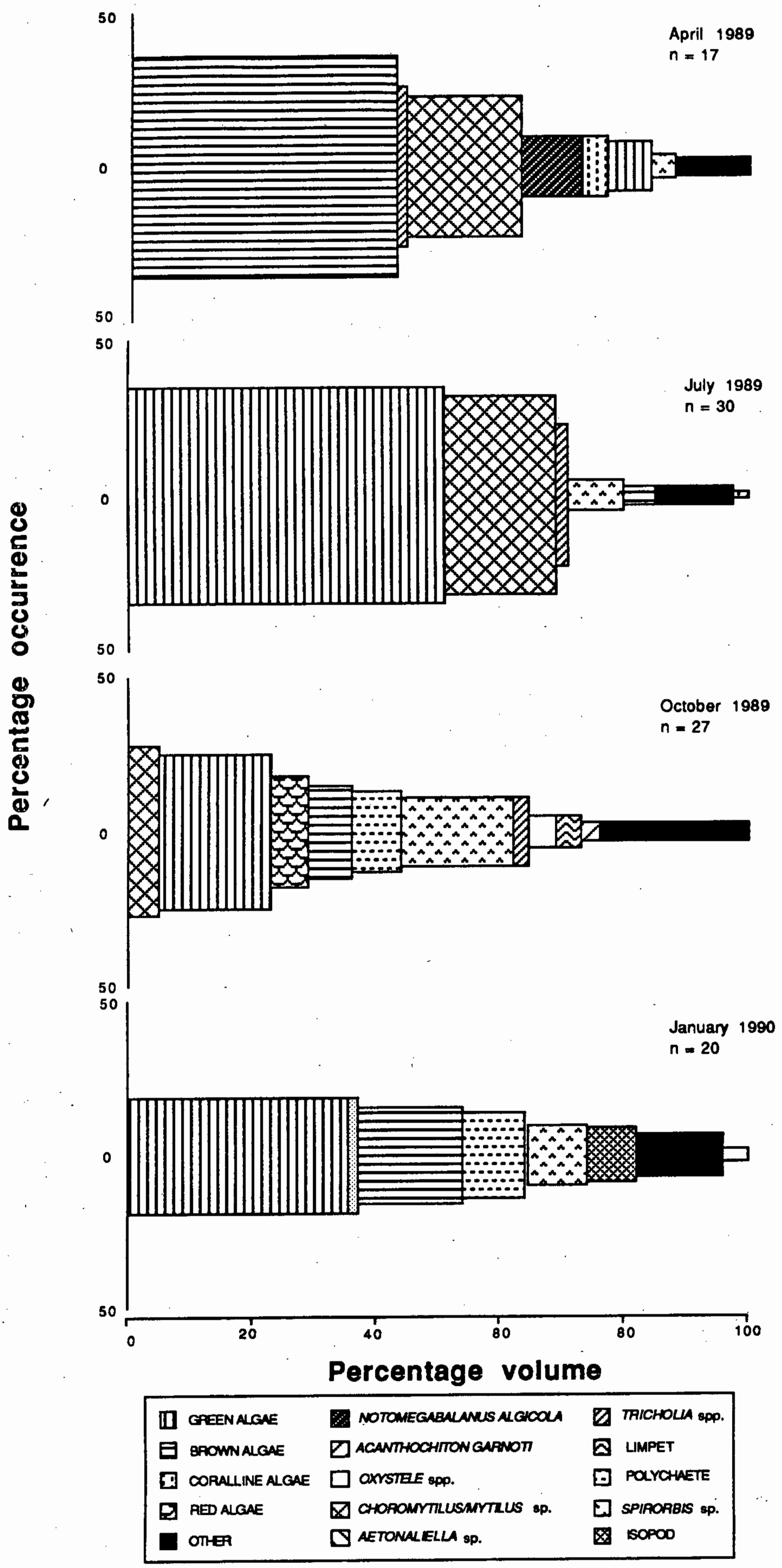


Figure 7. Percentage occurrence plotted against percentage volume of the cardiac stomachs of Plagusia chabrus taken from Oudekraal on the Cape Peninsula. Seasonal fluctuations in the diet are shown

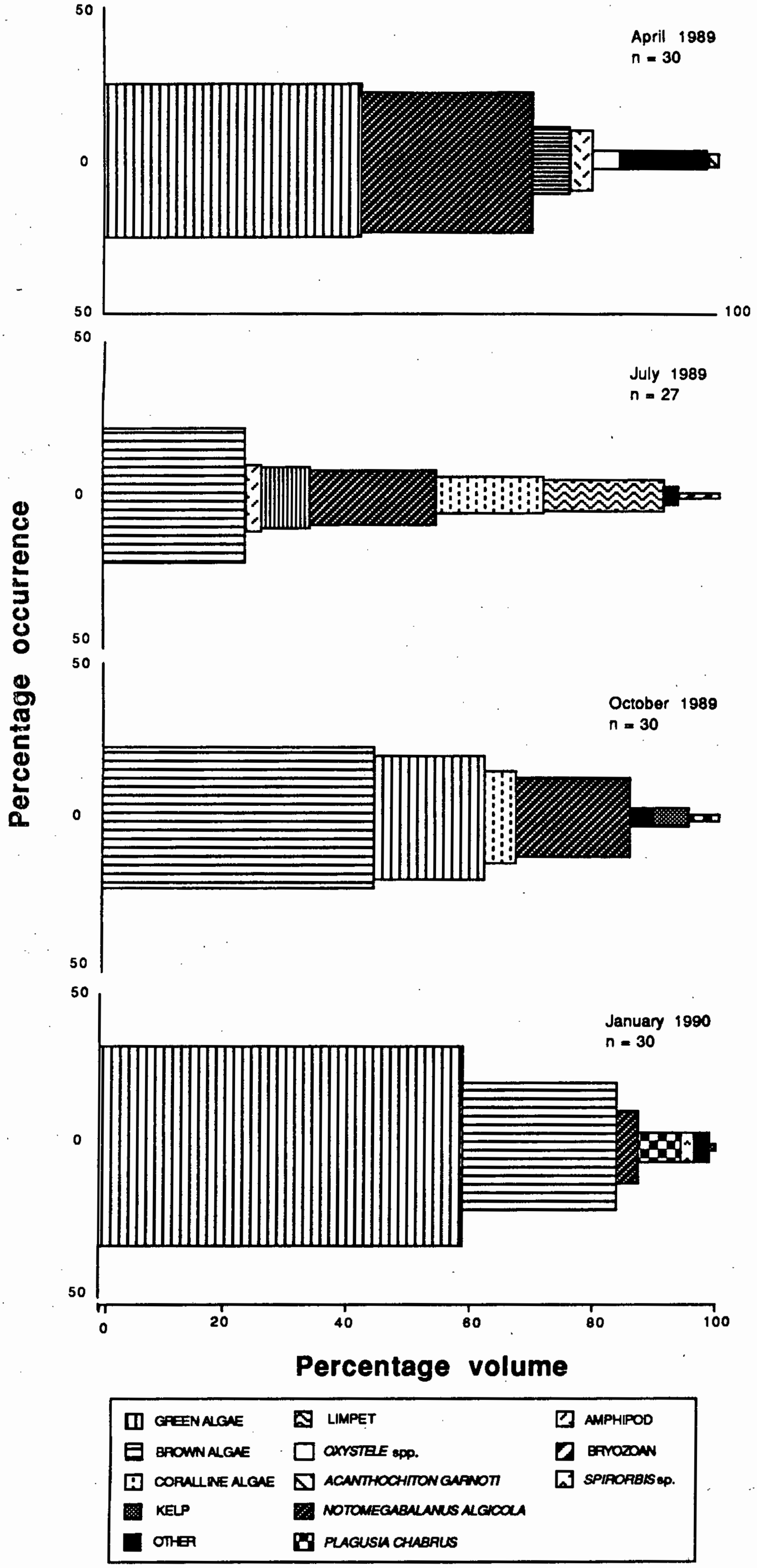


Figure 8. Percentage occurrence plotted against percentage volume of the cardiac stomachs of Plagusia chabrus taken from Kalk Bay in the Cape. Seasonal fluctuations in the diet are shown.

feature as important constituents of the diet (Table I). Limpets, *Oxystele* spp., amphipods and *P. chabrus* make up significant amounts of cardiac stomach volume at Kalk Bay. *Tricolia* spp., limpets, isopods (particularly *Exosphaeroma* spp. and *Paridotea* spp.) and *Acanthochiton garnoti* are significant components of *P. chabrus* diet at Oudekraal. Examination of the raw data shows that the diet of *P. chabrus* is more variable at Oudekraal than it is at Kalk Bay.

Table I and Figure 9 present dietary data for *Carcinus maenas. C. maenas* has a wide and flexible diet and is clearly a carnivore, algae constituting a very small part of its diet (Figure 9). *C. maenas* consumes the slow moving isopod *Paridotea* spp. (34 %occ, 29.4 %vol), members of the limpet genus *Patella* spp. (16 %occ, 24.3 % vol), assorted polychaetes (8.3 %occ, 24.6 %vol) and a variety of "other" less significant species from the point of view of percentage volume. These include gastropods, mainly *Aetonaliella* sp. and *Tricolia* spp. and the intertidal algae *Enteromorpha* sp. and *Ectocarpus* sp..

Enzymology

The fact that a full protein analysis could not be conducted on the enzyme extracts used in these assays means that no actual figures can be quoted. The results will be presented using ranges from high (+++) to low (+) levels of activity.

C. maenas had large quantities of amylase and moderate amounts of azocasein in the hepatopancreatic extract and so we presume in the cardiac stomach (Table II). Chitinase levels are suprisingly low, but as expected the largely carnivorous crab has low levels of cellulase, alginase and laminarinase.

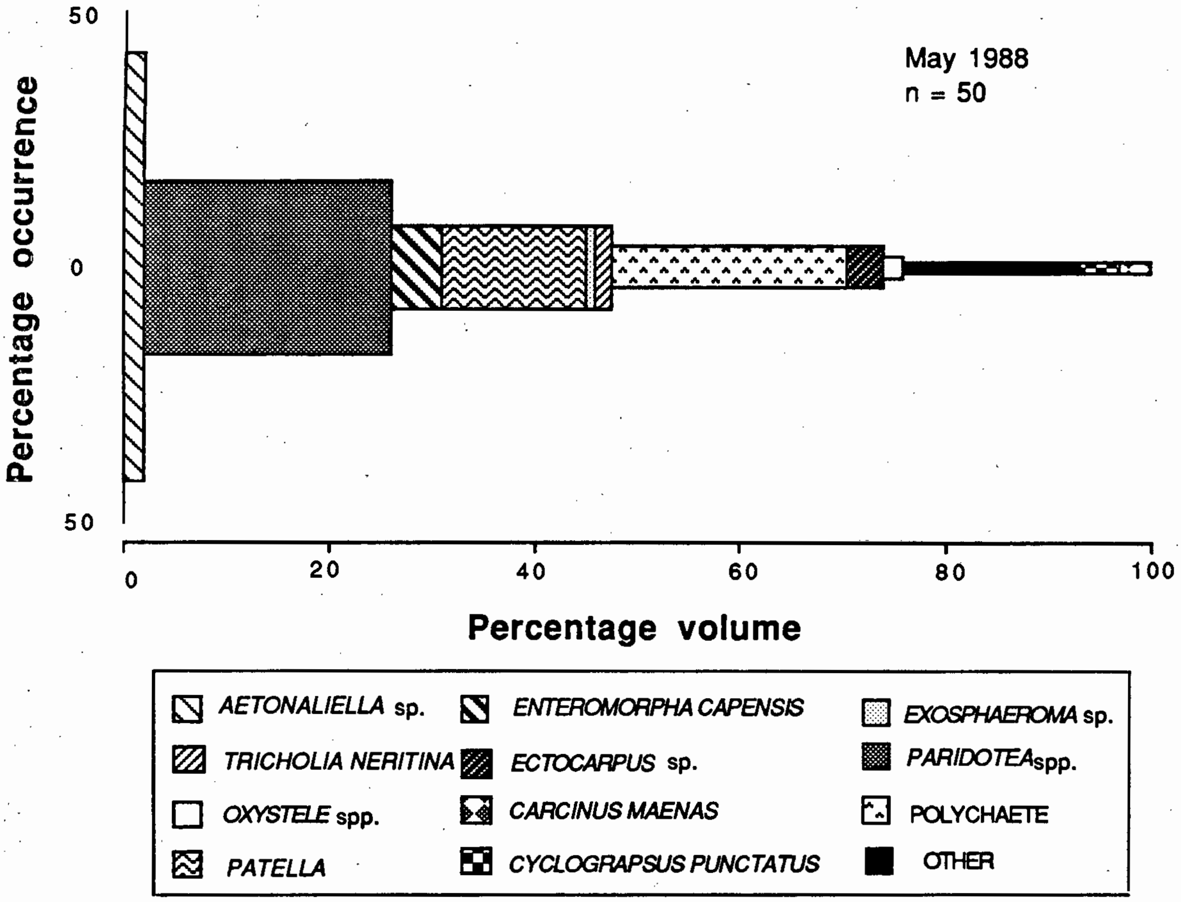


Figure 9. Percent occurrence plotted against percent volume of the cardiac stomachs of Carcinus maenas taken from Bloubergstrand in the Cape.

Plagusia chabrus had high levels of protease enzymes (amylase, chitinase and azocasein) and moderate levels of cellulase and alginase. Laminarinase activity was very low.

Cyclograpsus punctatus had high levels of amylase but low quantities of the other two proteases tested, chitinase and azocasein (Table II). The crab had very high levels of cellulase, alginase and laminarinase activity relative to the other two species.

Differences in chitinase activity recorded in this study must be interpreted with caution, in view of the fact that this enzyme is synthesized in varying quantities depending on the stage of the moult cycle the individual crab is entering.

