# Predation of infaunal bivalves by <italic>Carcinus maenas</italic> (L.) in the Burry Inlet, South Wales.

## Abbas, Saeed Abdulla Mohamed

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# PREDATION OF INFAUNAL BIVALVES BY *Carcinus maenas* (L.)
# IN THE BURRY INLET, SOUTH WALES

A THESIS SUBMITTED TO THE UNIVERSITY OF WALES

BY

SAEED ABDULLA MOHAMED ABBAS

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# ABSTRACT

Laboratory experiments and field studies in the Burry Inlet were designed to investigate the impact of crab predation on population of burrowing bivalves. Sampling of *Carcinus maenas* in the Inlet indicated that significant numbers of adult crabs move on to the sand banks at every flood tide for all but the coldest months of the year, but it proved difficult to estimate actual numbers. Settlement of first stage crabs occurs in July. These young crabs live in nursery areas near HWNT until about one year old. Stomach contents analysis demonstrated that large *C. maenas* feed mainly on infaunal bivalves. The priority food varied from one season to another and between juveniles and adults.

Laboratory experiments were conducted on the predatory behaviour of the crab, on four infaunal bivalve species. Methods used by crabs to open the bivalve shells are described and shown to be related to shell strength. For any given crab size, there was an optimal prey size where the prey value was at a maximum. Other experiments showed that crabs selected prey of a size close to the predicted optimum both for *Cerastoderma edule* and *Macoma balthica* even when they were buried in the sand.

Burrowing behaviour of both *M. balthica* and *Scrobicularia plana* was found to significantly reduce crab predation, but it had little effect in the case of the shallow burrower *C. edule*. Crabs preyed heavily on those bivalves that occurred close to the sand surface. When crabs were offered similar sized, small specimens of three species of bivalves buried in sand, they actively selected cockles.

Protection of small cockles from various predators by the use of cages in the field decreased their mortality.

It was concluded that crabs must be considered serious predators of first and second summer cockles.

# SECTION I

# GENERAL INTRODUCTION

During the last few decades, there has been increasing interest shown in the influence of predators on marine benthic populations. The work of Connell (1961) on the effect of dog-whelks (_Nucella lapillus_ L.) on intertidal barnacle populations in Scotland is one example. Pettitt (1975) reviewed information about predators of _Littorina_. Paine (1966) working on the west coast of the United States demonstrated the importance of starfish in shaping the pattern of intertidal populations of mussels and barnacles. In Europe, Crothers (1983) has demonstrated the influence of crab predation (and wave action) on shell morphology of _Nucella_. Comprehensive studies on predation of epifaunal bivalves have been reported in a series of papers by Hughes and Elner (see bibliography).

Predation studied from the viewpoint of the predator has resulted in the development of such concepts as prey value, optimal foraging and prey switching (see reviews by Pyke _et al_, 1977 and Krebs, 1978).

The present study was particularly concerned with the special situation of a crab predator foraging for buried bivalve prey; in particular predation of _Cerastoderma edule_ (L.) and other estuarine bivalves by the shore crab _Carcinus maenas_ (L.) as seen in the local estuary, the Burry Inlet.

The crab (_C. maenas_) which is variously known as the shore crab (UK) or the green crab (US), is a member of the family Portunidae. It is one of the commonest and most adaptable crabs around the British Isles. The crab is opportunistic and feeds on a wide variety of living and dead animal matter. Crothers (1968) in a literature review, lists 38 species of organisms eaten, including 14 species of molluscs. It is generally held to be a serious pest of commercial shellfish (Walne and Dean, 1972; Dare and Edwards, 1976; Walne, 1977). Its importance as a pest was reported as early as the 1920s when it was found feeding on the edible cockle in the field (Orton, 1926).

Estuaries are often found to be favourable places for production of natural populations of bivalves and some of these populations are harvested. In some estuaries bivalves are actually managed by putting down spat in suitable areas for fattening, for instance oysters in Milford Haven.

There are few surviving commercial cockle fisheries in Britain based on intertidal stocks. The Burry Inlet fishery is unique in that it continues to thrive using a collecting technique going back hundreds, perhaps thousands of years. Although the stocks of cockles fluctuate, the fishery recently provides a full-time livelihood for about 100 people (Franklin, 1976). By comparison, the fishery in the Thames Estuary is larger but is based on dredging sublittoral stocks and considerable modernisation by fishing methods has been introduced. The once flourishing Morecambe Bay fishery no longer exists having collapsed, it appears, through a combination of factors including over fishing.

Occasional low stock levels of cockles in the Burry Inlet may be due to a variety of factors including adverse physical conditions, poor settlement and serious predation. Little can be done about the first two, but some attempt has been made to control one predator, the wading bird known as the oyster-catcher (<u>Haematopus</u> <u>ostralegus</u> L.)

Three groups of predators attacking the bivalves are present in the Burry Inlet:

1. Birds, particularly when the tide is out.
2. Shore crabs, when the tide is in.
3. Various fish species, when the tide is in.

In the past, there has been great emphasis on the importance of the obvious predator, the oyster-catcher, on the cockles (Hancock and Urquhart, 1965; Davidson, 1967). However, the role of crabs predating cockles and other buried bivalves has not previously been studied in any detail, and this therefore, forms a main theme in the present study.

The Burry Inlet seems to be an ideal place to carry out such a study because of the presence of one crab species and large numbers of a few species of infaunal bivalves, including one which is commercially important, the edible cockle.

The present thesis considers the various aspects of the problem as follows:

| | |
|---|---|
| Section II | Describes the features of the study area, its geography, hydrology and other characteristics as well as giving a review of information available on the different bivalve populations in the Inlet. |
| Section III | Examines the recruitment, size structure and density of the shore crab population in the area, together with studies of its behaviour, in particular its tidal and seasonal movement patterns. |
| Section IV | Describes studies directed at determining the natural diet of juvenile and adult crabs in the Inlet. A comparison of the diet in respect to size, sex and seasons was made. |
| Section V | Describes the different techniques used by the shore crab to open four species of bivalves and examines the shell strength of these species. The dynamics of crab foraging strategy, the influence of hunger on their daily consumption and the fore-gut clearance rate were also determined. |
| Section VI | Attempts to assess the impact of predators on field populations by excluding them from areas where small cockles are abundant. |

Finally Section VII reviews these findings and draws some conclusions.

# SECTION II

# BIVALVES IN THE BURRY ESTUARY

## II.1

## THE BURRY INLET

The Burry Inlet, also known as the Loughor Estuary, is situated approximately in the centre of the South Wales coastline (Fig. I.1.1). It consists essentially of the combined estuaries of the rivers Loughor, Lliw and Llan, forming a tidal inlet with an east-west orientation and discharging into the eastern side of Carmarthen Bay around Burry Port and Whiteford Point at the north west corner of the Gower peninsula.

Historical, geomorphological, hydrological and environmental features of this estuary system were discussed in the Burry Inlet Symposium of 1976, the proceedings of which were published as a handbook edited by Nelson-Smith and Bridges (1977).

The river Loughor which is the main source of fresh water, flows south to join the smaller rivers at Loughor following a relatively narrow channel westward to the constriction between Llanelli on the north and Crofty at Salthouse Point on the south shore. Below Salthouse Point, the Inlet widens and the main river bed is directed more towards the northern side, leaving a wide expanse of relatively stable flat sand banks to the south known as Llanrhidian Sands which is the most important site for cockle fishery in Wales (Hancock and Urquhart, 1965).

The estuary has a surface area of nearly 45 $km^2$. The east-west length is about 13 km and at the widest point it has a width of approximately 6.5 km.

The tidal range in the Inlet varies from nearly 9.0 metres at mean spring tide to approximately 5.5 metres at mean neap tide. Volumes of water present within the estuary at the time of high water are estimated at $1.40 \times 10^9$ $m^3$ at average spring tides (8.7 m) and $1.04 \times 10^9$ $m^3$ at average neap tide (6.6 m). The volume of fresh water discharge varies from 515,850 $m^3$ per tidal cycle in January to 154,440 $m^3$ in June (Moore, (1976).

At high water, the Inlet experiences a gradient of salinity from normal sea water at the mouth to almost fresh water near the head. When the tide retreats the bed of the Inlet emerges as extensive flats where more than 80% of it dries out leaving only a few narrow drainage channels (Davidson, 1967). More detailed information on the topography of the area is given by Hancock and Urquhart (1966). The sediment, however, ranges in particle size from medium grained sand at the mouth to mud near the head (Moore, 1976). The cockle beds are a predominantly sandy mixture of sand and mud.

The Inlet is a low-medium energy environment (Carling, 1976), the middle and upper parts are moderately sheltered, but the outer part near the mouth receives much more wind and wave action. The depth of the black layer beneath the surface gives an indication of the degree of aeration of the sediment (Holme, 1949). This layer varies according to the season and the shore level in the Inlet (Poopetch, 1980).

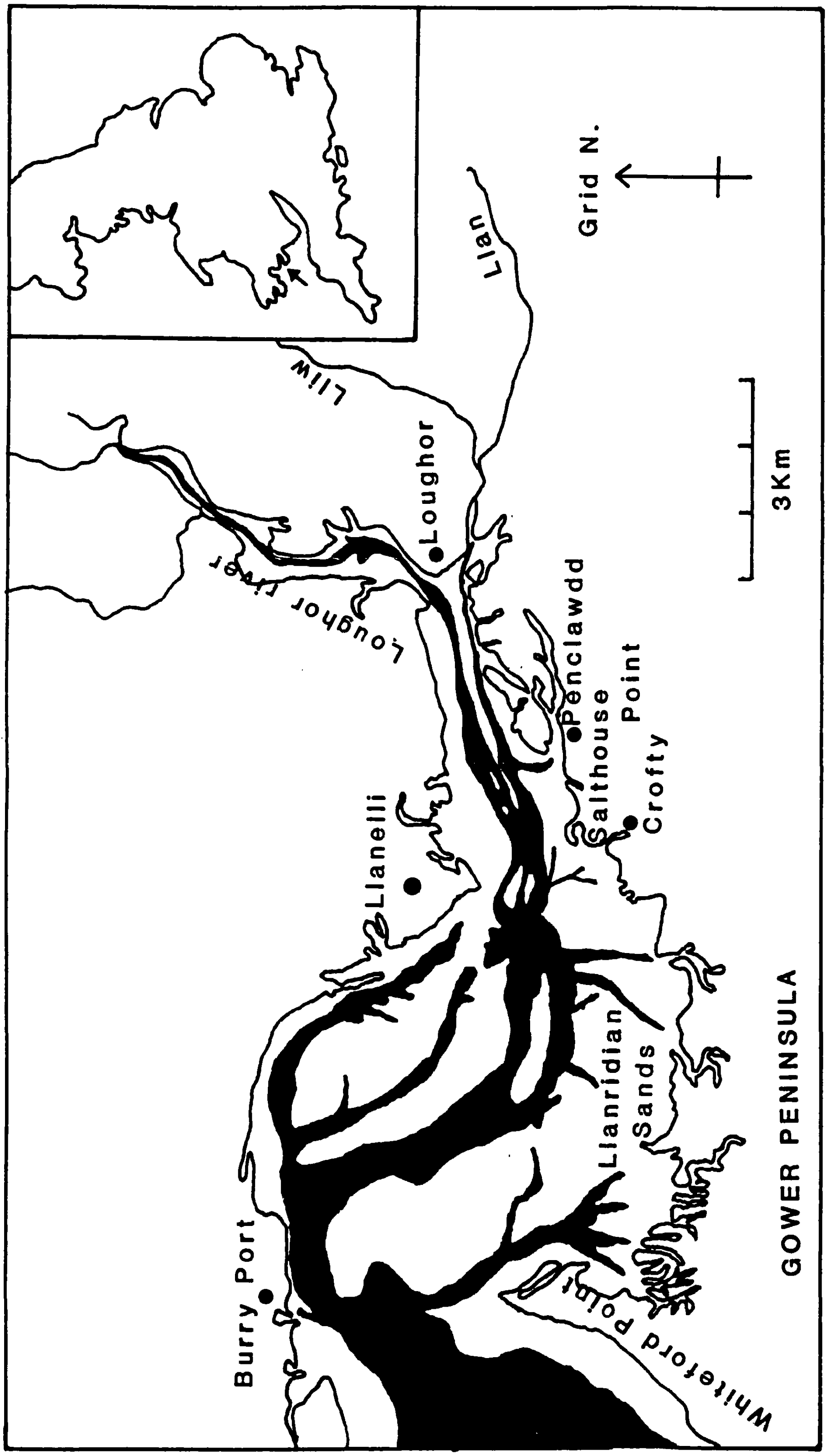
One feature of the Inlet is the remains of a 'training wall' which was erected at the end of the last century diagonally down stream from Salthouse Point with the aim of channelling the river flow to the northern shore to scour Llanelli docks of sediment. However, this resulted in the harbour at Penclawdd soon becoming silted up (Nelson-Smith, 1976). Remains of the training-wall appear now as witness to the dramatic change in the area.