Mechanical advantage

Handedness in crabs is simply a measure of interchelal dimorphism. *Cyclograpsus punctatus* and *Plagusia chabrus* are not handed. *Carcinus maenas* is, however, handed with one chela developed into a large crushing instrument. The "hand" may vary from the left to the right. Of the five species compared (Table III), the crusher-chela of *C. maenas* has the highest mechanical advantage (± 0.375). Suprisingly this is followed by the chelae of male *C. punctatus* (± 0.340). Then, in order of decreasing mechanical advantage (MA), *Cancer pagurus* (± 0.329), male *P. chabrus* (± 0.304), the fast chela of *C. maenas* (± 0.281), female *P. chabrus* (± 0.248), the "strong" chela of *Macropipus depurator* (± 0.248), female *C. punctatus* (± 0.245) and the "fast" chela of *M. depurator* (± 0.177).

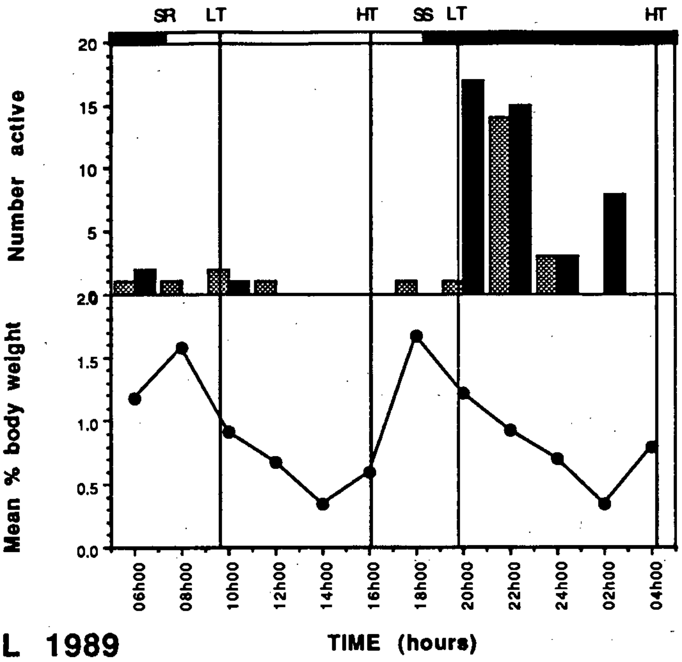
The difference between the MA value of male and female *C. punctatus* is the result of a 34 % increase in the distance between the pivot and the point of insertion (L_1) and a 26 % greater length of the dactylus (L_2) in males. In *P. chabrus* the difference in MA between male and female chelae is the result of a 36 % difference in the length of L1 and a 23 % increase in the length of L2 in males. Warner and Jones (1976) state that a 32.72 % increase in the length of L1 and a 6.22 % increase in the length of L2 in "strong" chelae is responsible for the difference in MA of "strong" and "fast" chelae of *M. depurator.*

The reflected tooth on the "strong" chela of *M. depurator* and the teeth on the crusher-chela of *C. maenas* increase the crushing strength up to 4 times. The chelae of *C. punctatus* do not have teeth. *P. chabrus* has teeth on the chelae, but they are smaller than those of *C. maenas.*

Activity

Figures 10 - 13 show the diurnal activity patterns and feeding rhythms of *Cyclograpsus punctatus* during April, July and October at Onrus, while figures 14-17 show similar data for *C. punctatus* in False Bay. Figure 18 shows the AR and feeding cycle of *Plagusia chabrus* on Kalk Bay Harbour wall during two spring and one neap tide.

The data indicate that *C. punctatus* is nocturnal with the majority of the activity, at all sites, occurring in the early part of the night. Intertidal observation confirms this result with very few crabs being seen during the day. The only exception to this was July 1989 in False Bay (Figure 15). Here a significant number of crabs were active during the daytime low tide. Examination of the raw data reveals



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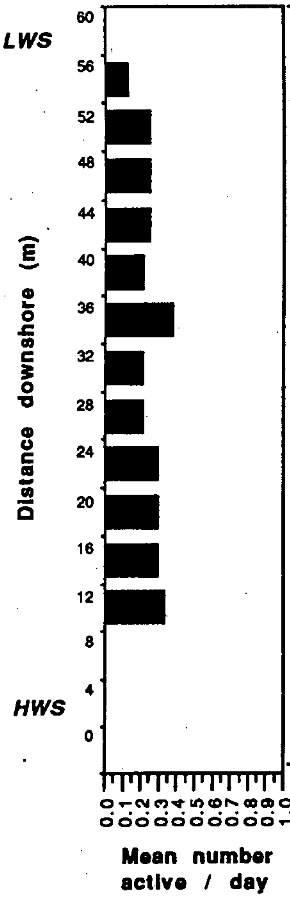
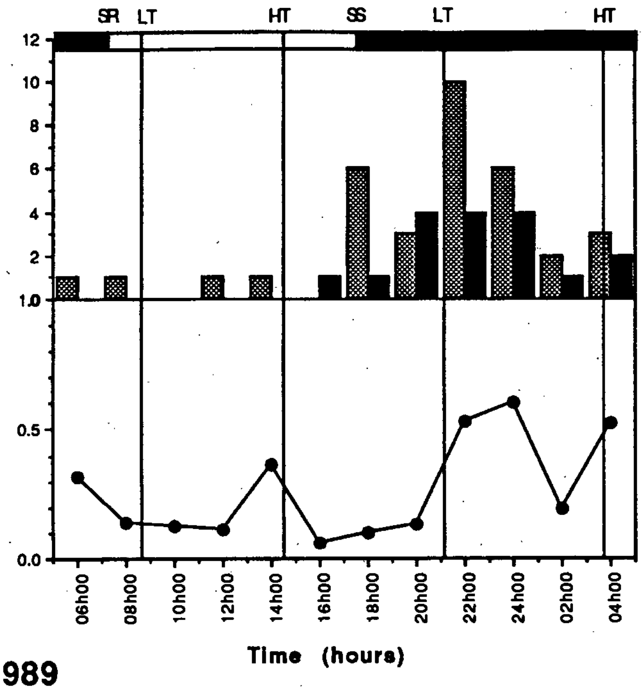
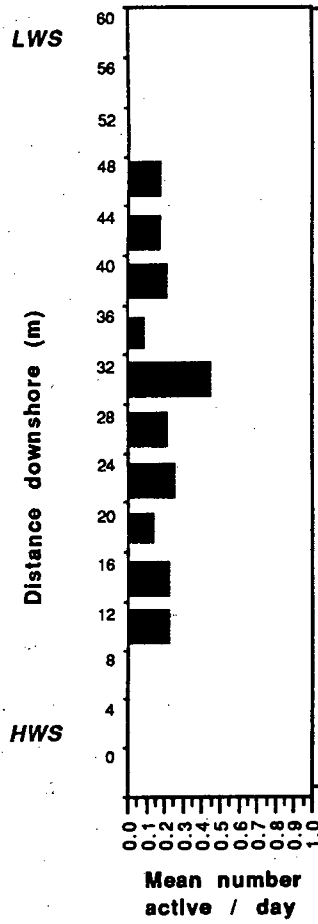


Distance downshore (m)	% Bed rock	% Boulder	% Pebble/sand	% Algae	% Kelp	Boulder diameter	# *Oxystele*	# Littorinids	# *Acanthochiton*	# *Ligia*	# *C. punctatus*
60											
56		70	30		<1	362	46				4
52		90	10		<5	240	101				6
48	<5	100					54				5
44	<5	60	55		<1	273	30				5
40	10	50	32		<1	283	64		1		10
36	15	55	45			218	65				10
32		65	50			228	50				5
28	10	55	75		<1	155	55				3
24	30	30	40		<1	131	45				4
20	20	55	35			191	77			5	7
16	10	55	50		25	260	28				6
12	70	65	20		<5	288	4			<100	10
6		60	35		<5	237		200		<50	
4	100										
0	100										

Figure 10. Top- the number of Cyclograpsus punctatus active on two transects at Onrus and the mean percentage of crab body weight made up by the gut contents. Bottom - The mean number of crabs active down the length of the shore (m) per day and, a table showing other parameters measured at each station (APRIL 1989). The two shadings on the "number active vs time" graph above shows the two different transects.

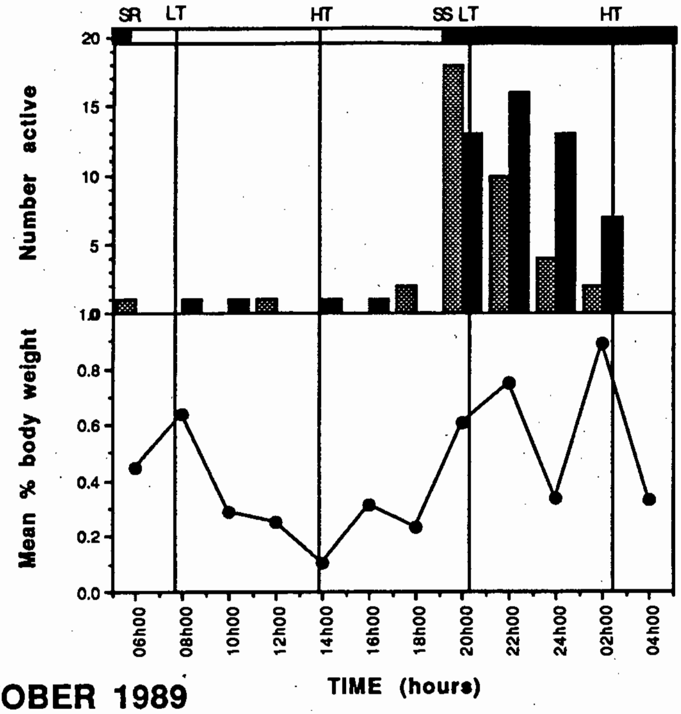


JULY 1989

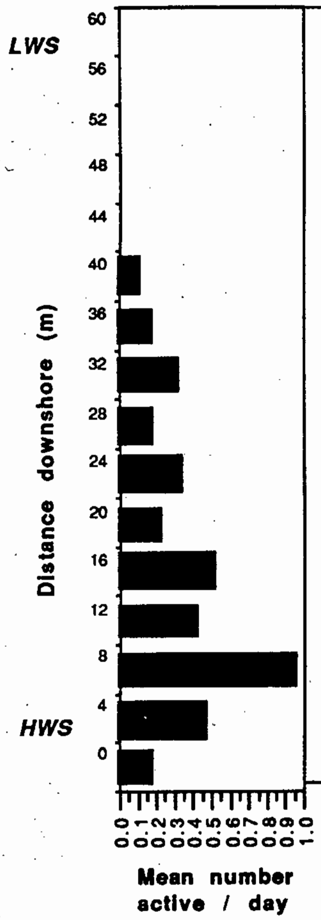


Distance downshore (m)	% Bed rock	% Boulder	% Pebble/sand	% Algae	% Kelp	Boulder diameter	# *Oxystele*	# Littorinids	# *Acanthochiton*	# *Ligia*	# *C. punctatus*
60											
56											
52											
48	100	50	35		<2		73		1		4
44	<15	60	30		<1	224	>100				8
40	50	50	10		<1	283	60				4
36	30	70	20			530	>100				11
32	90	40	15			114	120				1.0
28	5	85	<15		<2	245	88				12.5
24	47	90	10		<5	238	94				12
20		70	30		<1	238	68			5	4.5
16	10	80	25		25	246	28			10	2.0
12	<5	70	20		<10	209	2	230		<100	4.5
8	30	80	20		30	308				>300	
4	100	25	7.5		3.5	155				>300	
0	21.8		50		20	172				>350	

Figure 11. Top - the number of Cyclograpsus punctatus active on two transects at Onrus and the mean percentage of crab body weight made up by the gut contents. Bottom- The mean number of crabs active down the length of the shore (m) per day and, a table showing other parameters measured at each station (JULY 1989).

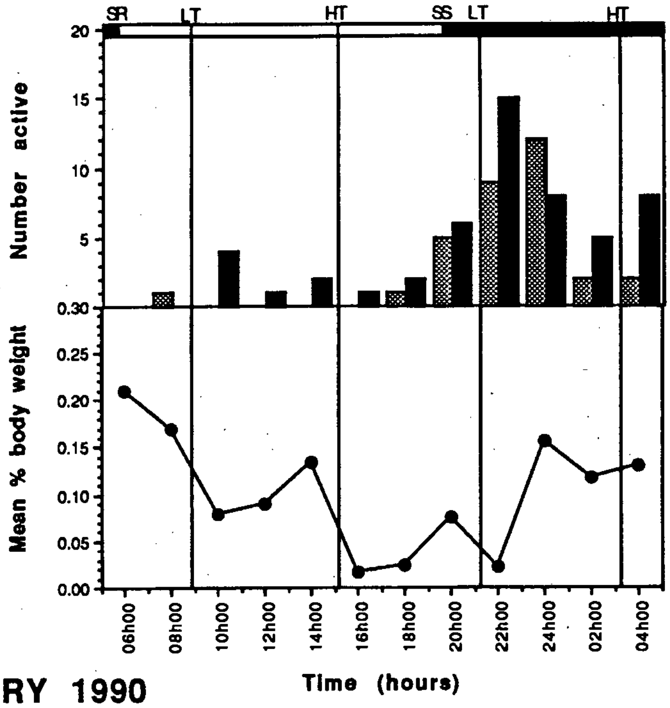


OCTOBER 1989

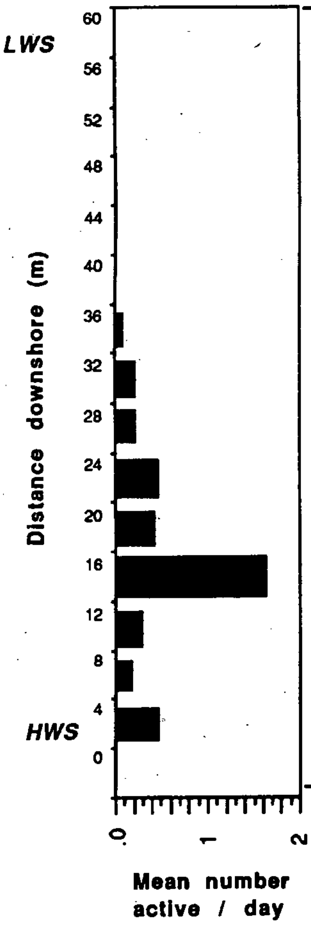


Distance downshore (m)	% Bed rock	% Boulder	% Pebble/sand	% Algae	% Kelp	Boulder diameter	# *Oxystele*	# Littorinids	# *Acanthochiton*	# *Ligia*	# *C. punctatus*
60											
56											
52											
48											
44											
40	35	55	30			220	42				8
36		60	30			301	55				10
32	<5	75	35			170	55				5.5
28	15	45	40			201	73				7
24	<5	70	30	<1		210	96				8
20	5	70	25		1	246	65			5	7.5
16	40	25	25			180	9			9	2
12	50	40	15		<1	277	3	20		4	9.5
8	20	65	15		2	284		30		16	10
4	60	20	22			193		>50		>100	
0	35	50	40		2	178				45	

Figure 12. Top - the number of Cyclograpsus punctatus active on two transects at Onrus and the mean percentage of crab body weight made up by the gut contents. Bottom - The mean number of crabs active down the length of the shore (m) per day and, a table showing other parameters measured at each station (OCTOBER 1989).