During the 1930s, the cord grass, Spartina anglica was planted on a small area to aid its reclamation. The salt marsh extended progressively throughout the years, mainly on the southern side to cover more than 16 $km^2$ fifty years later (Rojanavipart, 1981).

Upper shore hard stratum habitats (with stones and pebbles) which provide ideal nursery grounds in such an environment for juvenile shore crabs (see Poopetch, 1980) are limited to four areas scattered around the estuary (Burry Port, Llanelli, Salthouse Point and Loughor).

As well as the cockle fishery, the Inlet is an area for a small amount of commercial fishing, predominantly for sea-bass and flat fish, by small boats operating from Penclawdd.

Figure II.1.1 Geographical view of the Burry Inlet and the main channels at low tide (inset shows the location of the Burry Inlet)


Grid N.
Llan
Lliw
Loughor
Loughor river
3Km
Penclawdd
Salthouse Point
Crofty
Llanelli
Llanridian Sands
GOWER PENINSULA
Burry Port
Whiteford Point

# II.2

# BIVALVE POPULATION IN THE INLET

## Introductory review

Molluscs are one of the commonest macro-benthic invertebrate groups in the marine environment. The wide range of species, their appropriate size, sedentary habits and high density make them one of the most plentiful types of potential prey for both invertebrate and vertebrate predators.

Not suprisingly, molluscs employ a variety of defences against predation and these vary between the different classes. Most prosobranch gastropods have a strong shell which may have spines, narrow apertures, low spires, etc. (see review by Vermeij, 1978). These morphological characteristics have been shown to defend gastropods from predators such as crabs and fish (Vermeij, 1976 and 1978; Zipser and Vermeij, 1978; Palmer, 1979; Elner and Raffaelli, 1980; Bertness and Cunningham, 1981). A comparative study in the European waters by Crothers (1983) showed that crab predation was one of the factors influencing the variation in the shell of the dog-whelk, Nucella lapillus. However, Vermeij (1982) reported that N. lapillus became adapted phenotypically following the establishment of Carcinus maenas in North America. Opisthobranch gastropods often employ chemical deterrence (Thompson, 1960).

All lamellibranchs possess two shells. Many shell features associated with epifaunal and shallow burrower bivalves reduce their vulnerability to predators. These features were reviewed by Vermeij (1978) as including a strong, inflated shell, presence of ornamentations, reduction of permanent gape, etc. However, the deep burrowing bivalves lack many of these features, and this can be correlated with their burrowing behaviour (Stanley, 1970; Vermeij, 1978).

In a previous survey of the invertebrate macrofauna of the Burry Inlet, Poopetch (1980) listed 48 invertebrate species, five of which were burrowing bivalves. He found that the most abundant infaunal bivalves were: *Cerastoderma edule* (L.); *Macoma balthica* (L.); *Scrobicularia plana* (Da Costa) and *Mya arenaria* (L.). The fifth species *Tellina tenuis* (Da Costa) reported by the same author is found mainly in clean sand near the mouth of the Inlet. Non-burrowing species abundant on stony sites are *Mytilus edulis* L. and *Lasaea rubra* (Montagu).

The objective of this chapter is to review the relevant features of the four burrowing species.

## The four bivalve species studied

(for full taxonomic descriptions of the shell see Tebble (1966))

### 1. The edible cockle Cerastoderma edule (Plate II.2.1)

Shell description

Strong, rounded with prominent radiating ribs crossing fine concentric ridges, pale brown to yellow or white.

The cockle is a filter feeder with short siphons, and is a shallow burrower occurring just below the surface of the substratum. The ribs and the inflated shape reduce the ability for burrowing. However, those ribs may help to stabilise the shell in the substratum (Trueman et al, 1966).

Maximum shell length recorded in this study was 35 mm. Farrow (1972) related the smaller size of cockles in the Inlet to those from other British cockle populations (which sometimes exceed 50 mm) to the situation of the cockle flats near neap high water mark. He suggested that growth is arrested during tidal cycle when shells were exposed to the air. Cockles are abundant in the Inlet and concentrated in beds. The main bed is located at Llanrhidian Sands where densities of up to 7000 cockles per $m^2$ have been recorded (Farrow, 1972). They are highly abundant at 5-6 metres above Chart Datum (just above MSL), mainly where there are sediments of slightly muddy sand. Banister and Poopetch (1976) also reported that very high densities of cockles were found at the edges of pills (drainage channels), which agrees with what has been suggested by Boyden (1972) that running water is an essential environmental requirement for them.

The larvae are pelagic for about three weeks and settlement normally occurs in late spring-early summer (Franklin and Pickett, 1979).

Cockles have been exploited commercially in this estuary for a very long time. Regular monitoring has been conducted on the population in this area by the staff of MAFF (Ministry of Agriculture, Fisheries and Food) since 1958. An estimate of the stock at Llanrhidian Sands from 1958 to 1971 is summarised in Table II.2.1 (adopted from Franklin and Pickett, 1979). Studies on density, distribution, causes of mortality and recruitment of cockles in the Inlet have been reported elsewhere (see Hancock, 1970 and 1973). The effects of variations in fishing effort and strategies and the predation by oyster-catchers were discussed in relation to the yield of cockles and stability of the fishery by Horwood and Goss-Custard (1977).

## 2. Macoma balthica (Plate II.2.2)

### Shell description

Strong, rounded, swollen, narrowing somewhat towards the hinder end with fine concentric striations. Variable in colour from white, yellow, reddish to dark grey.

Generally, Macoma is a deposit feeder during low water time and a suspension feeder when covered by the tide (Brafield and Newell, 1961). This clam has a vertical migration in the sediment related to variation of day length throughout the seasons. They were nearest the surface in June and buried deepest in December (Reading and McGrorty, 1978). A horizontal migration or orientation daily, related to the position of the sun, was also recorded (Brafield and Newell, 1961).

The largest specimens recorded in this study measured 20 mm shell length (about average for this species). As in the case of cockles, the maximum density was recorded from muddy-sandy substrates (Banister and Poopetch, 1978). However, this species lives deeper in the sediment than cockles, large animals were found in the same study at about 5 cm below the surface. No detailed study has been made on the bivalve population in the area.

### 3. Scrobicularia plana (Plate II.2.3)

Shell description

Fragile flattened shell, rounded in outline, greyish white with brown ligament.

Although primarily a deposit feeder, Scrobicularia obtains some of its food by filtering suspended matter from the sea (Hughes, 1969).

The largest specimens recorded in this study were 42 mm SL. These are found to a depth of 15 cm below the surface (Banister and Poopetch, 1976). This bivalve species occurs in patches and concentrates between 6-6.5 metres above Chart Datum at areas with more muddy substrates. The study by Banister and Poopetch (1976) showed that in addition to the Inlet proper, S. plana was recorded in an area near Loughor village which suggests that the animal is more tolerant of lower salinities than the other three species. No detailed study has been made on the population of this bivalve in the area.

A study by Green (1957) in a neighbouring estuary in South Wales (the Gwendraeth Estuary) showed that a high density of S. plana was recorded in some patches; in one of them a population of 1025 per $m^2$ was found. By using the growth rings as an indicator of age, in the same study, Green concluded that some individuals appear to live for about 18 years.

In a comparison of M. balthica and S. plana as estuarine species, Eltringham (1971) stated that Macoma and Scrobicularia are not natural neighbours because the former is a boreal, cold water form while the latter is a southern species, but in Britain, their ranges overlap. Macoma is the more hardy under intensely cold conditions and its specific name of balthica refers to the Baltic sea which regularly freezes over. During the extremely cold British winter of 1962-3, Macoma was hardly affected but Scrobicularia was wiped out in many areas and decimated in others (Crisp, 1964).

### 4. *Mya arenaria* (Plate II.2.4)

#### Shell description

Fragile, elongated oval in shape, permanent gape at posterior end, right valve slightly larger than left, outer surface covered with rough striations, greyish-white or dull-brown.

This bivalve is a filter feeder. Large specimens exceed 10 cm SL and are often found at about 30 cm below the surface.

According to Flores (1983) this clam occurs in patches throughout the estuary with the exception of the areas at the mouth where there is more wave action and at the very muddy areas to the east. The upper limit of their vertical range is set by the edge of the *Spartina* marsh. They do not extend down to the lowest tidal levels.

Settlement of spat does not occur before mid June. The major size group in the population of the Inlet ranges from 70 to 90 mm. The highest density of *Mya* recorded by Flores (1983) was 45.4 clams per $m^2$ within the patches.

It was concluded by Poopetch (1980) that salinity and substratum type are the major factors controlling the horizontal distribution of the bivalves in the Inlet, while tidal level, composition of substratum and exposure appear to be the most important factors governing their vertical distribution. Nevertheless other factors are clearly important on a smaller scale. *Mya* populations for instance are easily destroyed by meandering drainage channels (Flores, 1983).

Plate II.2.1 External features of the edible cockle *Cerastoderma edule* (L.)

Plate II.2.2 External features of Macoma balthica (L.)

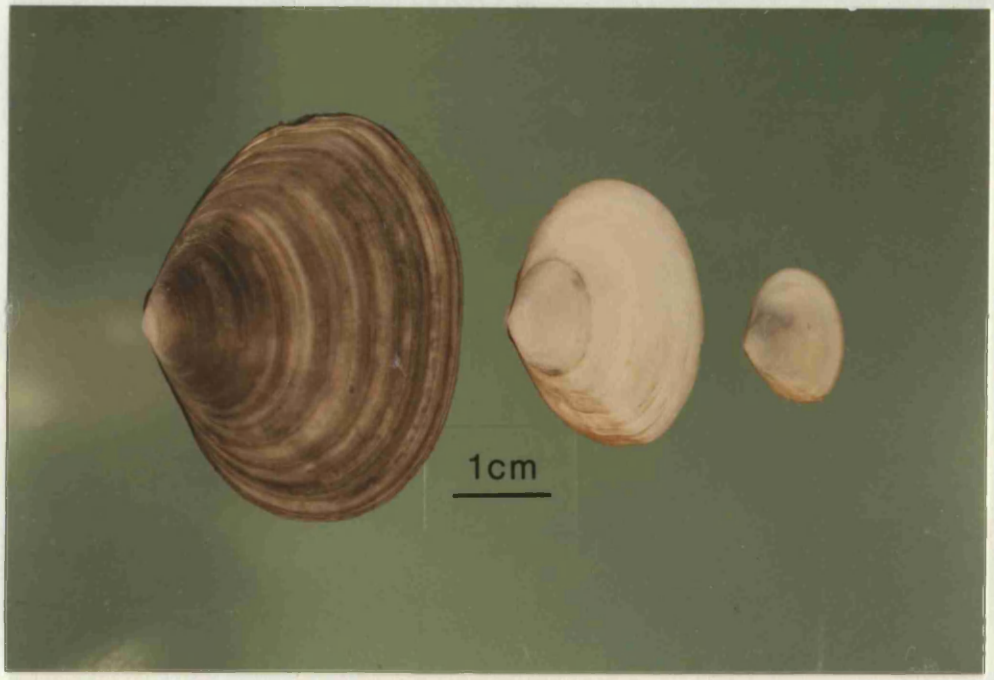


Plate II.2.3 External features of Scrobicularia plana (Da Costa)

Plate II.2.4 External features of Mya arenaria (L.)

Table II.2.1 Llanrhidian Sands. Summary of stock estimates - November 1958-1971. Numbers in millions (to the nearest ten million)

| Year | 1st year | 2nd year | 2+ year | Total |
|---|---|---|---|---|
| 1958 | 2 840 | 80 | 150 | 3 070 |
| 1959 | 2 580 | 920 | 70 | 3 570 |
| 1960 | 4 970 | 900 | 160 | 6 030 |
| 1961 | 3 300 | 850 | 160 | 4 310 |
| 1962 | 2 650 | 1 070 | 280 | 4 000 |
| 1963 | 10 620 | 10 | 100 | 10 730 |
| 1964 | 190 | 3 190 | 40 | 3 420 |
| 1965 | 5 720 | 30 | 1 780 | 7 530 |
| 1966 | 310 | 410 | 1 030 | 1 750 |
| 1967 | 4 170 | 50 | 650 | 4 870 |
| 1968 | 800 | 1 580 | 350 | 2 730 |
| 1969 | 1 210 | 230 | 800 | 2 240 |
| 1970 | 3 930 | 370 | 320 | 4 620 |
| 1971 | 1 530 | 990 | 200 | 2 720 |

After Franklin and Pickett (1979)

# SECTION III

# THE SHORE CRAB POPULATION

# INTRODUCTION

The shore crab, Carcinus maenas is the commonest British crab found between tide marks. However, it also regularly occurs down to a depth of 3 fathoms ≈ 6 metres (Marine Biological Association, 1957; Naylor, 1962) and some individuals have been found as deep as 60 metres (Chumley, 1918). The factors limiting their seaward distribution were discussed by Crothers (1969).