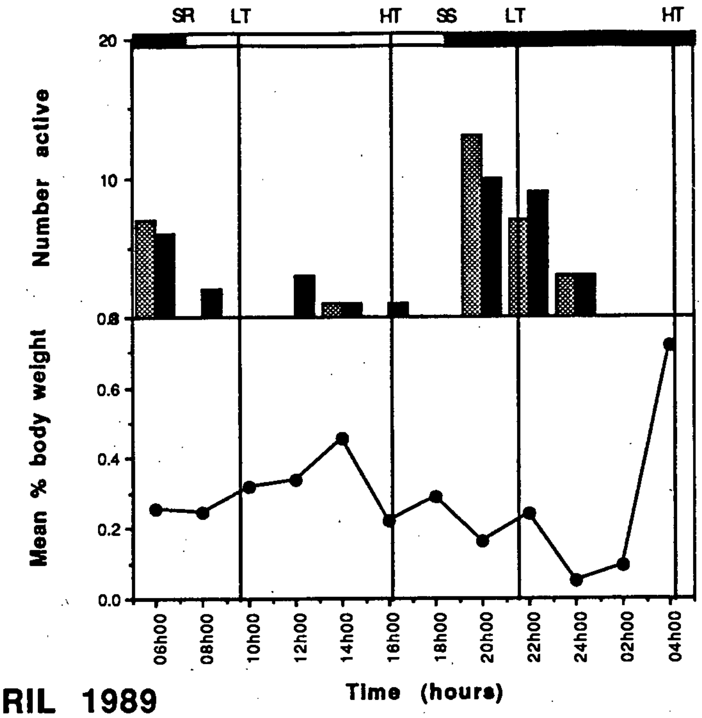


JANUARY 1990

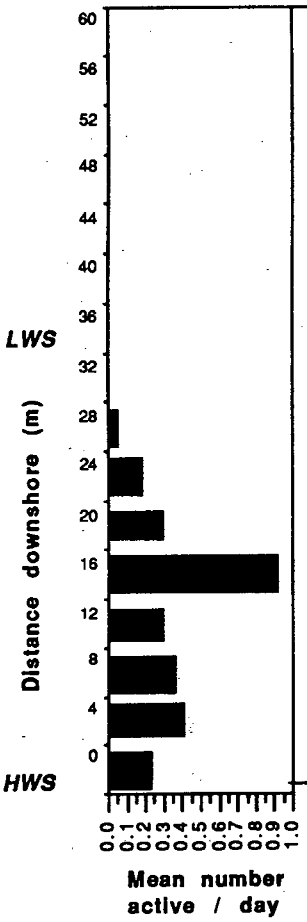


Distance downshore (m)	% Bed rock	% Boulder	% Pebble/sand	% Algae	% Kelp	Boulder diameter	# *Oxystele*	# Littorinids	# *Acanthochiton*	# *Ligia*	# *C. punctatus*
60											
56											
52											
48											
44											
40	35	55	30			220	42				8
36	25	90	10		1	468	108				3
32	25	60	17		<2	270	100		2	<10	5.5
28	25	85	13			181	<150		1		12.5
24	30	60	20		<2	235	<250		1		7.5
20	35	55	22		<5	255	42			>25	3.5
16	5	80	15		<5	292	>150			>25	22
12	15	60	45		<5	179	10			>25	1.5
8	50	65	12			238				>250	2
4	15	70	20			155		>100		>50	2.5
0	40	45	12		25	185				10	

Figure 13. Top - the number of *Cyclograpsus punctatus* active on two transects at Onrus and the mean percentage of crab body weight made up by the gut contents. Bottom - The mean number of crabs active down the length of the shore (m) per day and, a table showing other parameters measured at each station (JANUARY 1990).

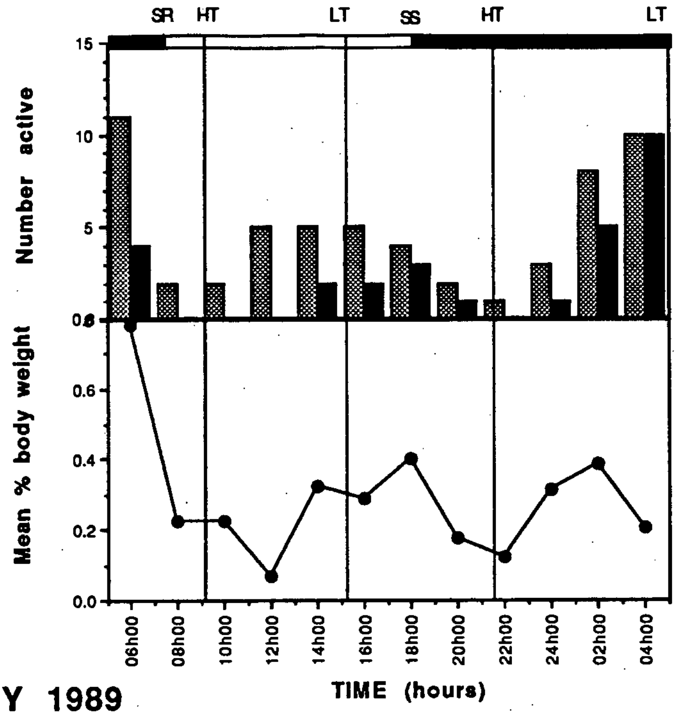


APRIL 1989

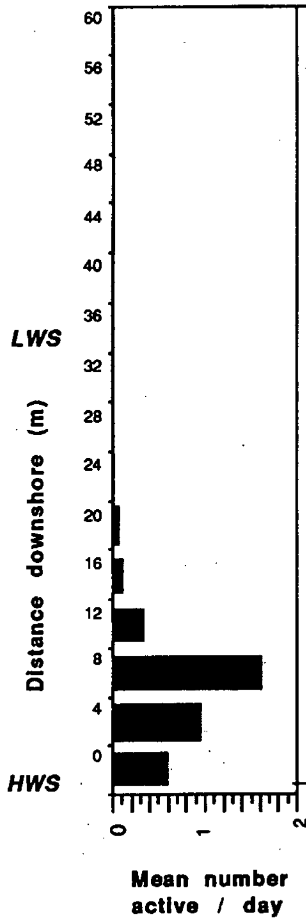


Distance downshore (m)	% Bed rock	% Boulder	% Pebble/sand	% Algae	% Kelp	Boulder diameter	# *Oxystele*	# Littorinids	# *Acanthochiton*	# *Ligia*	# *C. punctatus*
60											
56											
52											
48											
44											
40											
36	100			25			9				
32	100		<5	15			12		9		
28	100	20	10	<5		120	38				
24	75	<15	18	22		137	30		5.5		0.5
20	60	22	22	<5		192	8.5				2
16	100	<10	30	<10		97	20		<5		
12	100	25	25	<5		224	28				4.5
8	60	70	12		<5	274	21		1		8.5
4	100	100				238	5				8
0	100	100			<2	273	16	1			6.5

Figure 14. Top - the number of Cyclograpsus punctatus active on two transects at False Bay and the mean percentage of crab body weight made up by the gut contents. Bottom - The mean number of crabs active down the length of the shore (m) per day and, a table showing other parameters measured at each station (APRIL 1989).

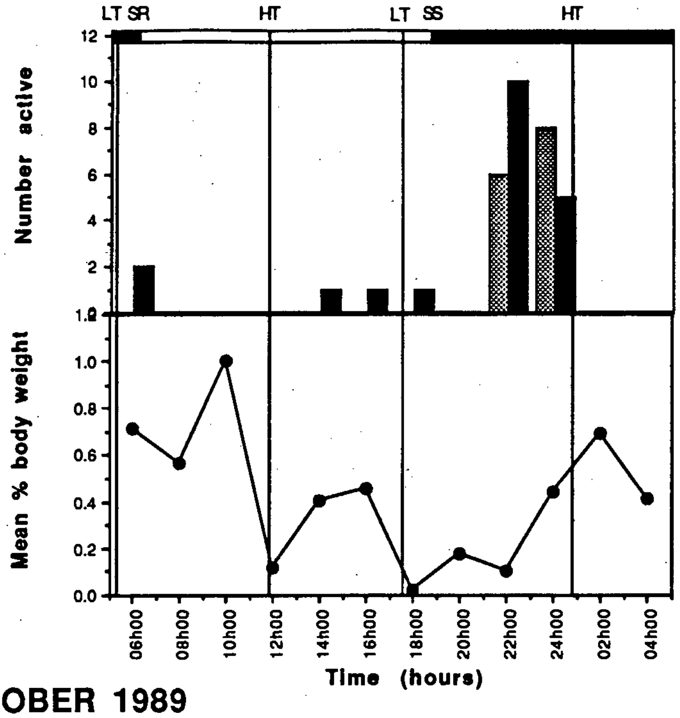


JULY 1989

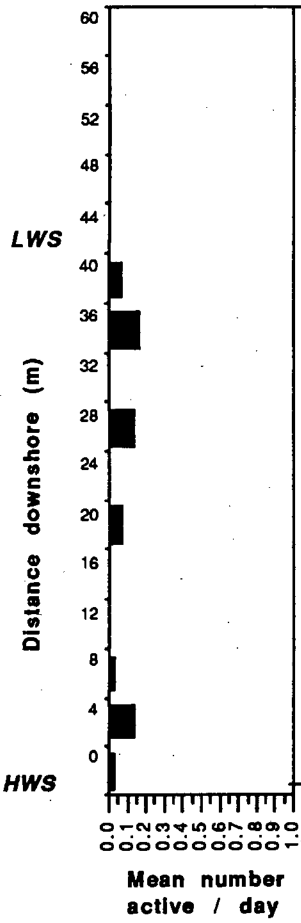


Distance downshore (m)	% Bed rock	% Boulder	% Pebble/sand	% Algae	% Kelp	Boulder diameter	# *Oxystele*	# Littorinids	# *Acanthochiton*	# *Ligia*	# *C. punctatus*
60											
56											
52											
48											
44											
40											
36											
32	100	100									
28	100	50		20							
24	100	15		<10		442	40		2		
20	100	20	<5	<5		134	24		3		1
16	100	15	2.5	<5		301	13		7		0.5
12	100	30	25	5		362	69				2
8	100	60	35	<5		484	83				
4	20	70				232	29				4.5
0	10	90				291	48	3			12.5

Figure 15. Top - the number of Cyclograpsus punctatus active on two transects at False Bay and the mean percentage of crab body weight made up by the gut contents. Bottom - The mean number of crabs active down the length of the shore (m) per day and, a table showing other parameters measured at each station (JULY 1989).

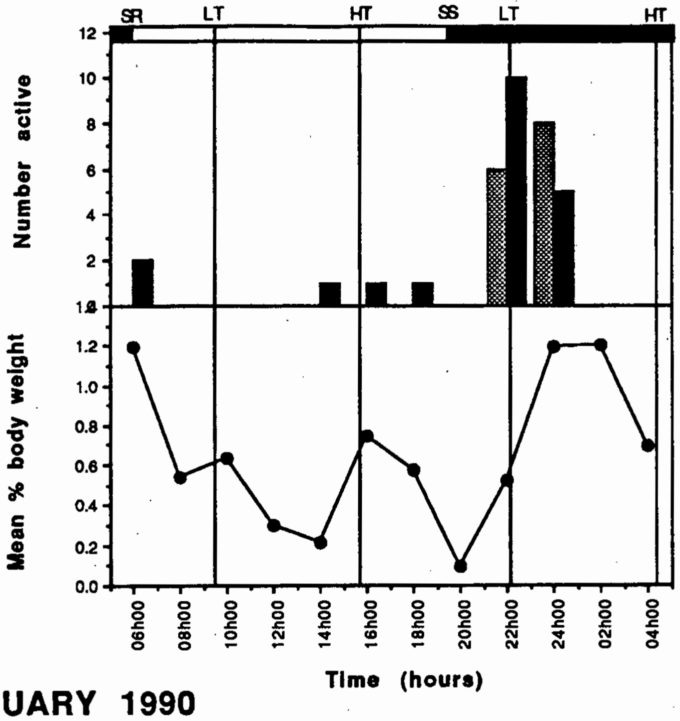


OCTOBER 1989

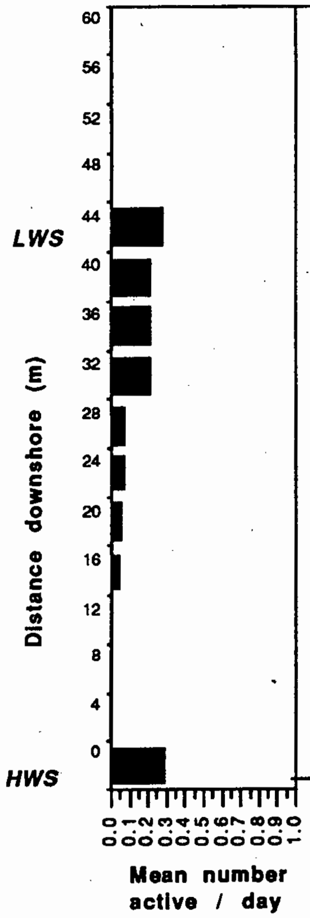


Distance downshore (m)	% Bed rock	% Boulder	% Pebble/sand	% Algae	% Kelp	Boulder diameter	# *Oxystele*	# Littorinids	# Acanthochiton	# *Ligia*	# *C. punctatus*
60											
56											
52											
48											
44											
40	15	70	50			204	48				7
36		90	15	2	<2	173	104	25	<5		10
32	75	25	<10			277	36				3.5
28	50	50	10		<2	222	31	>150			3
24	50	85	<10		<2	210	18	>250			4.5
20	<5	65	35			225	2	>150			0.5
16	40	20	55		<2	190		<150			
12	40	25	40		<2	137		>200			0.5
8	5	70	25			179		>200			1.5
4	45	60	15			133		>100			1
0	35	20	50			125		>75			0.5

Figure 16. Top - the number of Cyclograpsus punctatus active on two transects at False Bay and the mean percentage of crab body weight made up by the gut contents. Bottom - The mean number of crabs active down the length of the shore (m) per day and, a table showing other parameters measured at each station (JANUARY 1990).