It is a European species recorded throughout Europe from northern Norway to North Africa (see Bouvier, 1940; Crothers, 1968). In the Mediterranean it is replaced by C. mediterraneus, a closely related species. The crab was introduced accidentally to the east coast of North America where it is now endemic (Scattergood, 1952; Macphail et al, 1955; Elner, 1981). Crothers (1968) reviews the world distribution of related species of Carcinus. In addition to reporting original data, Crothers (1967 and 1968) has given a fairly comprehensive review on the biology of the crab. In the Dutch waters, development, growth and distributions of the crab were studied by Broekhuysen (1936).

There is little information available about variation in the life-cycle of the shore crab in different areas around the British Isles, but Crothers (1967) suggested that the normal cycle in south-west Britain is: copulation July to September, eggs January to April, zoeae April to June, megalopae June to July and settlement of young crabs July to August.

The presence of C. maenas in the Burry Inlet was reported by Hancock and Urquhart (1965) during their study of the natural mortality of the cockles in the area. Although they failed to catch many adult crabs, they appreciated the need for more study of the shore crab's feeding on the cockles.

Since there has been no previous study of the C. maenas population in the Burry Inlet, overall assessment of the impact of the crab population on bivalves necessitated a thorough understanding of the various population processes; patterns of activity, seasonal, diurnal and tidal; seasonal changes of size frequecny distribution; and overall abundance and fluctuations with time.

This section presents the results of this study of the crab population, divided into three parts as follows:

1. Studies on juvenile crabs, to determine the time of settlement, to discover nursery areas and record recruitment of annual cohorts, and record their movement patterns.
2. Studies on adult crabs, to determine the period of their presence on the sand-flat, to investigate the population structure and their activity patterns.
3. Assessment of crab density on the sand-flat, to estimate the number of adult crabs feeding in the buried bivalves areas.

# SECTION III.1

# POPULATION STUDIES ON JUVENILE CRABS

## III.1.1 INTRODUCTION

Ecological studies reported in the literature concentrate on adult crabs; the literature on juvenile (O-group crabs) is comparatively poor. Some of the more important studies will be listed here. Rearing experiments in which growth rate was determined, proved to be the most popular field for many workers since the early part of this century such as Meek (1902), Williamson (1903), Shen (1935), Orton (1936) and Demeusy (1958). Crothers (1970) made a detailed study of the distribution of juvenile and adult C. maenas (as well as other crabs) in one particular self-contained locality, the rocky shores of the Dale peninsula, South Wales. The most comprehensive study on juvenile crabs was undertaken in the Dutch Wadden Sea by Klein-Breteler (1975a, b, c and 1976a, b).

Unlike the adult crabs, juveniles usually over-winter on the shore (Naylor, 1962; Atkinson and Parsons, 1973; Klein-Breteler, 1976a; Eriksson and Edlund, 1977). Rasmussen (1973), however, working in the non-tidal brackish Isefjord of Denmark, found that all crabs, including juveniles, leave the shore and move to the 'deep' water (presumably just sublittoral) in autumn. Settlement of early crab stage occurs usually in summer around June or July (Holme, 1949; Klein-Breteler, 1976b; Pihl and Rosenberg, 1982). However, in the cold waters of the Isefjord, Denmark, the settlement of megalopae was not only delayed to late August-early September, but in many years no settlement was recorded (Rasmussen, 1973).

As in the case of locomotory behaviour of adult crabs, juveniles move about actively at high water, especially during night time (Powell, 1962b). In the winter months the juveniles displayed only circadian activity with peaks towards the end of the night (Atkinson and Parsons, 1973).

To augment the central theme which is a study of adult crabs as predators of infaunal bivalves in the estuary and in view of the general lack of information about the mechanisms of recruitment to the adult population, it was decided to make a special study of the juvenile crabs in the Inlet.

Preliminary observations revealed that small (O-group) crabs overwintered intertidally where there was a plentiful supply of large stones for them to shelter under. Such sites are comparatively rare in the Burry Inlet since the upper shore usually grades into salt marsh. However, certain artificial structures provide a suitable substrate. One such is on the south shore near the village of Penclawdd at a site known as Salthouse Point. Here a stone causeway runs seawards from high tide level for about 250 metres, terminating in an angled construction of boulders and rubble, faced with concrete. The base of this structure is located at high water level of neap tide (HWNT). Part of it has collapsed scattering many stones over a wide area which has resulted in a good habitat for the small crabs (Plate III.1.1). The population there was adopted as the subject of this special study of juveniles.

## III.1.2 MATERIALS AND METHODS

Regular sampling was carried out monthly from January 1981 to December 1982. In the summer when rapid changes take place, fortnightly sampling was undertaken. Crabs were sampled by using a 1 metre quadrat frame; on each sampling day four randomly selected 1.0 $m^2$ were sampled when the site was emersed. Care was taken to ensure that all small crabs in the quadrat were collected. Firstly the obvious ones were collected after turning the stones in the sampling area. After that, a 1.0 mm mesh sieve was used to sieve about 3 cm depth of the sand (using a nearby stream) in order to catch the smaller and buried individuals. Soft crabs were stored separately from the others to decrease the possibility of them being eaten.

Back in the laboratory, the crabs were preserved in 4% sea water formalin. They were then promptly examined to record externally visible features. Maximum carapace width (CW) was measured to the nearest 0.1 mm with Vernier calipers for large crabs (carapace width >10.0 mm). Smaller crabs were examined under a stereomicroscope and measured using a calibrated eye piece micrometer. The moult cycle state and the sex of each crab was recorded.

Apart from small crabs sheltering under boulders it was usually possible to find some wandering about on the mud nearby when the tide was low. To record the numbers of juvenile crabs wandering on the mud flat in this way throughout the year, a transect was established near the regular sampling area towards the main river (Fig. III.1.1). Eleven stations - 15 metres apart - were located on the transect. Recording was carried out during daytime low tide once a month for a year. The number of crabs was recorded within a 1.0 m wide band, 5 metres in length at right angles to the transect line (Fig. III.1.2). Apart from collecting the mobile crabs by hand, a trowel was used to probe suspicious marks to reveal any crabs buried in the sand inside the sampling area.

## III.1.3 RESULTS

Small crabs were present in the sampling area throughout the year (Fig. III.1.3). The numbers and size range, however, varied considerably from month to month.

In the winter months (November to February) all the crabs present measured less than 20.0 mm CW. In the spring and early summer (May to June) there was a sudden drop in the total number of crabs in the quadrats, accompanied by an equally abrupt change in the size structure of the population. Some larger crabs appeared in the sampling area under the stones with the small ones. At the same time it was evident that the over-wintering small crabs (though reduced in numbers) were also growing larger, some exceeding 20 mm. Increase in the population size was noticeable again when the new settlers joined the population in July. There was another considerable increase in the crab numbers in October, November and December (see Fig. III.1.4). In the same figure, it is obvious that crabs which are <5.0 mm CW represented a high proportion of the population in mid-summer, while the crabs with a carapace width between 15.0 and 20.0 mm showed a considerable increase in spring and early summer.

Soft crabs appeared in the period between May to November (Fig. III.1.5) and their peak was in August and June in 1981 and 1982 respectively, while no soft crabs were found in the period between January to March.

Fig. III.1.6 shows that for crabs collected in the summer period of both years, clearly distinguishable peaks and troughs of size were present. These peaks lay at regular distances and had a regular form. Five distinguishable peaks were present for the smallest crabs (measuring less than 7.0 mm CW). Table III.1.1 shows the mean, standard deviations, and growth percentage for the five peaks in the present study as well as other data from different areas for comparison. More peaks were found in the period from mid-July to mid-August which correspond to the growth of the new settlers (Fig. III.1.7). As soon as the crabs increased in size ( >8 mm) the peaks were fused and overlapped which made them difficult to distinguish.

Three different cohorts are shown in Fig. III.1.8, I, II, and III representing that of 1980, 1981, and 1982 respectively. Rapid growth occurred in warm months from April to October while on cold months no growth in the population was recorded. For the 1981 cohort the mean carapace width was 2.2 mm in July with a range from 1.5 to 4.0 mm. Entering their first winter they reached a mean size of ≈ 8.0 mm and ranged from 3 to 20 mm. By July 1982 ie. when they become one year old after settlement they reached mean size of 14.8 mm and ranged between 10 to 25 mm. Because of the small numbers of large animals stranded under the boulders in the summer months, it was difficult to follow the cohort accurately.

The sex-ratio of the juvenile crabs in Salthouse Point sampling area indicates similarity in numbers for males and females throughout the year (Fig. III.1.9) in marked contrast to the migratory crabs.

Distribution of juvenile crabs in the transect area at low tide (Fig. III.1.10) shows that their numbers varied from month to month and appeared to be directly related to temperature changes. July was an exception; there were only a few animals in the area. In general, the number of small crabs wandering on the sand decreased the further one moved away from the Salthouse Point boulders (Fig. III.1.11).

## III.1.4 DISCUSSION

It is apparent from the results of this study that unlike their adults, juvenile C. maenas in the Burry Inlet do not exhibit a seasonal on-shore/ off-shore migration, and do not move down shore at each low tide, rather their habitat is the upper shore. The non-migratory mode of life for juvenile crabs in the Inlet agrees with what other workers recorded in other areas of South and West Wales (Naylor, 1962; Crothers, 1968; Atkinson and Parsons, 1973).

The highest density the juveniles reached (170 crabs $m^{-2}$ in December 1981), was not a reflection of new settlement at that time as crabs of less than 5.0 mm CW represented only 12.5% of the population, while in August and September it usually exceeded 40% of the population. It is explained by the movement of crabs, which previously wandered on the mud flat, in the warm months, into the stony area. This is presumably a response to avoid the effects of winter weather. Support for this explanation comes from Fig. III.1.10 which shows a close relationship between air temperature and the number of crabs wandering on the sand flat. In the warm months, while air temperature was considerably higher, many of these small crabs were found mainly shallowly buried in the sand, and it seems that when the temperature dropped, fewer crabs were found on the sand flat.

The decrease in the crabs' density at the boulder area was obvious in June 1981 and July 1982 (Fig. III.1.4.), and also found between crabs which wandered on the mud flat in July (Fig. III.1.10). This reduction is related to various factors. First of all following a period of rapid growth as demonstrated in Fig. III.1.8. Many of them now exceed 20-25 mm CW (almost one year after settlement). At this size, they start to leave their juvenile mode of life and join the other part of the population in their tidal migration (Klein-Breteler, 1976a). Data from Section III.2 support this interpretation since all (except one) migratory crabs caught in the baited traps exceeded 20 mm CW. As more crabs leave the nursery area, no crabs replace them until the new settlers arrive which is usually in the second half of July.

The second factor can be explained as follows. As mentioned before, the distribution of the crabs on the mud flat is linked to their density under the boulders. In winter crabs hide under stones and leave the mud flat, while in warm months, more crabs wander on the flat and few retreat into the stony area. A third factor, undoubtedly, is the role of different predators, and finally, anglers search under the boulders for soft crabs to use as bait.

When the numbers of crab in each station of the transect are combined for the whole year (Fig. III.1.12), it is evident that progressively fewer crabs are found wandering on the flat as one moves away from the stony area. This cannot be related to tidal level since the whole transect was on level ground. The recorded distributions are possibly related to high tide activity of these crabs. In the warmer months, they probably wander further away from the stones at high tide.

The appearance of crabs >30 mm CW in the sampling area in April 1981 and May 1982 respectively (Fig. III.1.3) is clearly not a result of rapid growth of the small ones which settled in the previous summer and had spent the winter in the area. These crabs show a similarity in the size with crabs caught in the pots. The latter crabs also started to arrive from their winter range in March-April (see Section III.2). This part of the population moves actively up and down the shore with every tide except in winter when they remain sub-tidal (Naylor, 1962). Some individuals are clearly less migratory than others and stay on the shore at low tide.

Recruitment of the new season post larvae to juvenile population occurred in summer. The first crab stage appeared in the sampling area in the month of July for each of the two successive years (1981 and 1982) of the study. This agrees with what Holme (1949) and Klein-Breteler (1976b) reported on the settlement of crab larvae in Exmouth Estuary and the Balgzand area in the Dutch Wadden Sea. On the other hand, a study by Berrill (1982) on the shore crab population in colder water than Europe (Gulf of Maine, North America), showed that larvae in that area settle at a later time (September).