JANUARY 1990



Distance downshore (m)	% Bed rock	% Boulder	% Pebble/sand	% Algae	% Kelp	Boulder diameter	# *Oxystele*	# Littorinids	# *Acanthochiton*	# *Ligia*	# *C. punctatus*
60											
56											
52											
48											
44	55	45	<10			153	56				3.5
40	45	70	5			204	106		5		10
36	35	75	10		2	257	95		3		13
32	50	50	<15			175	54		1		10
28	5	65	35			206	63		1.5		11
24	20	55	<30			212	45		<2		8
20	65	35	30			172	55				1.5
16	50	35	35			256		<150			0.5
12	100	25	<15		2	142	30	>300			3
8	55	12	45			195		>200			
4		80	20			206	5	>100			1.5
0	100	50	5			202	30	>400			1.5

Figure 17. Top - the number of *Cyclograpsus punctatus* active on two transects at False Bay and the mean percentage of crab body weight made up by the gut contents. Bottom - The mean number of crabs active down the length of the shore (m) per day and, a table showing other parameters measured at each station (JANUARY 1990).

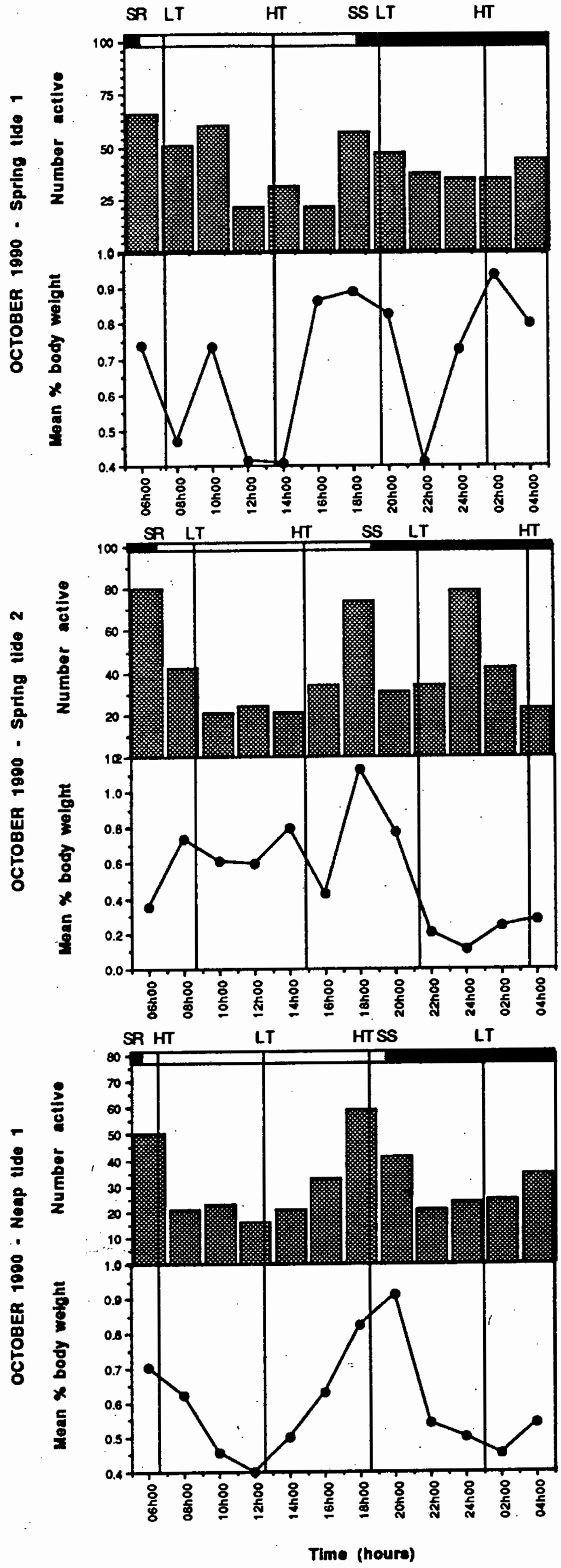


Figure 18. The number of Plagusia chabrus active on 60 m of the Kalk Bay harbour wall over three 24 hour periods. The mean percentage of crab body weight made up by food is also plotted (OCTOBER 1989).

that this is an artificially elevated figure. A large rock with a long, deeply shaded, damp overhang formed part of the transect. Crabs could be observed under the rock, moving in the comparative protection of the overhang throughout the day.

Figures 10 - 17 also show that *Cyclograpsus punctatus* is most active at or just after the nocturnal low tide. There are two exceptions to this trend, April 1989 and October 1989 at False Bay. Sampling also revealed a general feeding cycle which has a peak which coincided fairly closely with the peaks in activity. Figures 10, 12, 13, 14 and 15 show a second feeding peak at or near the daytime low tide. The two peaks are seldom of the same magnitude (day, night ; 0.68 % body weight ± 0.45 ; 0.888 % body weight ± 0.45). Figures 11, 16 and 17 also show a second feeding peak which corresponds to one of the daily high tide times. Observation of the intertidal at high tide while skindiving showed that no *C. punctatus* were active on the transects. It would appear that while the first feeding peak is relatively constant the second is more variable and follows between six to 12 hours after the first.

At Onrus and to a lesser extent at False Bay (Figures 11 and 15) maximum activity drops during July (peak, x others ± s_d ; 10, 16.6 ± 1.5 ; 11.0, 13 ± 2.12). The continued decline in peak activity in False Bay during October, however, cannot be attributed to a seasonal effect (see discussion). The quarterly nature of the data makes any further treatment of possible seasonal effects on activity difficult.

Activity downshore shows very few consistent trends, despite the fact that shore profiles were very similar. Very few of the other parameters correlate with the distribution of *C. punctatus* activity. Peak activities are usually asociated with high percentages of boulder cover and stations in which there is at least 10 % pebble and sand cover. The presence or absence of bed rock seems to play very little role in determining peak activity as do, boulder diameter, percentage algae, percentage kelp, the number of littorinids, chitons and *Ligia* sp. (Figures 10-17). Peak activity was very rarely not associated with abundant *Oxystele* spp. but was not linked to peak *Oxystele* sp. number. The frequency distributions of *C. punctatus* and *Oxystele* spp. did not match (Figures 10-17). Figures 10-17 also show that *C. punctatus* is a relatively inactive species. the numbers of crabs caught at each station often far exceeded the peak activity recorded at that station. On average, only 6.6 % (± 5.53 %) of the crabs caught on any transect were seen to be active over a particular 24 h period.

Figure 18 shows that *Plagusia chabrus* has no distinct preference for diurnal or nocturnal activity. Fairly high numbers of crabs are active throughout the day. Subtidal observation supports these findings, the authors being able to dive on *P. chabrus* at any time of the day and catch numbers of individuals. Activity is, however slightly elevated at night in all cases. The species does have a definite activity rhythm characterised by two distinct peaks, one at dusk and one at dawn (Figure 18). The dusk and dawn activity peak is clearly visible and is not influenced by tidal cycling. The shift from spring tide to neap tide did not alter the pattern at all. Dusk and dawn peaks are also of similar magnitude ($x \pm s_d$, dusk, dawn ; 66 ± 15, 65 ± 8.6) but the amplitude of the dusk peak is subject to more variability (Figure 18).

The feeding cycle of *P. chabrus* also remains relatively constant over the three tides and a clear pattern emerges despite the small sample sizes. The species does feed all day but the majority of the feeding is done at night and particularly

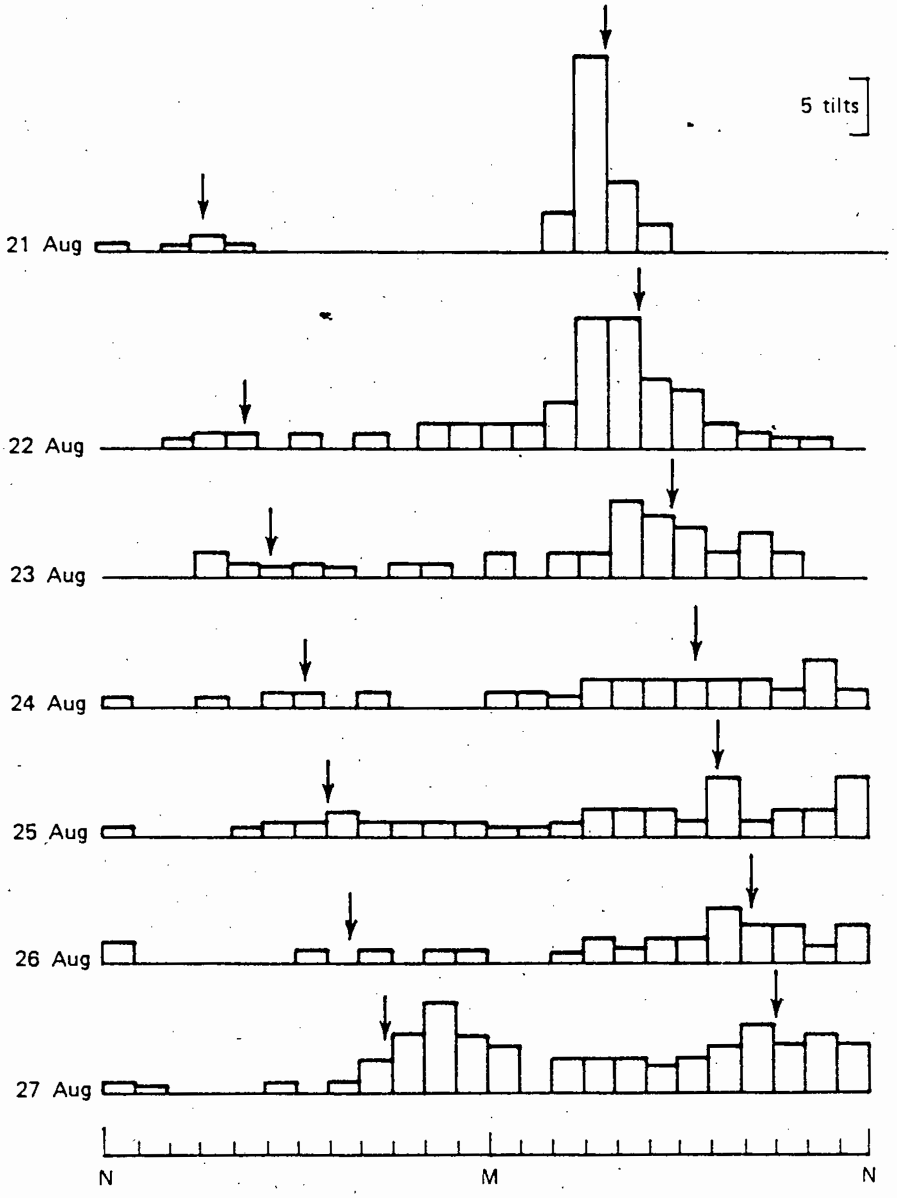


FIGURE 19. The mean hourly activity measured on an actograph of the green crab, <u>Carcinus maenas</u>. The arrows indicate the midpoints of the high tides. N = noon, M = midnight (after Naylor 1958, in Palmer 1974).

betwen 16h00 and 22h00. Figure 18a, the first spring tide sampled does differ slightly from this pattern. The feeding peak extends virtually throughout the night from 16h00 to 06h00. The decline in the mean percentage body weight of the food at 22h00 is considered to be a sampling error, a high percentage of animals being caught with empty guts. Feeding is also not tidally linked, the feeding pattern remaining constant in time despite changes in the tide.

Figure 19, shows the activity rhthym of *C. maenas*. The figure is adapted from Palmer (1974) and shows clearly that *C. maenas* is active at high tide, preferring the nocturnal high tide. No work was done on the activity rhthym of *C. maenas* on the Cape Peninsula, because this aspect of the animal's biology has been extensively examined by several other authors (see Naylor 1982).

DISCUSSION

Zonation and Habitat

Broekhuysen (1941) describes *Cyclograpsus punctatus* as a species which prefers the higher parts of the intertidal, frequenting broken up sections. Alexander and Ewer (1969) showed that *C.punctatus* frequented stony dykes constructed high in the intertidal, or excavated shallow burrows well above the water-line in the Kowie River estuary. Jackson (1988) stated that *C. punctatus* at Green Point lived high in the intertidal and that their distribution correlated with that of *Oxystele variegata*.