Under laboratory conditions, the rearing experiments of juvenile shore crabs show that animals of one year old ranged in size from 9.0 mm (Meek, 1902) to 30.0 mm (Rothschild, 1940). In order to compare the size of crabs from different localities, only field data on juvenile populations are present in the following table which gives the results of studies from different areas to show the size crabs reach at their first winter and after one year from settlement.

| Locality | 1st Winter Range (mm) | One year old Average (mm) | One year old Range (mm) | Author and date |
|---|---|---|---|---|
| Burry Inlet | 4-20 | 14.8 | 10-25 | Present study |
| Dutch Wadden Sea | 5-20 | | 11-35 | Klein-Breteler, 1976a |
| Gullmar Fjord (Sweden) | | 9.5 | | Eriksson and Edlund, 1977 |
| Central Maine (N. America) | 2-11 | | 7-17 | Berrill, 1982 |

It is clear from the table that the size range of crabs in the Burry Inlet is close to that in the Dutch Wadden Sea, while both are higher than those in Gullmar Fjord and Central Maine. The limiting factors for growth of Carcinus are temperature, salinity, and food (Klein-Breteler, 1975b). Temperature was behind the small size of crabs from the two localities as suggested by Eriksson and Edlund (1977) and Berrill (1982).

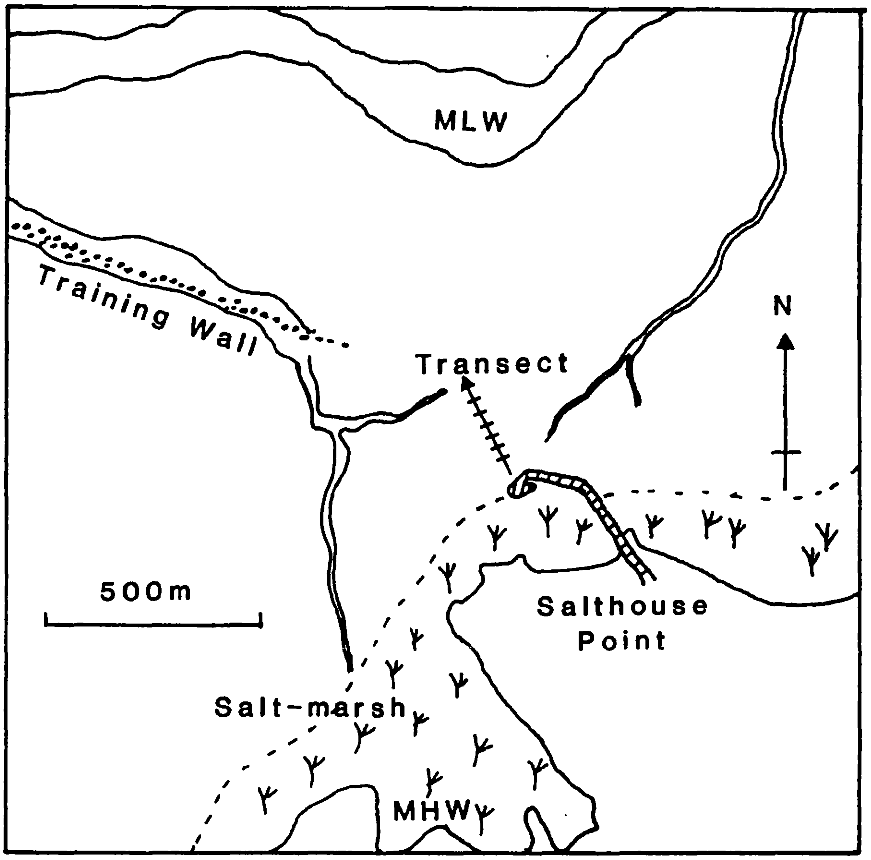
In July 1981 and 1982, there were at least three distinctive cohorts present in the juvenile sampling area which represent three parts of the population. The young ones (2.2 mm CW in 1981 and 2.7 mm CW in 1982) represent the newly settled crabs, and the second group (13.6 mm CW in 1981 and 14.8 mm CW in 1982) represent the one year old crabs, while the third and large ones (35.3 mm CW in 1981 and 34 mm CW in 1982) represent the migratory component.

The study of Naylor (1962) on the Mumbles crab population showed that newly soft crabs were found in all months of the year, but more in summer months. The present study which deals with juvenile crabs, showed that in two successive winters, no soft crabs were found. It seems that moulting ceases in the very cold months of the year. In the laboratory, the interval between moults of juvenile Carcinus gets longer at low temperature (see Klein-Breteler, 1975b). Furthermore, in an area where the cold period is longer (as in Maine) no soft crabs were found from mid-October to mid-May (Berrill, 1982).

The first new instars of the newly settled crabs were identifiable by their size at the beginning of their intertidal existence. The data in Fig. III.1.6. indicate that there were five recognisable instars in 1981 and 1982. The mean carapace width of each of the five instars is similar to that from Balgzand (Klein-Breteler, 1975a) and to that of crabs reared in the laboratory (Berrill, 1982). Recruitment to the population was rapid in summer, probably being concentrated into just a few weeks as Fig. III.1.7 indicated. As Lebour (1928) stated, following the first crab stage the skin is cast about once a week for the first month, after which there are longer intervals. While there were only three instars on 15.7.1981, at least five crab stages were present simulataneously less than twenty days later. Growth rate (linear) from one stage to another ranged between 30-38% and by the time the crabs had reached the sixth stage, it was difficult to distinguish between successive instars.

Figure III.1.1  Location of the transect at Salthouse Point

Figure III.1.2  Details of sampling areas on the transect


MLW
Training Wall
Transect
N
500m
Salthouse Point
Salt-marsh
MHW

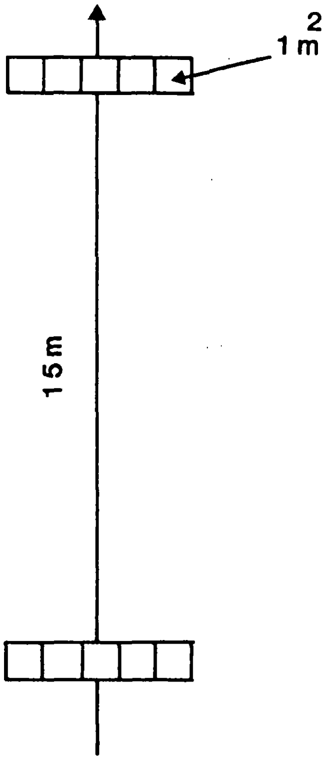
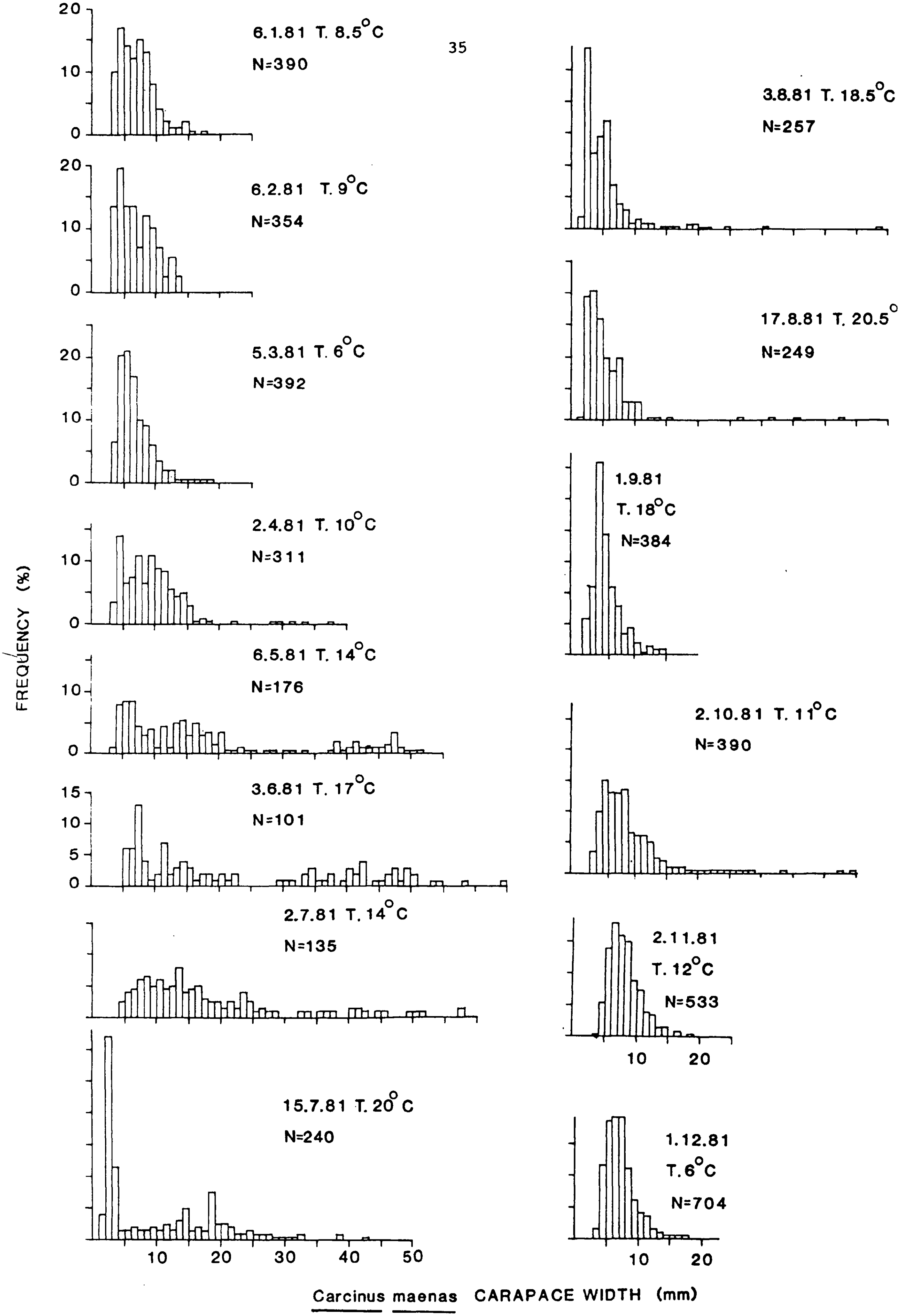

$1 m^2$
15m

Figure III.1.3 Size-frequency (%) distribution of juvenile *C. maenas* at Salthouse Point from January 1981 to December 1982


6.1.81 T. 8.5°C
N=390
6.2.81 T. 9°C
N=354
5.3.81 T. 6°C
N=392
2.4.81 T. 10°C
N=311
6.5.81 T. 14°C
N=176
3.6.81 T. 17°C
N=101
2.7.81 T. 14°C
N=135
15.7.81 T. 20°C
N=240
3.8.81 T. 18.5°C
N=257
17.8.81 T. 20.5°
N=249
1.9.81
T. 18°C
N=384
2.10.81 T. 11°C
N=390
2.11.81
T. 12°C
N=533
1.12.81
T. 6°C
N=704
FREQUENCY (%)
20
10
0
15
5
10
20
30
40
50
Carcinus maenas CARAPACE WIDTH (mm)