This study confirms the findings of Broekhuysen (1941) and Jackson (1988), showing clearly that *C.punctatus* is a strictly intertidal species (Figure 4), preferring the high shore (Figures 10 to 17). They are found in their highest densities in tumbled boulder fields which rest on shale bedrock and accumulated sediment. Their densities are lower when the rocks rest directly on sand, because there are fewer cavities beneath the rocks in which to shelter. They are far less abundant on Table Mountain Sandstone or granite (Kommetjie and Olifantsbos).

C. punctatus share their habitat with *C. maenas* where the two co-occur (Figure 4).*C. punctatus* also shares its burrows, with *Sesarma catenata* on occasion (Alexander and Ewer 1969). No evidence was found conclusively linking *C. punctatus* habitat preferences to *O. variegata* distribution.

The distribution of *C. punctatus* is similar to that of *Metograpsus thukuhar* on the East Coast of South Africa although this species is restricted to estuaries (Day 1974). It is also similar to that of *Pachygrapsus transversus* (Shumway 1983), *Cyclograpsus lavauxi* (Pellegrino 1984) which are found in Brazil and New Zealand respectively and to that of *Pachygrapsus crassipes* from the U.S.A. (Robles 1985).

Pellegrino (1984) found a relationship between crab size and boulder size in *C. lavauxi.* He also showed that large crabs predominated in high shore zones and small crabs in the low shore. He related this to distributional restrictions placed on smaller individuals by their surface area to volume ratio and the consequent danger of dessication. No evidence of such a trend were found in *C. punctatus.* There is no correlation between crab number or size and boulder size (Figure 3, 4). The point of peak density also varies with distance and time from shore to shore (Figure 2). This suggests that *C. punctatus* distribution is random and determined mainly by patchy "ideal" habitats, and localised food availability.

Plagusia chabrus is primarily subtidal (Figure 2). The primary reasons for this subtidal habitat are, that the species is stenohaline and stenothermic relative to *C. punctatus* and *Carcinus maenas* (Heeg and Cannone 1966 and Bevis-Challinor 1983). It prefers the subtidal because temperature and salinity fluctuate less (Bevis-Challinor 1983). In addition the green and brown algae upon which it feeds also only grows subtidally or in "subtidal gullies" which *P. chabrus* sometimes penetrates (Figure 2, Melkbosstrand). Shepherd (1973) considers Australian *P. chabrus* to be crevice dwelling emerging to patrol and forage over open rock surfaces. This study supports these findings. *P. chabrus* is similar in zonation and habitat to *Percon planissimum* and to *Plagusia depressa*, both of which can be found clinging to rocks on wave washed shores in Natal (Day 1974).

Carcinus maenas occupies the mid to low intertidal at Melkbosstrand and at Sea Point (Figure 2) the only sites that were sampled at which both species occur. Its subtidal distribution in South African waters is poorly understood. Muntz *et al.* (1965) states that *C. maenas* distribution in Lough Ine is limited and that it is most common, intertidally, among rocks. *C. maenas* distribution often does extend well below LWS, especially on mud flats where the tide recedes great distances (Dare, Davies and Edwards 1981). Up to 5 % of the crabs migrate as far as 600 m above LWS (Sanchez-Salazar *et al.* 1987a). All sites at which *C. maenas* is found to date in South Africa probably do not permit the extension of the species into the subtidal, given its well documented preference for sheltered water (Crothers 1967, 1968, Naylor 1965, Kitching *et al.* 1965, Sanchez-Salazar *et al.* 1987 a,b, Le Roux *et al.* 1990). Melkbosstrand and Table Bay Harbour are possible exceptions. Melkbosstrand is characterised by a long shallow subtidal flat before reaching reefs over which waves break (Field *et al.* 1980). It is possible that *C. maenas* may extend further here than recorded. Table Bay Harbour is man-made, highly sheltered and has a muddy bottom. The Cape Yacht Basin within the harbour (subtidal) supports huge numbers of this species (Barkai and Hanekom pers. comm.), and, it is certain that they extend in similar numbers throughout the harbour environment.

Shumway (1983) has shown that oxygen demand has a direct bearing on the relative distribution and habitat preferences of four species of Brazilian crab. *Petrolisthes armatus* with the lowest tolerance was only found in subtidal channels. *Pachygrapsus transversus*, a grapsid shore-crab had the highest tolerance and frequented the high intertidal. *Panopeus herbstii* and *Callinectes danae* tolerances fell between those of *P. armatus* and *P. transversus* as did their habitat preferences.

Pellegrino (1984) showed that the relative distribution of *Cyclograpsus lavauxi*, *Hemigrapsus edwardsi* and *Heterozilus rotundifrons* were related to their respective tolerance to dessication. *C. lavauxi* was the most tolerant frequenting the high shore. *H. rotundifrons* was the least tolerant and frequented the low shore.

The relative distributions of *Cyclograpsus punctatus*, *Plagusia chabrus* and *Carcinus maenas* are similarly determined. *C. punctatus* is tolerant of high and low salinities and can resist dessication (Heeg and Cannone 1966, Bevis Challinor 1983, Alexander and Ewer 1969) and consequently favours the high intertidal. *Plagusia chabrus* is the least tolerant of fluctuations in salinity and temperature (Heeg and Cannone 1966, Bevis-Challinor 1983) and is strictly subtidal. *Carcinus maenas* is also tolerant of dessication and variable salinities, but not to the same degree as *C. punctatus* and thus frequents the low to mid intertidal.

Diet

Gut contents

C. punctatus is a herbivore-cum-detritivore, feeding mainly on kelp wrack (Figures 7 and 8, Table I). Also significant in its diet are one or two selected gastropod species, particularly *Oxystele variegata* and *Acanthochiton garnoti* , and the isopod *Ligia dilatata. L. dilatata* are fast moving and as a consequence, it seems unlikely that *C. punctatus* pursues and captures them. They are probably trapped or scavenged. *C. punctatus* and *P. chabrus* fragments also appear in the diet. *C. punctatus* is not an aggressive species and it is therefore difficult to support the hypothesis that they actively prey on *P. chabrus*. The crab probably scavenges *P. chabrus* carcasses within the intertidal. Broekhuysen (1941) does note that hard-shelled *C. punctatus* may kill vulnerable soft-shelled individuals shortly after they have moulted. It would appear that *C. punctatus* may thus be cannabilistic under certain circumstances.

Both male and female *C. punctatus* chelae have high mechanical advantage (Table III). Male chelae are larger than females and so have a larger MA. Neither males or females have pronounced tubercles or reflected teeth on the cutting edges of their chelae. This suggests that force is fairly uniformly applied along the length of the cutting edge. Force is probably strongest at the dactylus insertion, as it is at the fulcrum of a pair of domestic scissors. It is suggested that these strong chelae are used as shears to "clip" and cut pieces of stipe, holdfast or frond from stranded kelp wrack. Kelp stipes and fronds are often several milimetres thick, rubbery and difficult to tear, yet *C. punctatus* can be seen cutting and consuming kelp with ease.

C. punctatus was observed feeding on the coiled gastropod, *Oxystele variegata* and upon the chiton, *Acanthochiton garnoti.* The chelae were used to break a "slot-like" opening in the shoulder of the body whorl of *O. variegata* and as much flesh as could be reached was pulled out. Alternatively the chelae were inserted into the gastropod, the operculum pulled off and as much flesh as possible consumed. No *O. variegata* shells were crushed outright and it appears that the large chelae of *C. punctatus* were a hindrance rather than a help, very few of the gastropods ever having all the flesh removed from them. *A. garnoti* were manipulated in the chelae until their foot was exposed and then in "chopstick" like fashion the flesh was scooped from under the valves. Schaeffer (1970) in a study of the gut morphology of *C. punctatus* notes that it has a crushing gastric mill. Presumably this is associated with the digestion of coarse kelp material and resilient gastropod flesh. The apparent inability of the crab to use its large chelae to crush prey may indicate that the large chelae of the male may be used during courtship, or in the establishing of dominance.

Animal prey is included in the diet. The increase in the amount of animal material in October and January at Onrus (Figure 5) and in January at False Bay sites (Figure 6) may be related to the moulting cycle of the crab. *C. punctatus* moults (and consequently grows rapidly) in spring and summer

(Broekhuysen 1941). The rapid tissue expansion associated with this process may necessitate the intake of more protein thus increasing the percentage of animal material in the diet. The diet of *C. punctatus* is similar to that recorded by Robles (1985) for *Pachygrapsus crassipes.* October to January is also the time of minimal kelp deposition on the shore (Stenton-Dozey and Griffiths 1983). It is possible that the incorporation of greater amounts of animal material over this period is simply a function of reduced kelp availability.

Plagusia chabrus is a subtidal omnivore which consumes selected green, brown and coralline algae (Figure 7, 8 and Table I). *P. chabrus* also consumes fair quantities of juvenile mussels, barnacles and amphipods. Most of the invertebrates consumed by *P. chabrus* are associated with algae or mussel beds. Many of the guts which were full of green or brown algae were characterised by relatively large strip-like pieces of thallus and a highly variable suite of invertebrates. The crabs can be seen grasping algal fronds between their chelae, perpendicular to the fronds axis. They are rarely seen consuming or tearing off chunks of algal material. The fairly evenly spaced occluding teeth and the spoon-like nature of the underside of *P. chabrus* chelae lead us to suggest that *P. chabrus* grasps algal fronds and then pulls the chelae backwards over the surface towards the mouth. As it does this, it fills the "spoon" with the long, strap-like, pieces of algae and numerous invertebrates seen in the gut contents. The chelae are then drawn to the mouth and the food is ingested. Guts often contain only juvenile *Notomegabalanus algicola* or juvenile mussels. It is suggested that *P. chabrus* is an opportunistic omnivore, consuming suitable prey as and when they are encountered during a foraging bout.

No data on moulting or growth cycles exists for this species. As a result, shifts in the percentage animal material in the diet with changing season, are difficult to interpret. The increase in percentage animal values in October at Oudekraal (Figure 8) and in July and October at Kalk Bay (Figure 7) may be related to the breeding cycle. Females require more protein for egg production during this period (September to February) and therefore may take in greater percentages of animal material just prior to or during this period. It is possible that the intertidal algal blooms, associated with summer (McQuaid 1985 in, Branch and Griffiths 1988) increase the local availability of algae, hence raising the percentage of algal material in the diet.

Female chelae are "faster" than the male (Table III), but both have medium to high MA. The high MA allows it to break and consume mussels and barnacles. No evidence was found to suggest that *P. chabrus* fed on the local abalone, *Haliotis midae* although the two species occur in the same habitats.

Carcinus maenas only consumed minimal amounts of algae. The crusher-chela of both males and females had the highest chelal MA of all three species this being a clear indicator of the carnivorous tendency of this crab. The diet of *C. maenas* in South African waters is very similar (at least in composition) to the diet of *C. maenas* in Maryland, U.S.A. (Ropes 1968). The only difference being that *C. maenas* in Maryland consume more bivalves than those in South African waters. It is possible that this difference is related to local prey availability. Most of the sites frequented by *C. maenas* in South Africa are not characterised by large, accessible mussel beds although they readily consume these species in the laboratory.

Enzymology

Several studies have suggested that the levels of digestive enzymes in certain species of crustacean may correlate with the amount and type of food being consumed (Stuart et al. 1985). The digestive arsenals of a number of invertebrates including some crabs and crayfish have been examined in varying levels of detail in the literature. *Pugettia producta*, the kelp crab, only eats algae when starved and contains an amylase enzyme which does not digest laminarin and fucoidin (Huang and Giese 1958). Laminarin and fucoidin are important constituents of algae.

C. punctatus has high amylase and very high cellulase, alginase and laminarinase activity relative to *Carcinus maenas* and *Plagusia chabrus* (Table II). This is consistent with the dietary information obtained by gut content analyses. Alginase is a common digestive enzyme in invertebrates which eat brown algae (Eppley and Lasker 1959). Cellulose is a constituent of many species of algae while laminarin is an important constituent of kelp.

Plagusia chabrus has high protease levels, moderate cellulase and alginase levels and very little laminarinase. These results seem to contradict the gut content analysis which suggests that the digestive arsenal of *P. chabrus* should have greater levels of algolytic enzymes. The authors contend that *P. chabrus* is more dependant on the invertebrate component of its diet than the gut content analysis indicates. *P. chabrus* has the highest chitinase activity (Table II). Although one must interpret this figure with caution, the high chitinase concentration seems consistent with the high intake of amphipods and other invertebrates with a high chitin content.

The results obtained for *Carcinus maenas* are consistent with those obtained by Hylleberg-Kristensen (1972). Chitinase values are surprisingly low (Table II) but the crabs digestive arsenal is clearly dominated by proteases (Table II). This is what one would expect from a carnivorous species (Figure 9).

It would appear that digestive enzymes in *Cyclograpsus punctatus*, *Plagusia chabrus* and *Carcinus maenas* do indeed correlate well with dietary information drawn from gut content analysis, this supports the work of Stuart et al. (1985). There is clearly very little dietary overlap between the three species.

Activity

It is a well-established fact, that many coastal marine organisms exhibit persistent circadian and circatidal rhythms (Naylor 1982). Several crab species have been the target of study in this regard. Palmer (1974) has worked extensively on activity in *Uca* spp. and has shown that *Uca* spp. are active at low tide during the day and the night. Naylor (1958, 1965 and 1982) has demonstrated that *Carcinus maenas* has a complicated circadian and circatidal rhythm. It is more active at night, but activity peaks on the nocturnal high tide (Figure 19). Wallace (1972) showed that the metabolic rate of *C. maenas* rose upon inundation and suggested that inundation provided the trigger for locomotary activity. Wallace (1972) does however, concede that the increase in metabolic rate may have been due to increased oxygen uptake by the gills. *Scylla serrata* spends the entire day inactive, emerging at night to feed. The period of time spent active, was related to the amount of food present. If no food was available, *S. serrata* spent half the normal time foraging (Hill 1979).

Data presented in this study do not lend themselves to a full analysis of activity as completed by Palmer (1974) or Naylor (1982). In order to make a full analysis, one would have to follow the activity of the species in question for a number of consecutive days. Given the logistics of this study and the fact that it was conducted in the field, this was impossible.

C. punctatus activity rhythm has a tidal and daily component (Figure 10 to 17), with one or two exceptions. The animal is active at both low tides and apparently feeds at both. The amplitude of the activity peak is increased at night as the circadian rhythm reinforces the circatidal component. The two exceptions (Figures 14 and 16) are difficult to explain. In Figure 16 the two low tides fall virtually at dusk and dawn, with the result that crabs would have had to emerge during the day. Here thecircatidal rhythm has been damped out and only the circadian rhythm is present, with low numbers of crabs emerging at night. The numbers are low because the usual reinforcement of numbers by the co-operation of tidal and daily rhythm is not evident.

It seems safe to say that nocturnal and diurnal feeding and activity peaks do coincide (Figures 10 to 17). The data is not conclusive however. A percentage of the variability is explained by the small sample sizes used to derive the feeding rhythm (*viz.* 10 individuals every two hours). It is possible however, that another, more cryptic rhythm, operates in the feeding cycle. Such a rhythm will only be detected using longer consecutive day observation periods.

Peak activity down-shore, appears to be random and is not apparently linked to season, crab number or, the distribution of prey species (Figures 10 to 17). It is probably a function of habitat characteristics and kelp or algal wrack availability.

Where the habitat is ideal, or food is plentiful, there the highest number of crabs will be active. The heterogenous nature of any intertidal, and the temporal instability of the food supply makes the peak activity individual to each transect laid and each site studied. No conclusive correlation can be demonstrated between *Oxystele variegata* distribution and that of *C. punctatus* as was done by Jackson (1988). Figures 10 to 17 also reveal that *C. punctatus* is not, generally, a very active species.

Plagusia chabrus on the other hand, has a definite bimodal circadian rhythm (Figure 18) peaking at dusk and dawn. No tidal rhythm is evident in the data (Figure 18). The feeding cycle also appears to be dominated by a circadian rhythm with a single peak at dusk. Palmer (1974) points out that animals taken from a harbour environment may have lost the tidal component of their rhythm. This is not a factor in this study. This study was conducted at a site which was exposed to incoming swell and experiencing a tidal range of ± 1.2 metres during the spring tides examined. Subtidal observation did not reveal any tidally related rhythm.

C. punctatus circatidal activity is probably triggered by emersion and circadian activity by day length and light level. The reluctance of *C. punctatus* to emerge at high tide may be a predator avoidance mechanism. *C. punctatus* is one of the favoured prey items of many clinid fish (Bennett et al. 1982). Activity in *P. chabrus* is probably triggered by changes in the light level.

It would appear that there is very little overlap between the activity rhythms of the three species considered in this paper. *C. punctatus* is active at night at low tide, *Carcinus maenas* mainly at night at high tide and *P. chabrus* is active at dusk and dawn with no circatidal component. The only possible overlap will occur when the circatidal components of *C. punctatus* and *Carcinus maenas* activity coincide, on shores where they co-occur. No such overlap will occur with *C. maenas*, *Cyclograpsus punctatus* and *Plagusia chabrus* since *P. chabrus* is spatially separated from the other two species.

CONCLUSIONS

1. *C. punctatus* is a strictly intertidal species, feeding on kelp wrack and selected gastropods. It has powerful clipping chelae and a digestive arsenal which matches its diet, consisting of very high levels of algolytic enzymes. It is active primarily at night on the low tide, but has two feeding peaks per day.

2. *Plagusia chabrus* is primarily subtidal on wave washed shores, only penetrating the intertidal via submerged gullies. It feeds highly omnivorously and has a digestive arsenal and chelal morphology which matches its diet, consisting of moderate to high levels of algolytic and proteolytic enzymes, in particular chitinase. It is active throughout the day but primarily at dusk and dawn. It feeds at dusk.

3. *Carcinus maenas* is a mid to low intertidal species, restricted to sheltered water. It has a massive crusher-chela, is carnivorous and has a digestive arsenal to match consisting of moderate to high levels of proteolytic enzymes and small amounts of enzymes associated with algal digestion. It is active by day and night during high tide and feeds on both occasions.

4. There is very little overlap between the three species and it is predicted that *C. maenas* will not impact populations of *C. punctatus* or *P. chabrus* to any significant degree. The possibility exists on shores where *Cyclograpsus punctatus* and *Carcinus maenas* co-occur that some displacement and carnivory of *C. punctatus* by *C. maenas* will occur.

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CHAPTER 5

ON THE MORPHOMETRICS AND POPULATION BIOLOGY OF THE CRABS *CYCLOGRAPSUS PUNCTATUS* (M.Edw.) AND *PLAGUSIA CHABRUS* (De Haan).

ABSTRACT

Cyclograpsus punctatus and *Plagusia chabrus* inhabit rocky intertidal and sublittoral shores along the Cape coast. Seasonal population, morphometric and reproductive data for these crabs is presented. Carapace widths were measured in the standard manner, number of males, females and females ovigerous were counted, egg masses were subsampled and the mass to number ratio used to estimate egg number. Male frequency distributions were skewed to the right and females slightly to the left. Recruitment occurred between July and January for *C. punctatus* and in July for *P. chabrus*. Males grew larger than females in *C. punctatus* (female, male ; 18.28, 42.38 mm) and in *P. chabrus* (female, male ; 17.3, 38.92 mm). *P. chabrus* grew larger at Oudekraal than at Kalk Bay (37.67 and 43.63 mm respectively) and *C. punctatus* grew larger at Onrus than in False Bay (20.3 and 17.02 mm respectively). Males consistently outnumbered females although sex ratio fluctuated seasonally, following the percentage ovigerous curve. A U-shaped sex ratio curve with respect to size was found in both species. Morphometric parameters scaled isometrically with CW except for abdominal width in *P. chabrus* and chela length and width in both species, which scaled allometrically. Changes in growth rate of the abdomen and the chela occurred at puberty.*C. punctatus* breeds between May and September, *P. chabrus* between September and February. The number of eggs increased allometrically with CW. *C. punctatus* proved to be more fecund than *P. chabrus*, (1890.3 and 1694.5 eggs/mm CW respectively) but both species are less fecund than the invasive *Carcinus maenas* (4021.7 eggs/mm CW).

INTRODUCTION

The grapsid crabs *Cyclograpsus punctatus* (M.Edw) and *Plagusia chabrus* (De Haan) are widely distributed throughout the southern hemisphere (Montgomery 1930, Barnard 1950). *P. chabrus* is found up to Port Shepstone and *C. punctatus* is abundant all along the South African coast. They are the dominant rocky shore crabs on the Cape Peninsula. Large numbers of the invasive European shore-crab *Carcinus maenas* are found in sheltered environments from Camps Bay to Saldanha Bay (Le Roux *et al.* 1990).

P. chabrus is a large, red, subtidal and intertidal rock-crab which although aggressive is fairly sensitive to changes in its external environment (Heeg and Cannone 1966, Challinor 1983). Despite its size, abundance and visibility, little was known about the biology of this species prior to the present study. Heeg and Cannone (1966) concluded that *P. chabrus* was sensitive to small changes in salinity and was in this respect far less robust than *C. punctatus.* Shepherd (1973) concluded that Australian *P. chabrus* has a dusk-dawn activity peak and is the major predator of *Haliotis roei* in Australian waters. Muir (1974) did an anatomical and morphological study on *P. chabrus* , while in an unpublished report Bevis-Challinor (1983) looked at temperature tolerance, energy budget and energetic efficiency of the species.

The small, brown, rocky-intertidal shore-crab *C. punctatus* is far less sensitive to a changing environment than *P. chabrus.* It is capable of tolerating prolonged periods of exposure to the air, fluctuating temperature (Bevis-Challinor 1983) and low salinities (Heeg and Cannone 1966). Much more is known about this species than about *P. chabrus.* Work has been done on its population structure at Strandfontein (Broekhuysen 1941) and at Green Point in the Cape (Jackson 1988). The ecology, habitat preference and zonation of *C. punctatus* in the Kowie river estuary was studied and compared to that of the mud crab *Sesarma catenata* (Alexander and Ewer 1969). Control of dominance heirarchies within populations (Caiger and Alexander 1971) and energetics (Bevis-Challinor 1983) have also been examined. The work done by Challinor was, however, inconclusive.

This study presents comparative morphometric, population and reproductive data for *C. punctatus* and *P. chabrus* populations from four sites in the south-west Cape - Onrus, Oudekraal, Gordons Bay and Kalk Bay (Figure 1). It is understood that seasonal sampling is not the optimal manner in which to conduct a population study. The data presented here was collected incidentally, while completing the main aims of the thesis which were to broaden our understanding of the biology of local crabs and assess the impact of *C. maenas* on local biota. It was felt that although the data were not ideal, it was nevertheless worth recording for use by future workers in the field.

METHODS

The crabs used in this study were collected between April 1989 and May 1990. *P. chabrus* were collected by hand while skin diving and *C. punctatus* by hand from the intertidal. Both species were sampled only at three monthly intervals owing to logistical constraints. *P. chabrus* was collected from Kalk Bay and Oudekraal (Figure 1). An attempt was made to capture 50 individuals at each sampling, but this was not always possible owing to the relative scarcity and agility of this crab. *C. punctatus* individuals were initially collected from

Wooley's pool at Kalk Bay and from Davie's pool in Onrus (Figure 1). The Wooley's pool site proved to be unable to sustain sampling pressure and was substituted for, in October 1989 and January 1990, with a similar site at Gordon's Bay (Figure 1). Fifty *C. punctatus* individuals were captured at each sampling. In all cases crabs were killed immediately and fixed in four percent formalin buffered in seawater.

The carapace width of each specimen was measured. For *P. chabrus* this was the distance between the most distal marginal teeth and for *C. punctatus* it was measured over the broadest region of the carapace. These data were subsequently used to plot size-frequency column graphs for each site. All measurements were taken to 0.01 mm using Vernier calipers. Other measurements taken were carapace length, left and right chela length and width, width of the fourth abdominal segment and the width of the merus of the fifth pereiopod (see Figure 2).

The crabs were weighed wet and then dried to a constant weight (36 hours at 80 °C) after which they were reweighed. A number of regressions were then plotted between these morphometric parameters. The results for both species were compared with morphometric work extant in the literature.

The crabs were sexed and the sex ratios calculated. The number of ovigerous females in each sample was counted and percentage ovigerous females calculated. The manner in which females of each species bears the egg plug is shown in Figure 3.

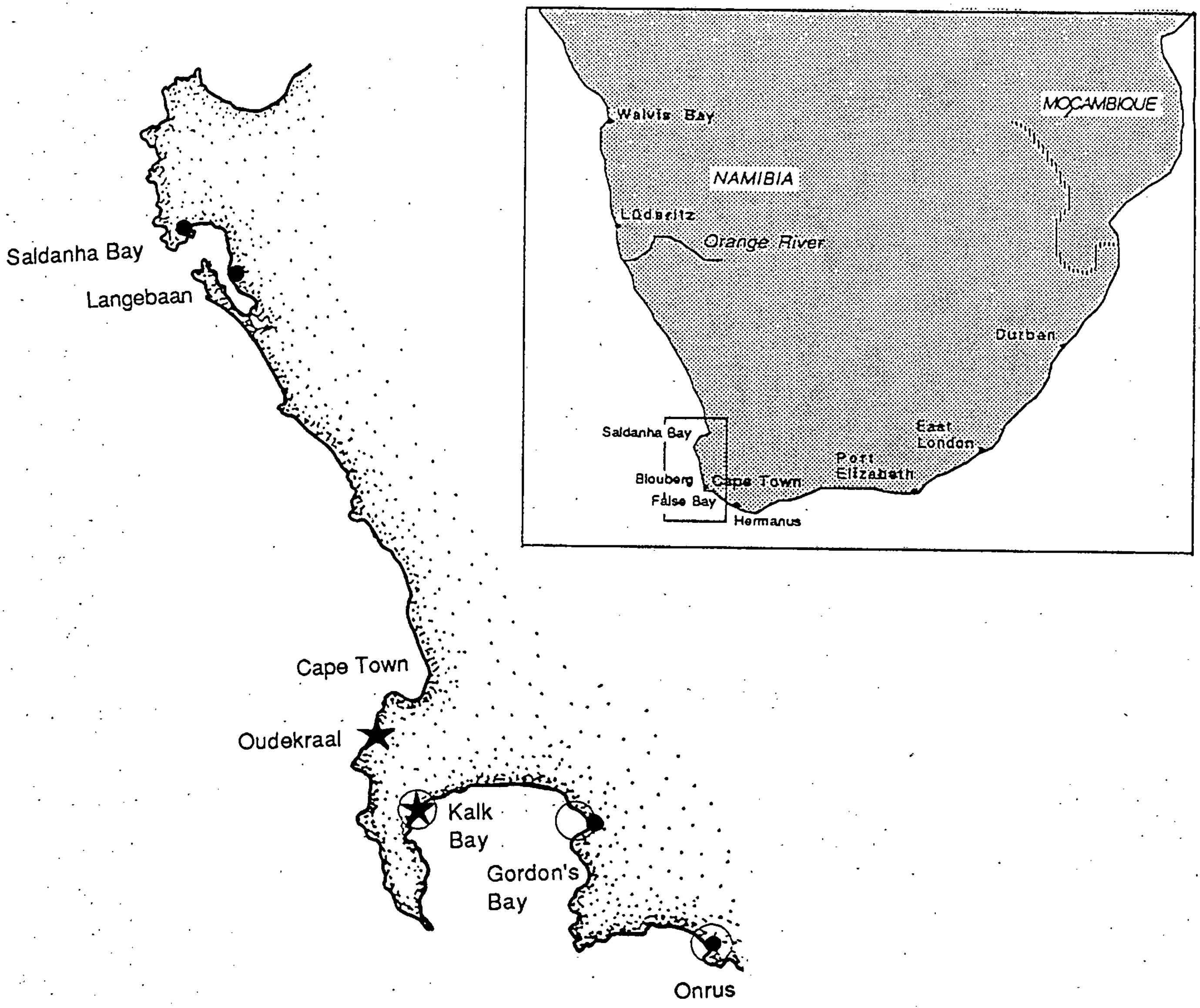

Figure 1. A map of the Cape Peninsula and surrounding areas showing the sites at which samples were collected for (★) - Plagusia chabrus and, (◯) - Cyclograpsus punctatus.