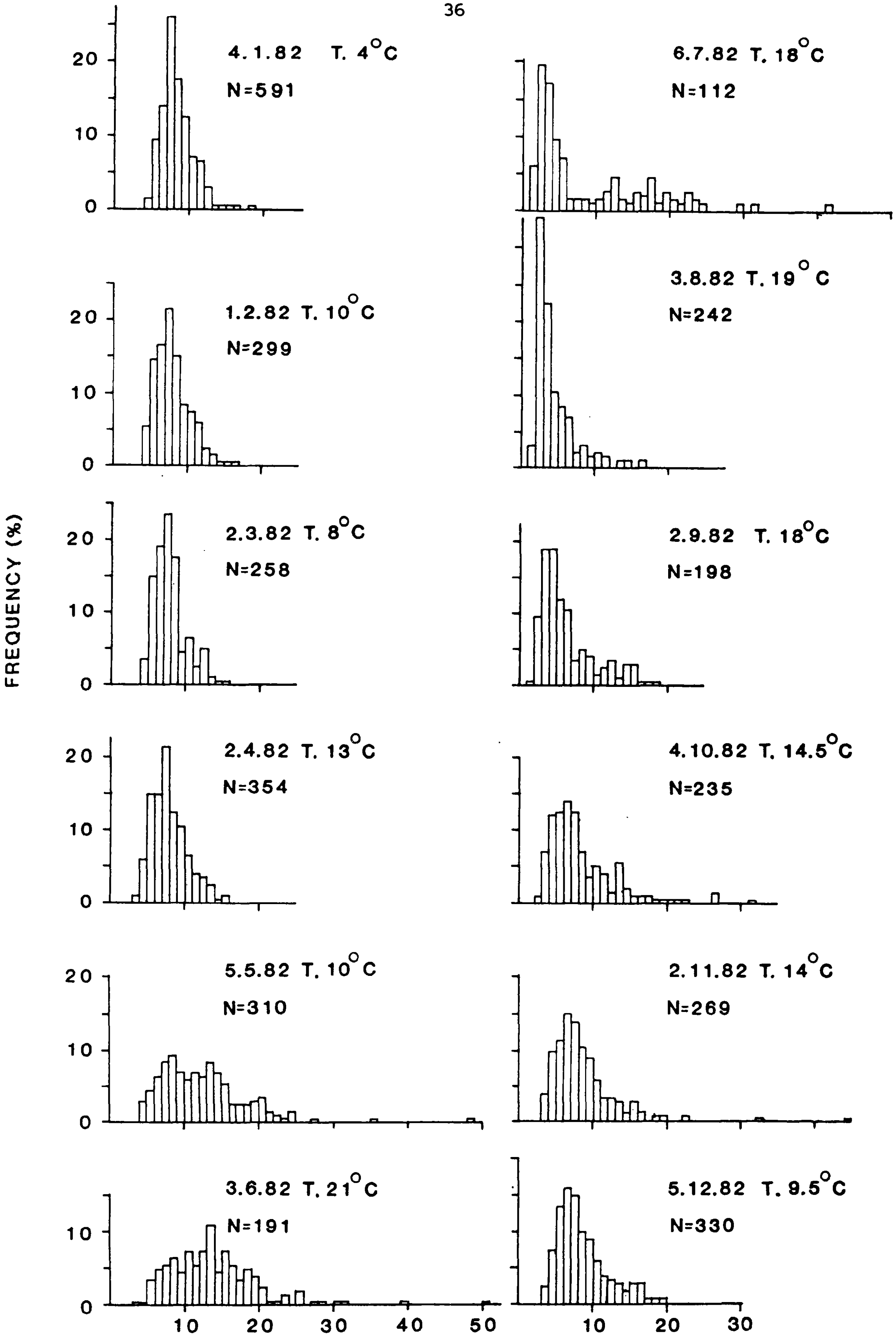


Fig. III.1.3 (cont.) <u>Carcinus</u> <u>maenas</u> CARAPACE WIDTH (mm)

Figure III.1.4 Monthly variation of different size groups of crabs present in the nursery area

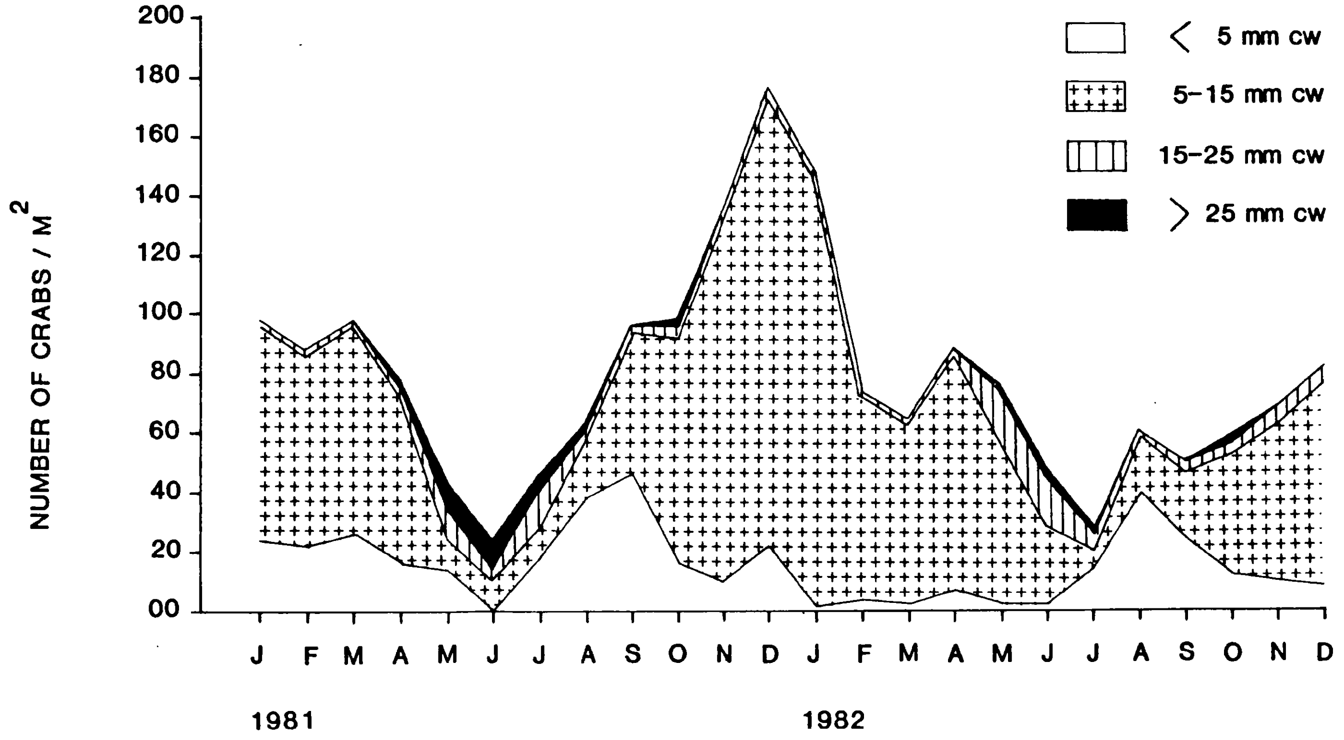

NUMBER OF CRABS / $M^2$
200
180
160
140
120
100
80
60
40
20
00
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
1981
1982
< 5 mm cw
5–15 mm cw
15–25 mm cw
> 25 mm cw

Figure III.1.5 Percentage of soft juvenile crabs in each month of the sampling

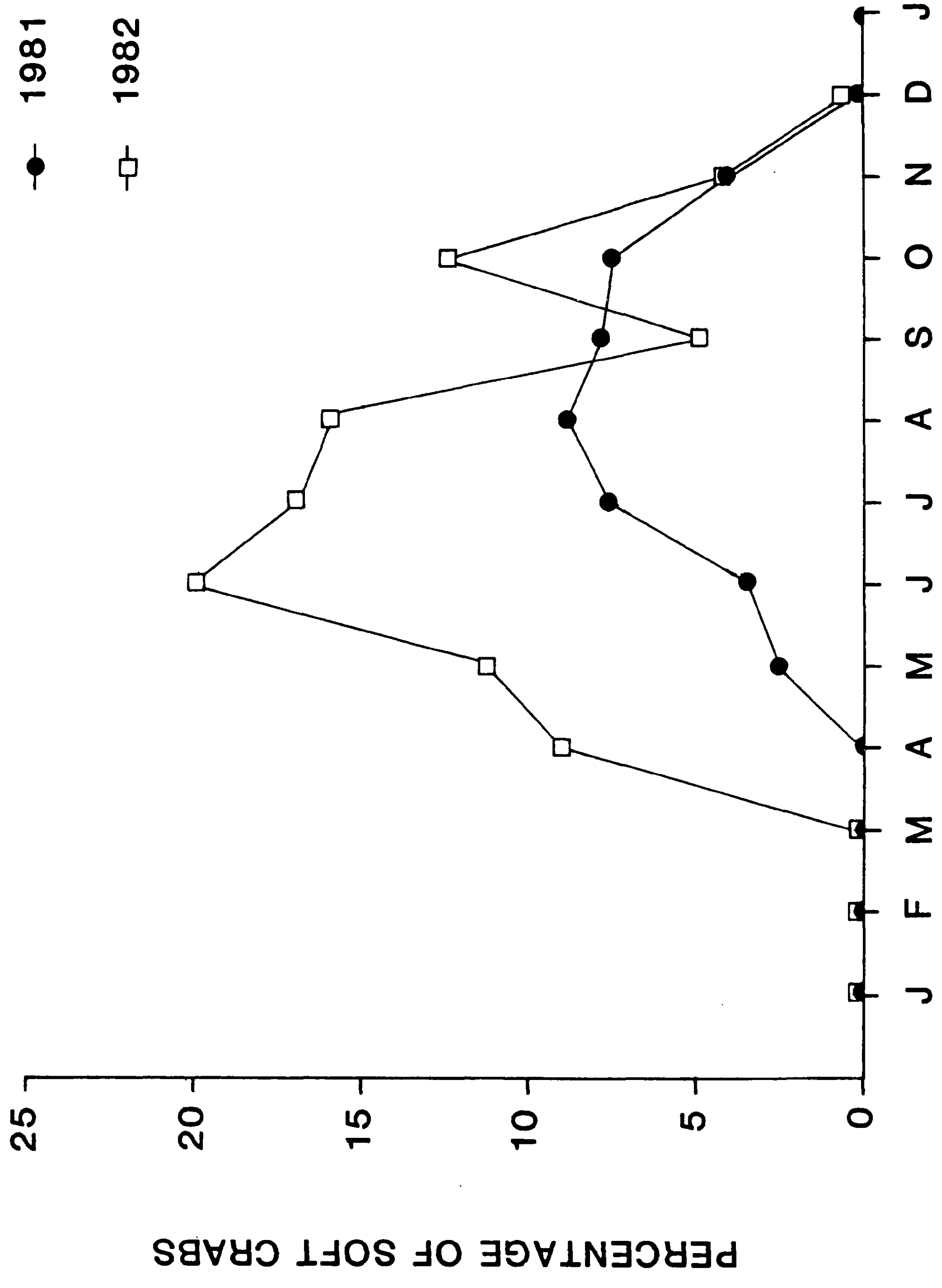

PERCENTAGE OF SOFT CRABS
0
5
10
15
20
25
J
F
M
A
M
J
J
A
S
O
N
D
J
1981
1982

Figure III.1.6 Size-frequency distributions of the carapace width of _C. maenas_ ( <20.0 mm) from the HWNT nursery area

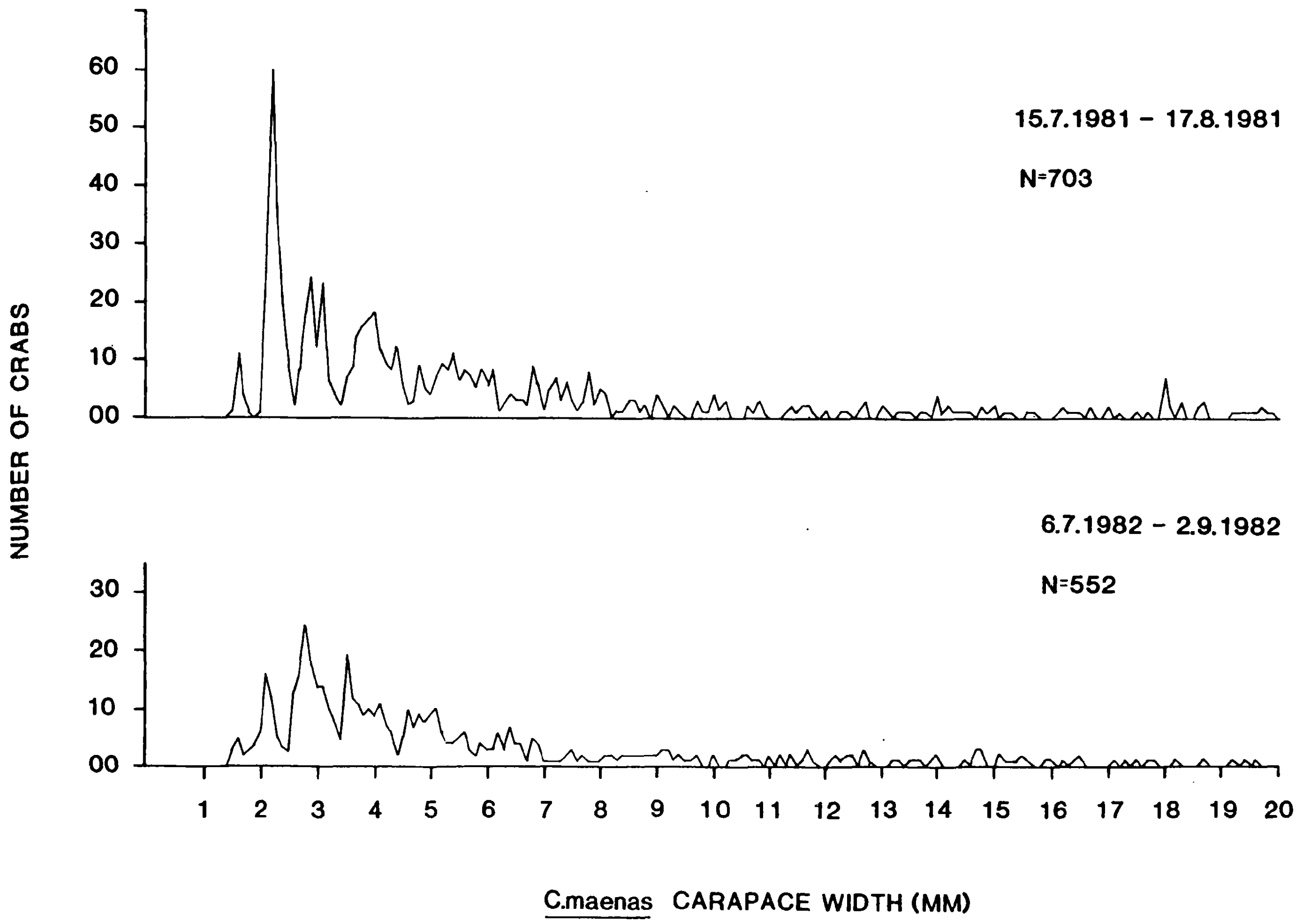

NUMBER OF CRABS
60
50
40
30
20
10
00
15.7.1981 - 17.8.1981
N=703
6.7.1982 - 2.9.1982
N=552
30
20
10
00
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
C.maenas CARAPACE WIDTH (MM)