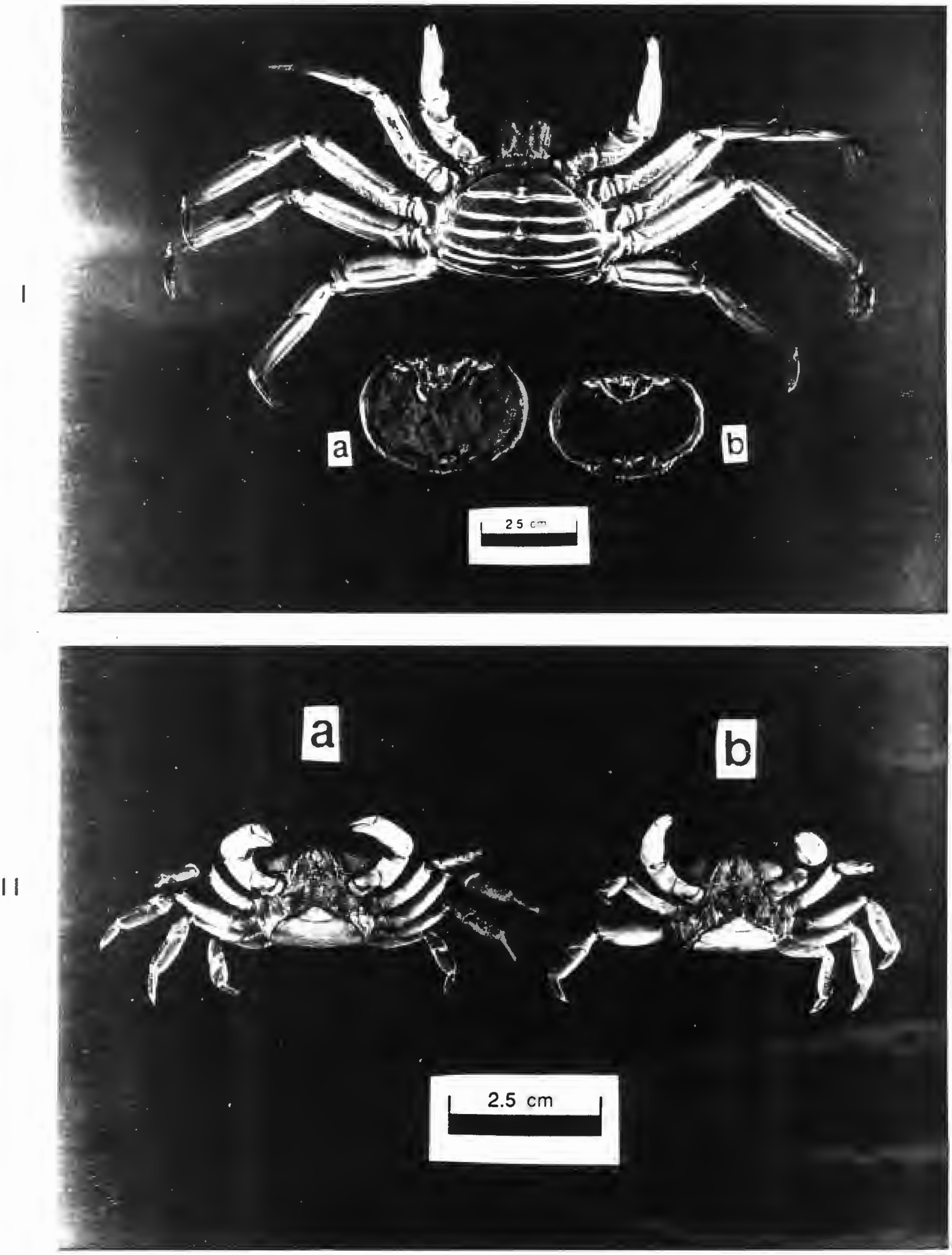

Figure 3. Photographs of female crabs in berry. I - *Plagusia chabrus* and II - *Cyclograpsus punctatus*, a - early egg development (orange) and, b - later development to the eyespot stage (brown).

III

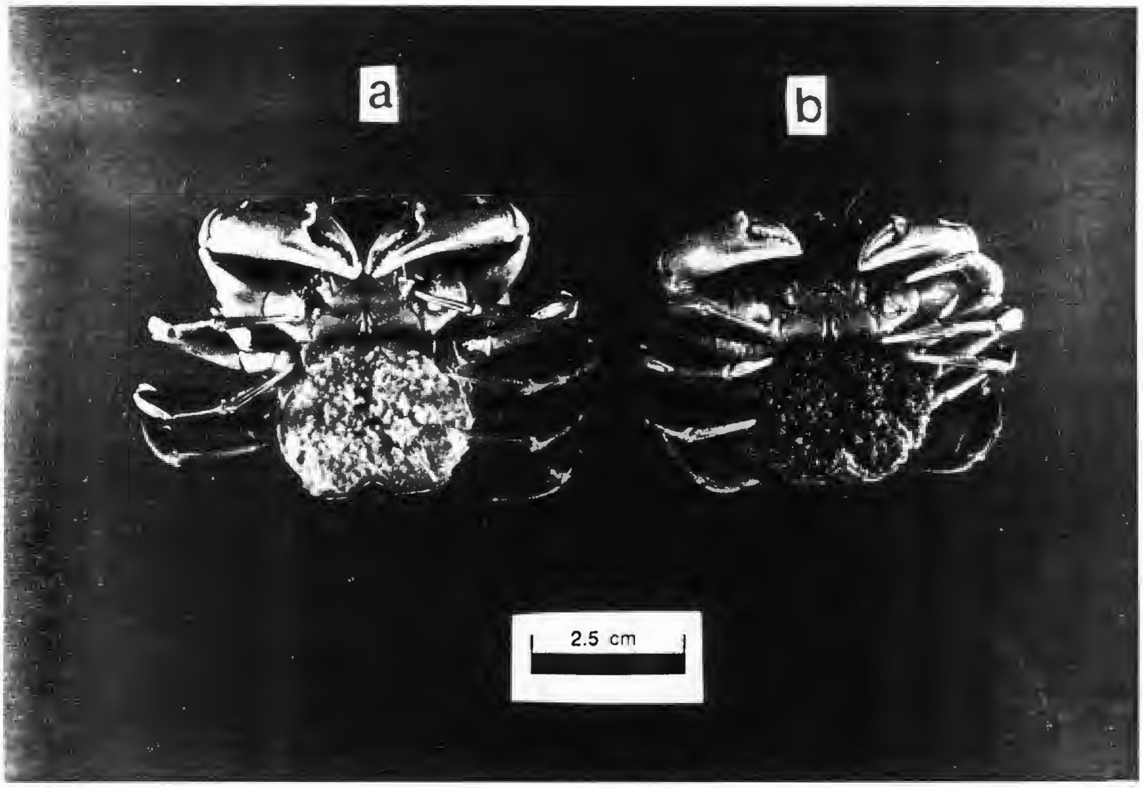

Figure 3 (cont). Photographs of female crabs in berry. III - Carcinus maenas, a - early egg development (orange) and, b - later development to the eyespot stage (brown).

Ovigerous females had their eggs removed and weighed wet to 0.01 g. A regression of egg wet weight on carapace width was then plotted for each species. Four small sub-samples were taken from the egg mass of each ovigerous female, weighed and the eggs separated and counted under a stereo- light-microscope. The mean number to mass relationship calculated from the four subsamples was then used to calculate the total number of eggs carried by that female. Regressions of total egg number on carapace width were plotted for both *C. punctatus* and *P. chabrus*. Comparisons were drawn between the fecundity of *C. punctatus* and *P. chabrus* and that of other local and overseas species.

RESULTS and DISCUSSION

Population biology

In the course of this study, 1350 *Cyclograpsus punctatus* and 750 *Plagusia chabrus* were collected and examined. The carapace width (CW) of male *C. punctatus* captured ranged from 8.8 to 32.25 mm, while that of male *P. chabrus* ranged between 16 and 65 mm (Figures 4,5). Female *C. punctatus* ranged in CW from 6 to 26 mm, while female *P. chabrus* ranged between 10 and 60 mm. The mean size of males ($x \pm s_d$, n ; 18.28 ± 2.18, n=270 ; 42.38 ± 6.04, n=216) was significantly larger ($t = 4.26$, $p < 0.05$; $t = 7.44$, $p < 0.05$) than that of females ($x \pm s_d$, n ; 17.3 ± 2.35, n=140 ; 38.92 ± 2.71, n=154) in both species. Crabs also differed significantly in size between sites. *C. punctatus* were significantly larger at Onrus than in False Bay ($x \pm s_d$, n ; 20.3 ± 1.3, n=200 ; 17.02 ± 1.94, n=200 ; $t = 19.8$, $p < 0.05$), while *P. chabrus* were significantly larger at Oudekraal than at Kalk Bay (x ± sd, n ; 37.67 ± 2.8, n=160 ; 43.63 ± 6.36, n=165 ; t = 5.06, $p < 0.05$).

Size-frequency distributions were largely unimodal with bimodality only evident following recruitment events over the year. In *C. punctatus* these occurred during July and October at Onrus and in January in False Bay (Figure 4). In *P. chabrus* juveniles were evident in April and July at Kalk Bay, but no clear pattern was revealed in the data from Oudekraal. The open nature of the site at Kalk Bay makes the capture of the agile juveniles of *P. chabrus* much easier. Owing to the heavy kelp growth and more difficult diving conditions at Oudekraal, smaller samples, which included fewer juveniles were collected, possibly masking any recruitment which may have occurred. The time of year during which recruitment occurs varies with changing species, latitude and prevailing sea temperature (Broekhuysen 1936, Crothers 1967,1968, Hill 1979 and Sumpton 1990). Broekhuysen (1941) could not show clear trends in recruitment or growth and failed to show distinct year classes in a population of *C. punctatus*. This failure was attributed to frequent, unpredictable moulting even in mature adults and to great variability in growth rates. The quarterly nature of the data presented here does not allow the formulation of any definite conclusions concerning recruitment. This paper does, however, suggest that recruitment in *C. punctatus* occurs primarily between July and January, while in *P. chabrus*, it occurs primarily in July.

Male size-frequency distribution curves for both species are distinctly skewed to the right, while those of females are slightly skewed to the left. This is a fairly common pattern in crabs, with many males occuring in the largest size classes skewing their curve to the left and those of the females slightly to the right

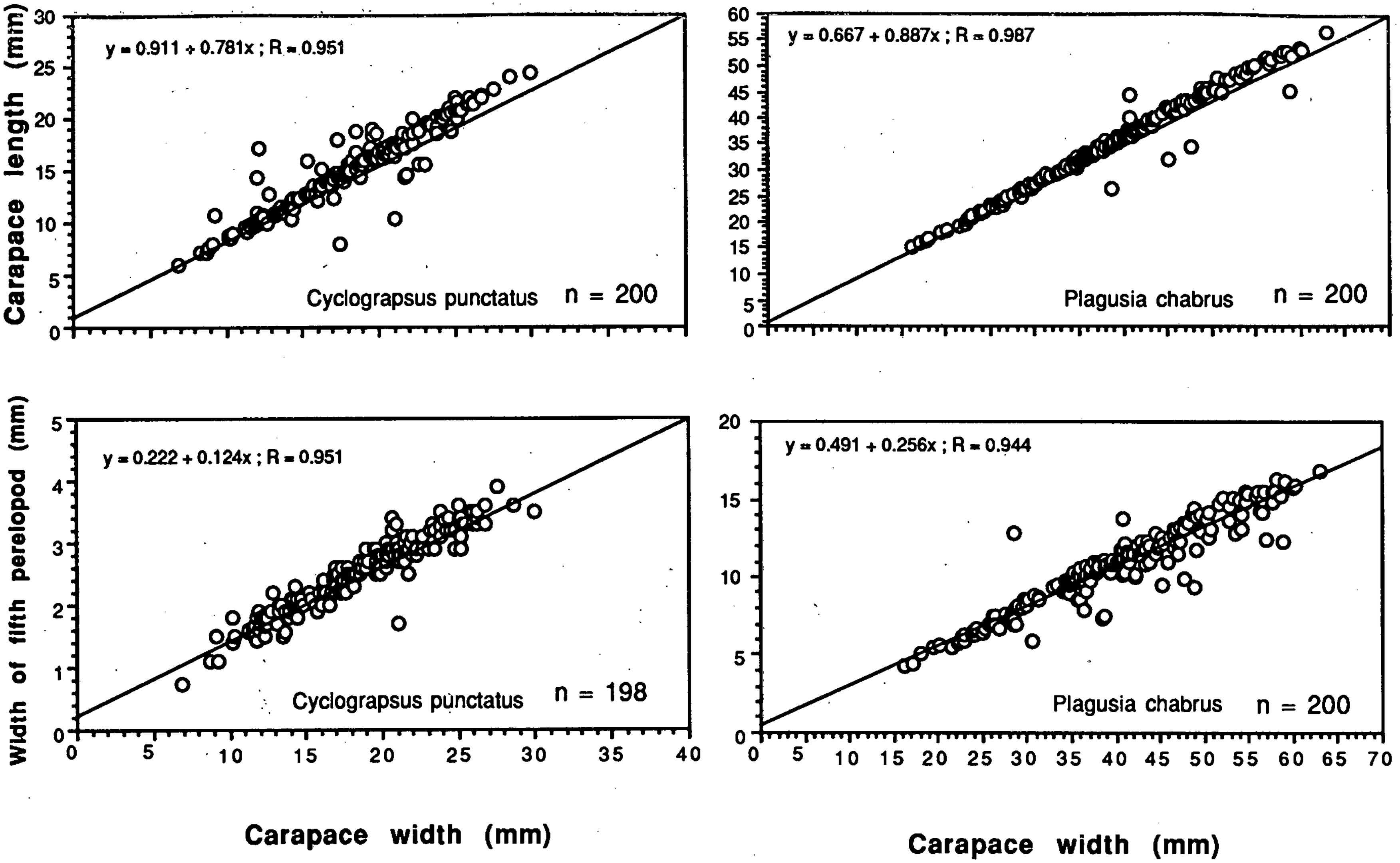

FIGURE 7. A plot of, A - carapace length (mm) and, B - the width of the fifth pereiopod (mm) against carapace width (mm). Data for Cyclograpsus punctatus and Plagusia chabrus is presented. Regression equations are shown for each curve plotted. n = the total number of individuals used in each analysis.