Figure III.1.7 Size-frequency distributions of the carapace width of juvenile crabs in summer 1981

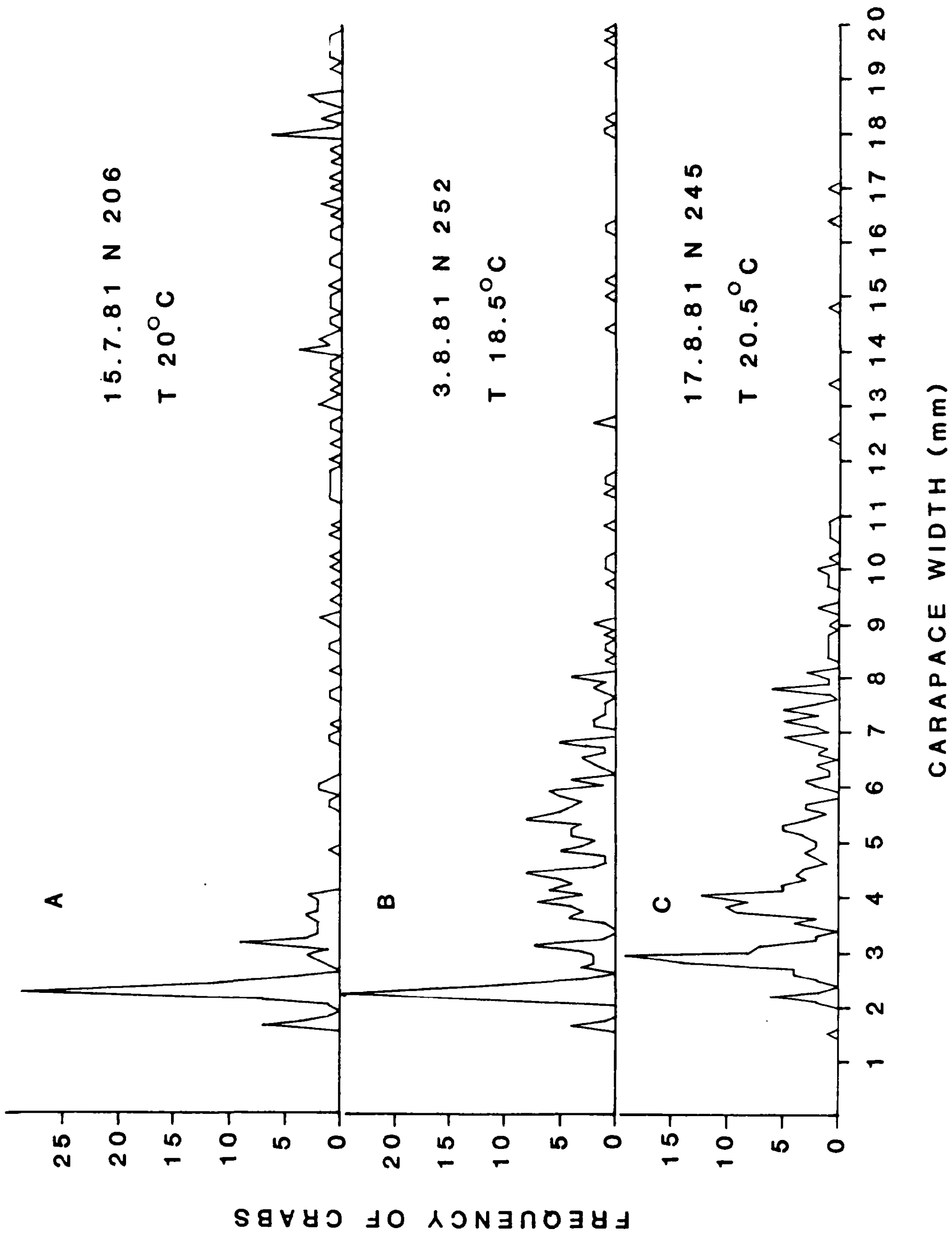

A
15.7.81 N 206
T 20°C
B
3.8.81 N 252
T 18.5°C
C
17.8.81 N 245
T 20.5°C
25
20
15
10
5
0
20
15
10
5
0
15
10
5
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
CARAPACE WIDTH (mm)
FREQUENCY OF CRABS

Figure III.1.8 Growth of *C. maenas* indicated by variation in mean size of cohorts with time

I 1980
II 1981
III 1982

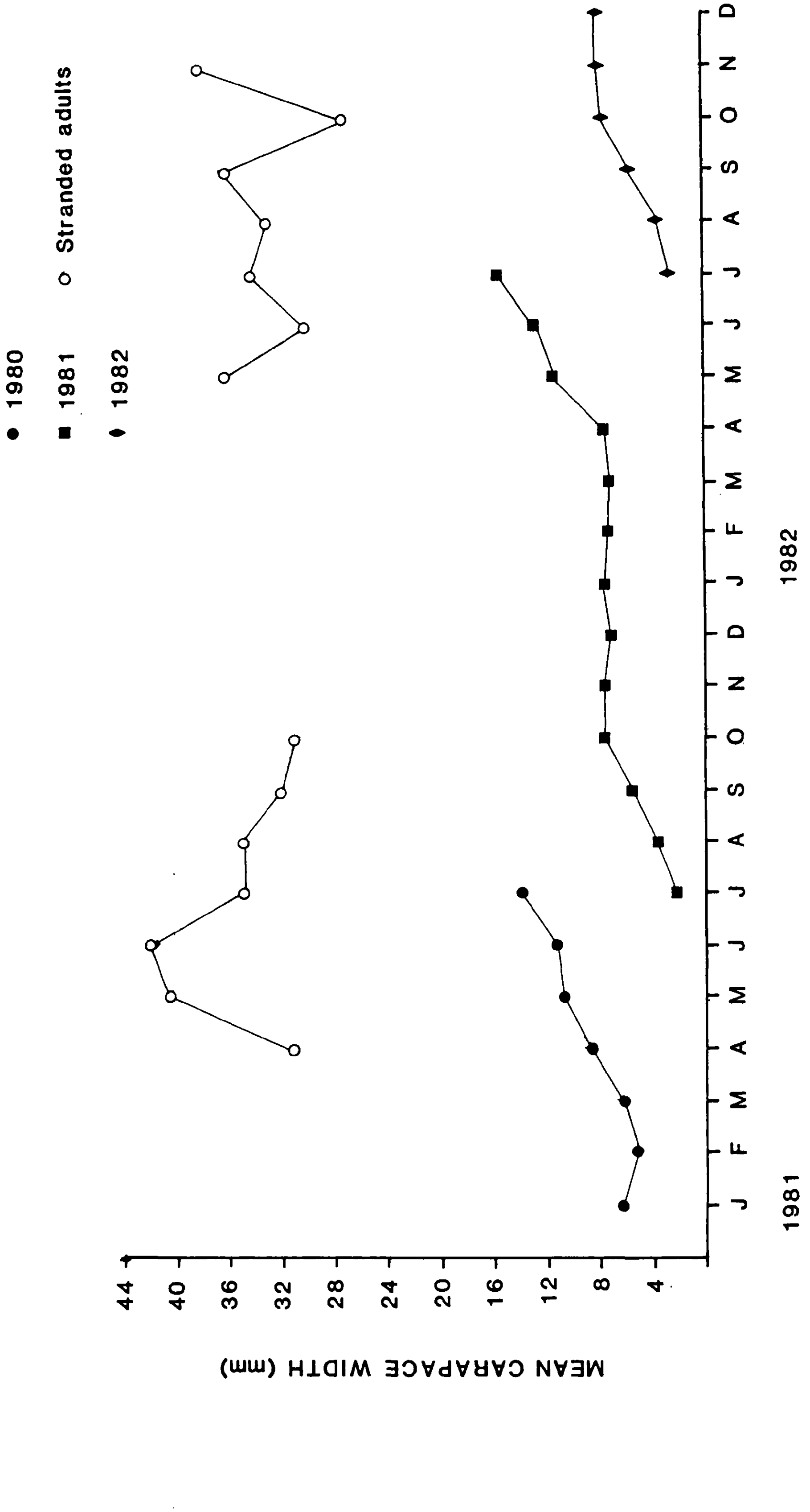

MEAN CARAPACE WIDTH (mm)
44
40
36
32
28
24
20
16
12
8
4
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
1981
1982
● 1980
■ 1981
♦ 1982
○ Stranded adults

Figure III.1.9 Monthly variation in the sex ratio of the juvenile crabs in the HWNT nursery area

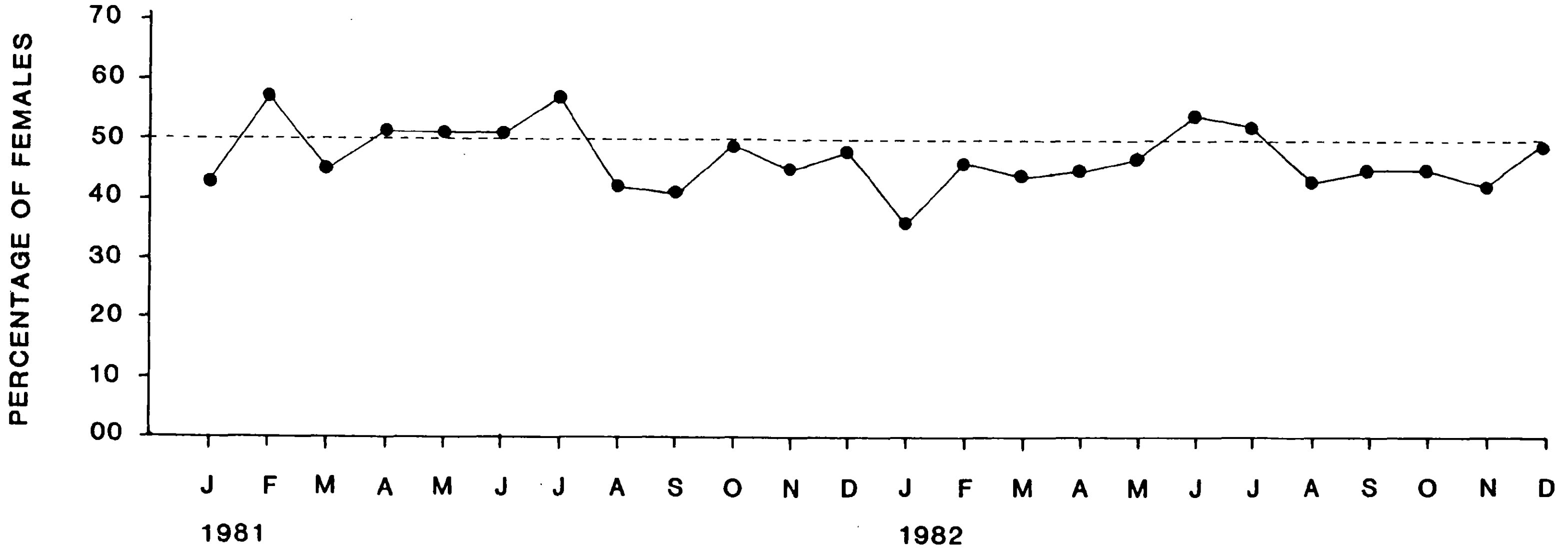

PERCENTAGE OF FEMALES
70
60
50
40
30
20
10
00
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
1981
1982

Figure III.1.10  Number of juvenile crabs recorded from the transect in each month plotted with air temperature