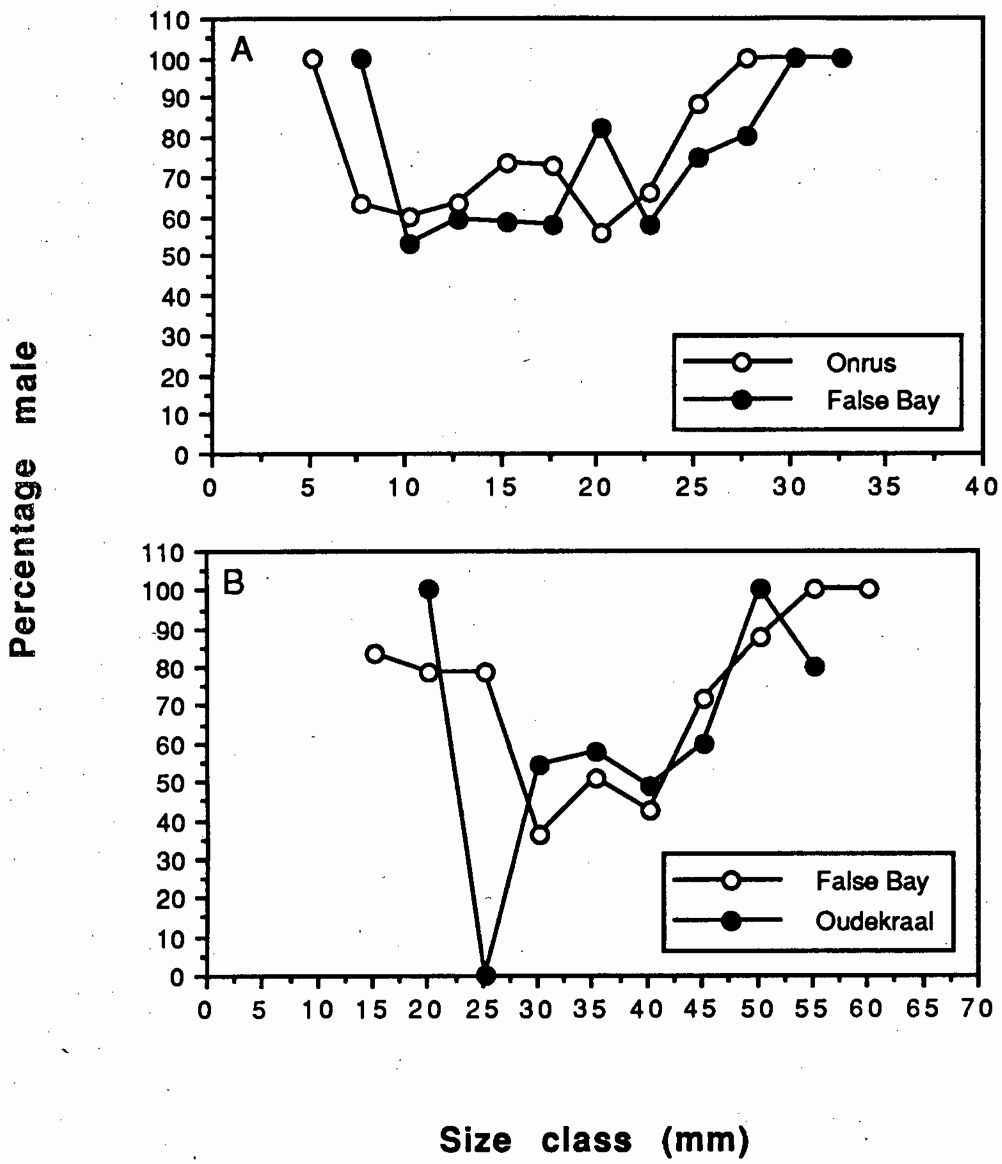

FIGURE 10. Variation in sex ratio with size of crab for, A - Cyclograpsus punctatus and, B - Plagusia chabrus. Sites at which the sampling was conducted are shown in the legends.

Reproduction

Copulation in *P. chabrus* and *C. punctatus* was very rarely observed, suggesting that both species copulate in hiding and that neither copulates for a protracted period of time. Females of both species were held sternum to sternum with the male superior. This technique is typical of most species of crab (Hartnoll 1969, Du Preez 1981). It was not possible to determine with any certainty whether or not *P. chabrus* females were soft shelled. *C. punctatus* females were soft shelled.

Percentage male data shows how the sex ratio varies with size in both species (Figure 10). At small sizes and very large sizes male *C. punctatus* and *P. chabrus* dominated the population of almost totally. *C. punctatus* was clearly male dominated with all size classes having percentage male values above 50 %. At intermediate sizes the sex ratio in both species approached 1:1. At the False Bay site the *P. chabrus* population was dominated briefly by females (30-35, 40-45 mm size classes). At Oudekraal, however, the population remained male dominated. Generally speaking , the patterns were similar for each of the two sites used for each of the two species. No 25.05-25.05 mm *P. chabrus* were collected from Oudekraal, hence the abberant point shown in Figure 10b.

The dominance of females at intermediate sizes was possibly a result of the tendency in reproductively active females to defer somatic growth in order to maximise reproductive output. This temporary deferment in *C. punctatus* and *P. chabrus* caused the females to accumulate in the 10-15 mm and 30-35 mm interval respectively. The tendency in ovigerous females to hide reduced the predation pressure on them, causing further accumulation. The fact that the

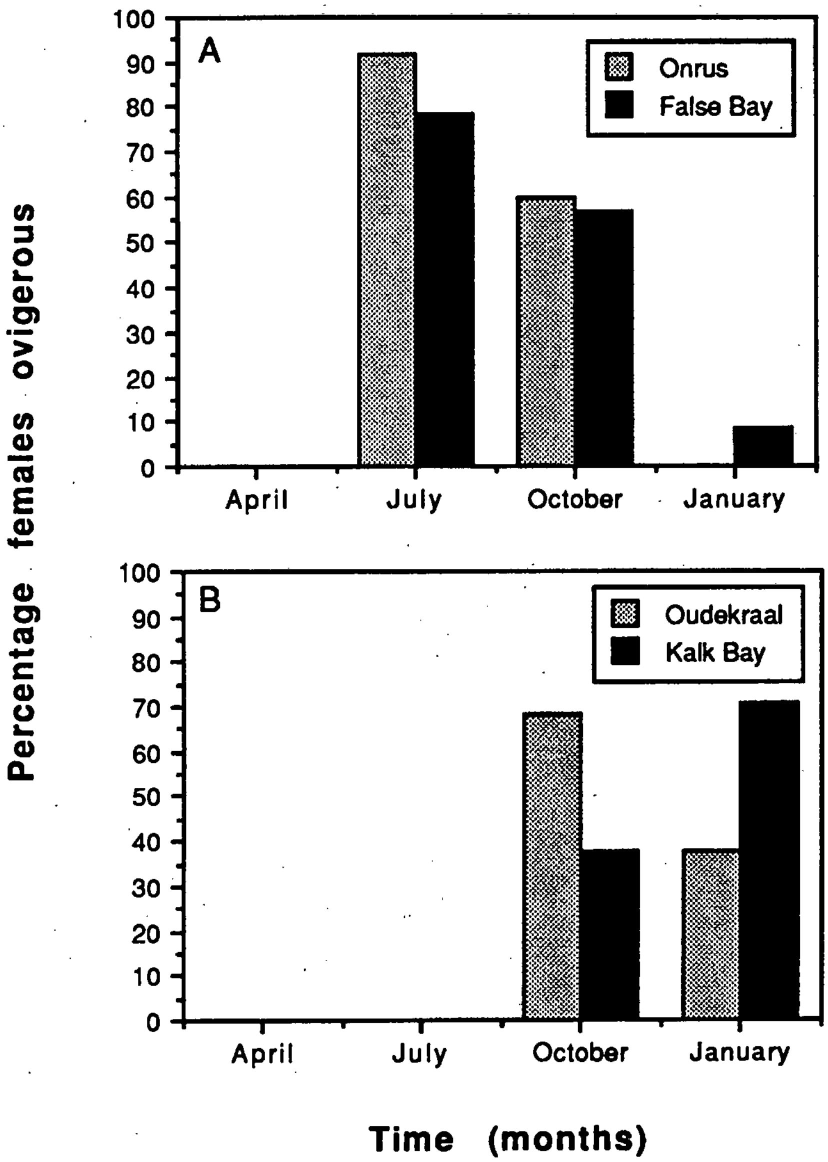

FIGURE 11. Percentage ovigerous plotted against time in months for, A - Cyclograpsus punctatus and, B - Plagusia chabrus. The sites at which sampling was conducted are shown in the legends.

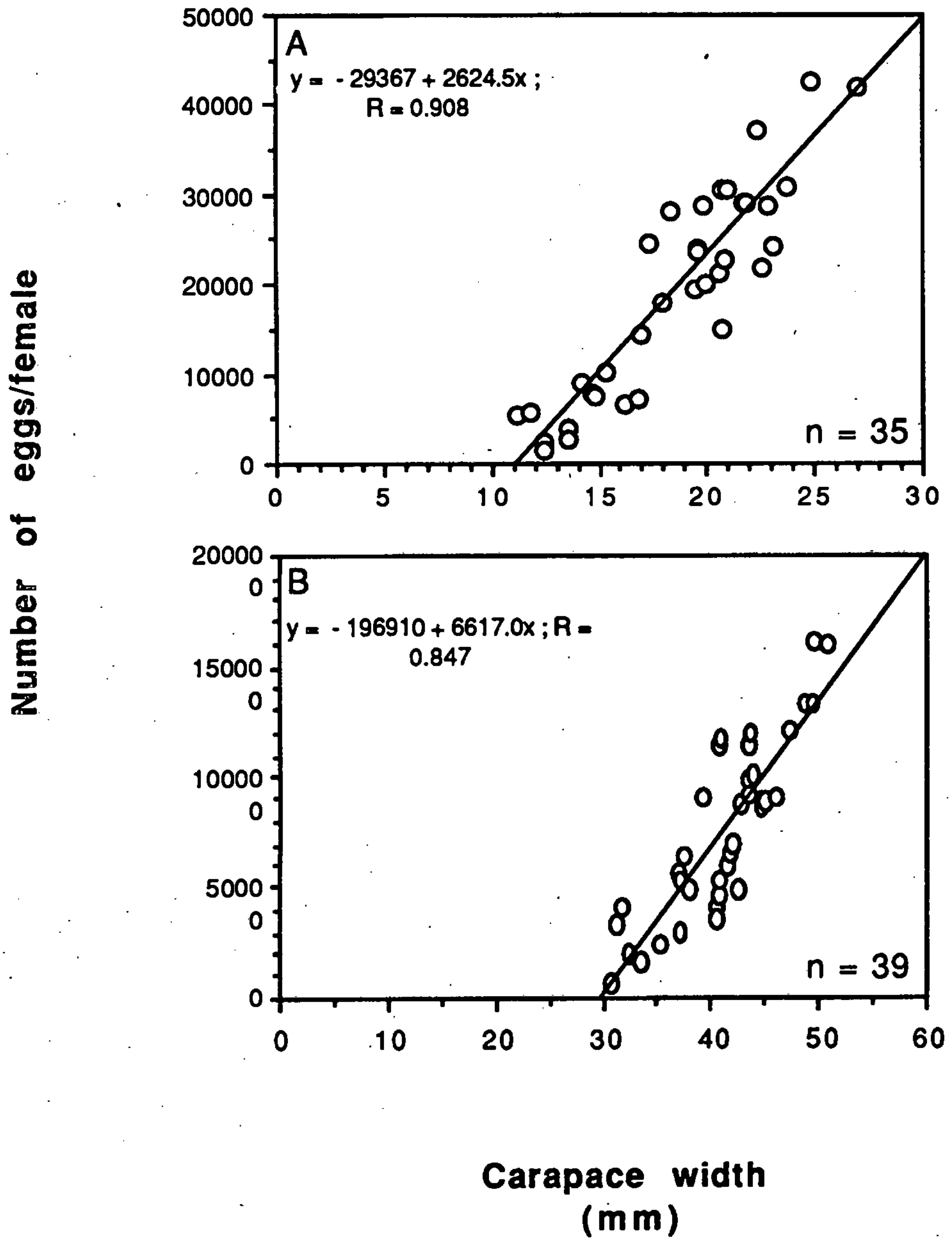

FIGURE 13. The number of eggs carried per female plotted against carapace width (mm) for, A - <u>Cyclograpsus</u> <u>punctatus</u> and, B - <u>Plagusia</u> <u>chabrus</u>. Regression equations appear on each figure, n is the number of females used in the analysis.

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