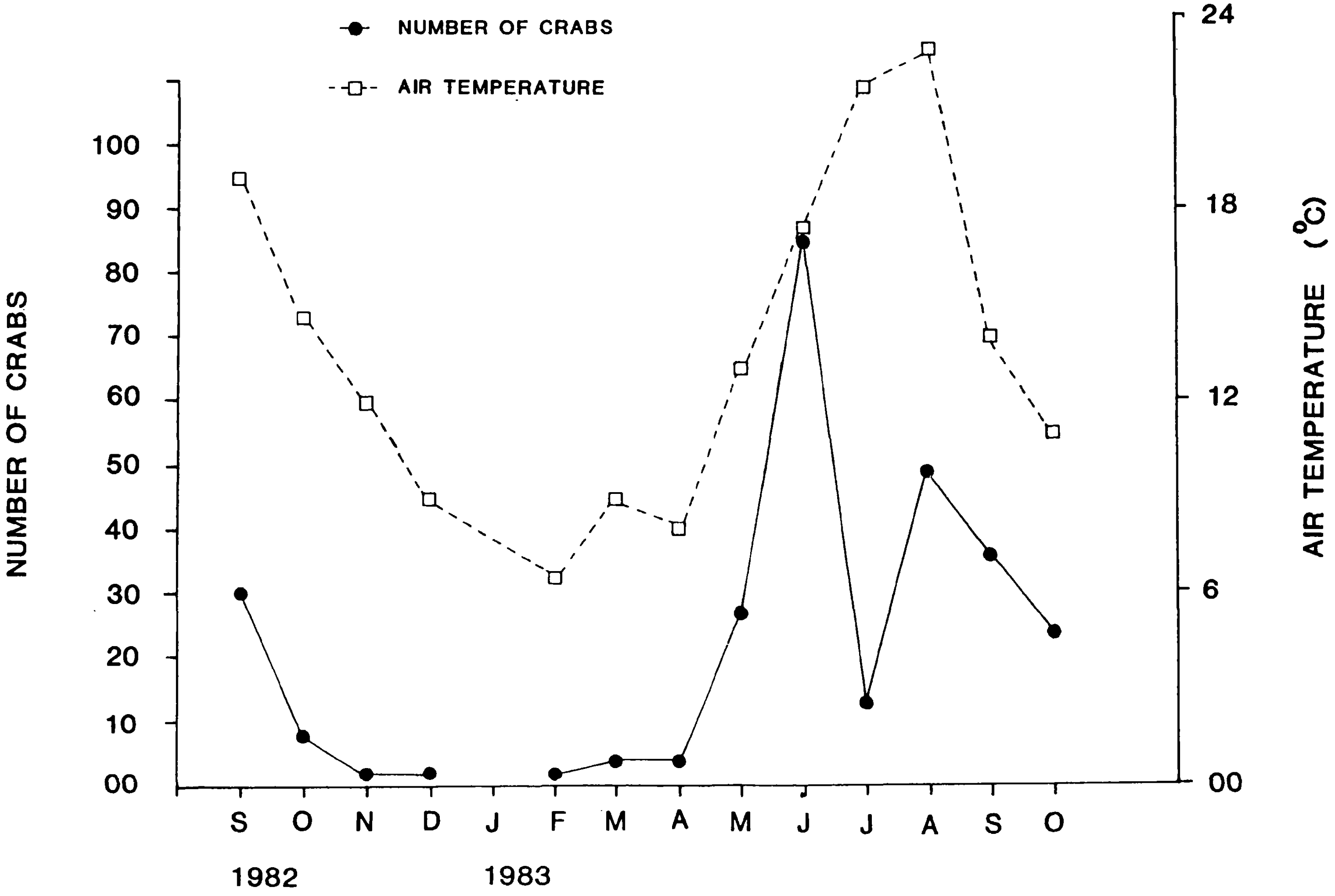

NUMBER OF CRABS
AIR TEMPERATURE
NUMBER OF CRABS
AIR TEMPERATURE (°C)
100
90
80
70
60
50
40
30
20
10
00
24
18
12
6
00
S
O
N
D
J
F
M
A
M
J
J
A
S
O
1982
1983

Figure III.1.11 Number of juvenile crabs wandering on the sand flat at low tide in 11 stations (data pooled for all months)

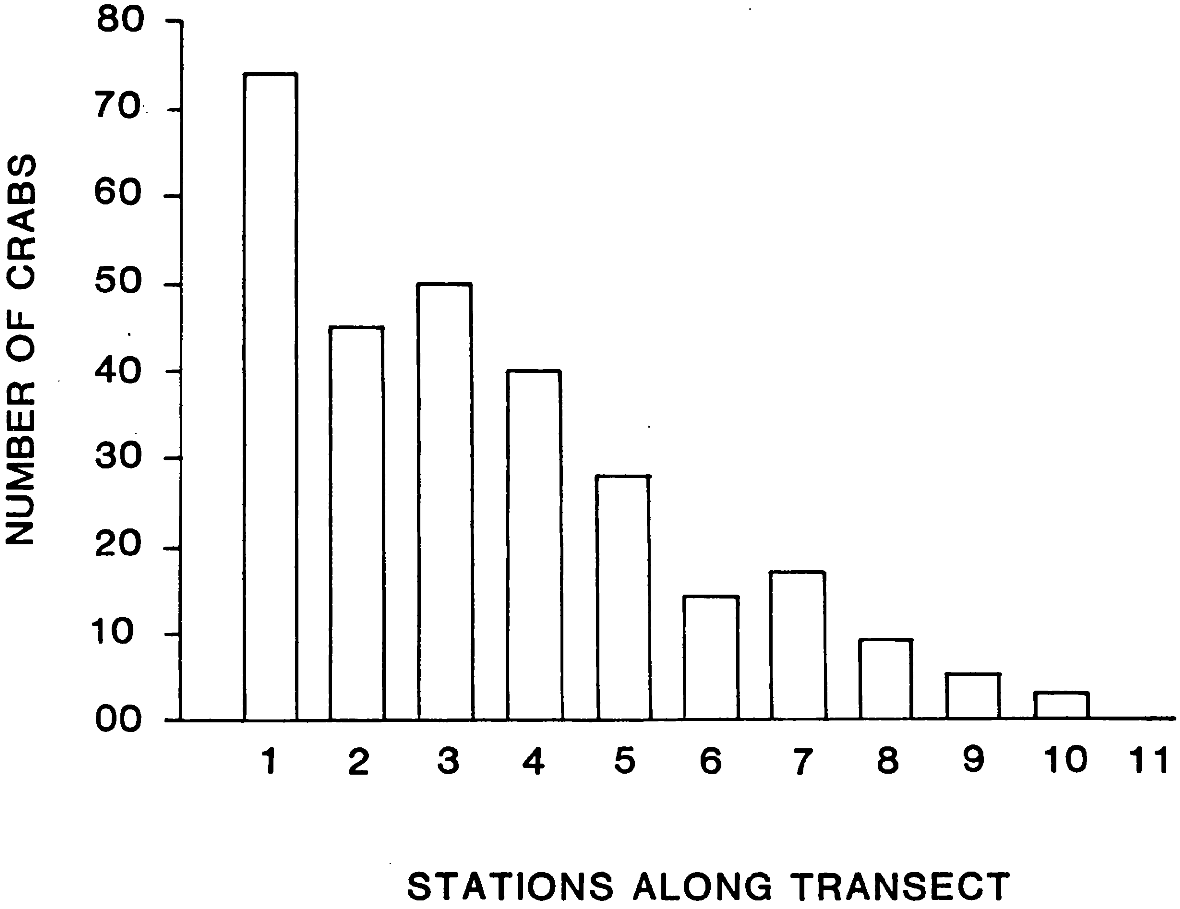

80
70
60
50
40
30
20
10
00
NUMBER OF CRABS
1
2
3
4
5
6
7
8
9
10
11
STATIONS ALONG TRANSECT

Plate III.1.1 Part of the nursery site of juvenile shore crabs at Salthouse Point

Table III.1.1 Mean carapace width, standard deviation, percentage of growth, and number of crab shown for the early stages of C. maenas from Salthouse Point, the Burry Inlet. Data from Balgzand, the Dutch Wadden Sea, and also crabs reared in the laboratory included for comparison

| Locality | Crab stage | Mean (mm) | SD (mm) | Growth (%) | Number of crabs | Author |
|---|---|---|---|---|---|---|
| Salthouse Point | 1 | 1.63 | 0.08 | | 18 | Present |
| 1981 | 2 | 2.26 | 0.12 | 39 | 150 | study |
| | 3 | 2.97 | 0.17 | 31 | 97 | |
| | 4 | 3.98 | 0.28 | 34 | 128 | |
| | 5 | 5.43 | 0.41 | 36 | 104 | |
| Salthouse Point | 1 | 1.59 | 0.07 | | 10 | Present |
| 1982 | 2 | 2.14 | 0.17 | 32 | 53 | study |
| | 3 | 2.92 | 0.22 | 35 | 122 | |
| | 4 | 3.84 | 0.27 | 31 | 96 | |
| | 5 | 5.0 | 0.36 | 30 | 88 | |
| Balgzand | 1 | 1.54 | 0.05 | | | Klein- |
| Dutch Wadden Sea | 2 | 2.26 | 0.10 | 44 | | Breteler |
| | 3 | 3.05 | 0.19 | 39 | | (1975a) |
| | 4 | 4.27 | 0.28 | 40 | | |
| | 5 | 5.87 | 0.45 | 43 | | |
| Crabs reared in | 1 | 1.53 | | * | 20 | Berrill |
| the laboratory | 2 | 2.19 | | 43 | 20 | (1982) |
| from megalopa | 3 | 3.02 | | 38 | 20 | |
| stage | 4 | 4.12 | | 36 | 20 | |
| (Central Maine, | 5 | 5.42 | | 32 | 20 | |
| North America) | | | | | | |

* computed from the data

## SECTION III.2

# POPULATION STUDIES ON ADULT CRABS

## III.2.1 INTRODUCTION

The previous part of the section dealt with populations of juvenile crabs in the Burry Inlet. It is now necessary to consider the population of adults.

Adult shore crabs inhabit a wide range of substrates in fully saline conditions including the whole range from bedrock to mud. They reach their maximum abundance on very sheltered shores (Crothers, 1970). They are able to tolerate salinities ranging from 4.0 to 34.0 ppt thereby allowing them to inhabit the estuarine environment (Broekhuysen, 1936; Green 1968; Wolff and Sandee, 1971). Laboratory and field studies have shown that crabs have the ability to withstand even lower salinity than 4 ppt when they shelter at low tide (Perkins *et al*, 1969).

The shore crab is not strictly diurnal or nocturnal. During the 24 hours, the animals show bursts of activity following a pattern representing two cycles of activity. The first one associated with the tides, and the second with the day-night cycle (Naylor, 1958). Naylor found that the activity was greatest when high tide occurred near midnight. Crabs collected from non-tidal conditions (eg. Swansea Docks) showed only the day-night cycle (Naylor, 1960). In the field, Crothers (1968) found that maximal activity occurred during the hours of darkness. Edwards (1958) had earlier studied the movement of individual members of a crab population in the littoral zone in summer and found that the majority of crabs took part in a movement up and down the shore, while some individuals become stranded under cover of rocks or weed when the tide left the area. From collecting crabs by hand and trapping them in creels at different tidal levels, Naylor (1962) deduced that the crabs moved actively with the tide throughout the year except in the coldest months. The activity rhythms of the *C. maenas* population at Mumbles in the

Swansea area were studied by Atkinson and Parsons (1973), who demonstrated a clear relationship between the appearance of the adult crabs in spring and the onset of endogenous tidal locomotor rhythmicity in the population, while in the autumn an off-shore migration of crabs accompanied by the loss of that rhythmicity. However, a recent study by Bolt and Naylor (1985) demonstrated that C. maenas in winter do not lose the ability to express endogenous circatidal locomotor rhythmicity since it is re-induced by the influence of an exogenous factor such as continuous exposure to low salinity. Temperature change has been suggested as the main factor controlling the seasonal migration (Naylor, 1963; Naylor et al, 1971). No satisfactory explanation has been advanced for the different behaviour of some members of the population.

The body colour of adult shore crabs varies from light green to dark red. In general, external colour of animals is due to chromatophores which are cells containing pigments. Melanin and carotenoid are the commonest pigments responsible for the visible colour pattern of animals (Goodwin, 1960).

Physiological colour changes are normally rapid and change the degree of pigment dispersion within the chromatophore. On the other hand, the formation and destruction of pigment results in a morphological colour change, which is relatively slow in occurrence (Kleinholz, 1961). In juvenile C. maenas the physiological change has been demonstrated by Powell (1962a and c) on the response of pigments to the background, temperature and light. Unlike juveniles, adult shore crabs cannot use their chromatophores to change their colour as a result of the thickness of the cuticle overlying the hypodermis and therefore the chromatophores (Crothers, 1968).

An attempt to assess the green-red colour variation of a crab population was made by Crothers (1968) who related the changes in colour to the depth of water the animals inhabit.

Many organisms have been recorded as associates settled on the carapace and the pereiopods of the shore crab (Crothers, 1968; Ingle, 1983). The distribution and orientation of barnacles on the carapace of a C. maenas population from North Wales were discussed by Heath (1976).

The shore crab has the ability to drop limbs which are badly damaged or seized by an attacker. Autotomy is the common word used to describe this phenomenon and occurs rapidly at the preformed breakage plane (Bliss, 1960). The value of autotomy to the individuals and the species was discussed by Needham (1954) who worked on a population of C. maenas and other crustacea. The mechanism of the process was reviewed by Mcvean (1975 and 1982) and the incidence of autotomy was studied for intertidal and sub-littoral populations of C. maenas (Mcvean, 1976; Mcvean and Findlay, 1979). Autotomised limbs can only be replaced by moulting. The size increment, however, may decrease since resources are diverted to the regenerated limbs (Warner, 1977).

In order to gather adequate information on the adult crab population in the area, investigation was concentrated on the season of migration, time spent foraging in the area, their monthly abundance, sex-ratio, size structure, recruitment pattern etc. These aspects form the main theme of this part.

## III.2.2 MATERIALS AND METHODS

A site was chosen near Salthouse Point at which to carry out regular sampling of the adult crab population. The site was located near the main river, between mean water level (MWL) and low water of neap tides (LWNT).

Following pilot trials, a standardised trapping method was employed. Four baited pots were used. They were cylindrical in shape, 30 cm high with a diameter of 28 cm (Fig. 111.2.1). The conical, non-return mouth was sited at the top. They were made of one inch (c. 24.5 mm) mesh galvanised wire roll 'Weldmesh' covered with 5.0 mm mesh plastic netting 'Netlon' in order to retain the smallest migratory crabs as well as the large ones. The traps were set up at 10 metre intervals (see Plate III.2.1), parallel to the advancing tide. Metal rods were used to keep them in position on the sand flat. Usually they were set up during the low tide period and left there over the period of one high tide only. All the catch was removed and the traps were reset for the following tide. Fresh bait (pieces of flat fish) was usually added after each catch, and was kept in a perforated polythene bag held firmly in the trap to prevent crabs from removing it.

In this way adult crabs were monitored on a monthly basis for more than two years. Each month the traps were set up on four successive tides, two during the day-time and the others at night. Neap tide was chosen for two reasons. Firstly, in the Swansea area, the shore crab is more active at neap tide when high tide coincides with darkness (Naylor, 1958). Secondly, it is more convenient to set up the traps and collect the crabs at low tide which happens to be in the early morning and afternoon in the case of neap tide.

The collected crabs were measured in the field across the greatest width of the carapace to the nearest 0.1 mm by using a Vernier calipers. Specimens were sexed, the colour of the abdomen, the presence of epifauna (barnacles and hydroids) on their exoskeleton, and missing limbs were recorded for every specimen. Some crabs were taken back to the laboratory to use them for feeding experiments or to examine their stomach contents. The remaining crabs were released in the estuary. To reduce the possibility of catching the same crabs in the following tide, they were taken back to the main river, away from the sampling site.

## III.2.3 RESULTS

The results of the baited trap experiments are set out in Figures III.2.2 to III.2.14 and Tables III.2.1 to III.2.3.

### III.2.3.1 Season of occurrence

Fig. III.2.2 shows that no crabs were caught during the cold months, between October 1981 and March 1982, nor again from December 1982 until February 1983. Only a few were caught at the beginning and the end of the season [November (1982), March, December (1983) and January (1984)].

### III.2.3.2 Size range

The following table indicates the extremes of size for each sex.

Size range caught in baited traps (mm)

| | Smallest | Largest |
|---|---|---|
| Male | 18.6 | 73.5 |
| Female | 20.3 | 63.5 |

The histograms in Figure III.2.2 indicate that the smallest migratory crabs (20-30 mm CW) appeared in the traps in summer, May-August in 1982, and May-September in 1983. The largest crabs were caught in the month of June. In both years, the very large crabs ( > 65.0 mm CW) disappeared from the catch starting from August.

### III.2.3.3 Changes in abundance

Annual variation in the abundance of C. maenas in the area is apparent in the histograms (Fig. III.2.2) and is reflected in the number of crabs caught per pot per tide (Fig. III.2.3). It shows a variation in their number throughout the season and from year to year. More crabs were caught in summer months and the maximum catch was in May 1983 (30.5 crabs per pot per tide). In general there was a low catch in 1982 compared to that of 1981 and 1983.

As Table III.2.1 shows, more crabs were caught at night than at day tides ($P < .001$). There were, however, some anomalies, which will be discussed later.

### III.2.3.4 Changes in the size frequency distribution

The pattern of changes was complex with no clear separation of cohorts. By the time crabs returned from their winter habitat, no change was recorded in the average carapace width of the population from that of the previous autumn; it now increased rapidly from a mean of 46.9 mm in April 1982 to 48.8 mm in May, and from 47.4 mm in the following April to reach 50.6 mm by June 1983 (Fig. III.2.4a). The figure shows as well a decline in the mean carapace width of the population starting from June 1982 and July of the following year. When the mean carapace width of males is considered separately from that of females (Fig. III.2.4b). It showed a rapid increase in size between April and June reaching a peak in May 1982 (52.9 mm) and June 1983 (54.8 mm), followed by a continuous decline to the minimum (46.0 mm) in September of both years. On the other hand there was a considerable late peak for the females, August to October in both years following a period of increase between July and August (Fig. III.2.4c), the maximum was in September, 47.0 mm (1982) and 48.0 mm (1983). The decline in the mean of the female carapace width is shown in the same figure reaching the minimum in June 1982 (43.6 mm) and July 1983 (44.8 mm). The lower point here precedes that of the males by three (1982) or two (1983) months.

Figure III.2.5 a and b show that mean carapace width of both males and females with red abdomen was bigger than that of animals with green abdomen all the time except the early months of 1983 in the case of males. A clear peak in the percentage of crabs >55 mm CW was recorded in May 1982 and June 1983 for the males, but there was no clear pattern in the case of females (Fig. III.2.6.).

As Figure III.2.7 shows, crabs < 35 mm CW increased in the catch in summer months and the peak was in July. This percentage in the catch was 13% in 1982 and 10.4% in 1983

### III.2.3.5 Sex ratio of catch

In most months, more females were caught than males (Fig. III.2.8). In July 1981, when the percentage of females was highest, it reached 89% of the catch. Figure III.2.9 shows the monthly changes in the different size groups of male and female. When crabs first started appearing in the traps in spring, males predominated (see results for April 1982 and March 1983). In May 1982 and April 1983 there was a sudden change to a predominace of females which continued to dominate all size groups except the large ones ( >60.0 mm CW) with a single exception of June 1983 when male numbers again exceeded females. By late summer and early autumn the dominance of females is obvious (July-August 1981, August-September 1982, and July-September 1983). However, this domination decreased at the end of the season.

### III.2.3.6 Berried females and copulating pairs

The number of females carrying eggs shown in Table III.2.2 indicates that they were caught from April to July only and in relatively small numbers (maximum of 4% of all females in any month).

Clearly no paired crabs were caught in pots since such crabs hide in cover. However it is perhaps worth putting on record at this point that some such paired crabs were found in late summer, high on the shore under boulders in the habitat of the juvenile crabs referred to in Section III.1. As mentioned there a few large crabs were found in this habitat in the warm months (but not in the winter). Of these a few were observed in copulation (see Table III.2.2).

### III.2.3.7 Body colour

In practice it was found that the great majority of crabs could be classified as either predominantly green or predominantly red coloured. The few intermediates that occurred (which represented no more than about 5%) were arbitrarily classified as green or red on the basis of any tendency observed in their coloration. Figure III.2.10a shows that the percentage of animals with green abdomen increased progressively throughout the season to reach their maximum in late autumn. When males were separated from females (Fig. III.2.10b) it was clear that the majority of male crabs were green in colour all the time. They peaked on two occasions in July and October 1982, and May/June and November (1983). On the other hand, females with green colour were few (5% in 1982) in spring, but their numbers increased progressively from July-August to reach their maximum in late autumn, November 1982 and December 1983.

If the results are grouped into three size classes (< 40 mm, 40-50 mm, >50 mm) as shown in Figure III.2.11, a correlation is found between crab size and body colour. The larger crabs include a far higher percentage (10-70%) with red coloration for most of the season. Crabs of the smaller size class nearly always include over 50% (up to 90%) green individuals.

### III.2.3.8 Autotomy

The number of crabs with missing limbs in 1982 was lower than that of 1981 and 1983 (Table III.2.3). The table shows also that crabs suffer more incidence of autotomy in chelae than walking limbs. The maximum of autotomy was 40% (March 1983) and the minimum was 5% (June 1982). Figure III.2.12 shows that incidence of autotomy between crabs with red abdomen was higher than those with green abdomen and particularly at the beginning and the end of the season.

### III.2.3.9 Epifauna

The common associates encrusting the integument of *C. maenas* in the Burry Inlet are: barnacles, *Balanus crenatus* Bruguière, and *Elminius modestus* Darwin; the bryozoa *Conopeum reticulum* (L.); and the hydroid *Sertularia cupressina* (L.).

Figure III.2.13 indicates that the presence of epifauna on the exoskeleton of crabs was at its highest in summer and decreased in autumn. It shows also that the percentage of crabs bearing epizoites was higher for females than males except in autumn, October 1982 and October and November 1983. Figure III.2.14 shows that the percentage of crabs bearing epizoites was higher for crabs with red abdomen than those with green abdomen at all times of the survey.

## III.2.4 DISCUSSION

### III.2.4.1 Main features of the population

#### III.2.4.1.1 Season of tidal migration

The tidal migration has an abrupt start and finish. As mentioned in the introduction to this section, the seasonal migration was found to be influenced by temperature. In Mumbles, South Wales, Atkinson and Parsons (1973) reported that crab populations moved off-shore in the autumn when sea temperatures dropped below 8°C, and moved on-shore when temperatures exceeded that value in spring. In the present study crabs showed similar behaviour. However, in mild winters a few individuals continued to move. A small number of crabs were caught in January 1984, but none in the following month when the experiment was terminated.

Since crabs caught in the traps usually exceeded 20 mm CW (only once a male of 18.6 mm CW was caught) even though the mesh size was $\approx 5.0$ mm, the trapping experiment shows that not only do all such crabs over-winter sub-littorally, but smaller crabs do not tidally migrate.

#### III.2.4.1.2 Tidal migration

In the Burry Inlet, tidal migration of adult crabs is almost complete. In warm months, few crabs were seen at low tide stranded on the upper shore at the juvenile nursery area where boulders are present. On some occasions some individuals were found covering themselves with sand in the drainage channels on the sand flat. The large majority take part in the tidal movement up and down the shore. Such behaviour has previously been recorded in the Wadden Sea. Where there was no shelter available, no crab >30 mm was found stranded on the mud flat at low tide (Klein-Breteler, 1976a). On the other hand, on rocky shores, many crabs are found stranded intertidally under covers at low tide (see for example Edwards, 1958; Naylor, 1962; Crothers, 1968). In the absence of covers, as in the case of Burry Inlet, it seems that crabs prefer to move away with the ebb tide rather than get stranded and facing the risk of being vulnerable to predators such as birds. It was also suggested by Klein-Breteler (1976a) that a high percentage of mud in such areas would deter adult crabs from inhabiting the flats at low tide.

### III.2.4.1.3 Diurnal pattern

Many studies had shown the higher activity of C. maenas during the hours of darkness (see Naylor, 1958; Kitching et al, 1959; Crothers, 1968). The present study is in agreement with that where the overall night/day ratio is about 1.45:1. However, on a few occasions slightly more crabs were caught during the day tide than during the night tide. The reason for this was not obvious but in retrospect it seems possible that on these occasions crabs had been moving actively to the intertidal area under the cover of high turbidity.

### III.2.4.1.4 Recruitment to the tidally migrating population

The maximum carapace width of O-group crabs which had settled in the previous summer and over-wintered on the upper shore would be still < 20 mm by April (see Section III.1). It was only from May onwards (when the size of these upper shore crabs exceeded 20 mm) that crabs ranging between 20-30 mm CW were first recorded in the baited traps (Fig. III.2.2). It is presumed that these small migrators had been recruited from the upper shore juveniles. The highest numbers of such juveniles were in July. However, some individuals of 20-30 mm size group were still to be found stranded under covers at HWNT. Although it is comparatively simple to follow the first year events of young crabs, it was not possible to separate year cohorts and relate size to the age group of the largest migratory crabs. The table below shows the maximum size reached by males and females of C. maenas in this and other localities.

| Area | Carapace width (mm) Male | Carapace width (mm) Female | Author |
|---|---|---|---|
| Burry Inlet | 73.5 | 63.5 | Present study |
| Swansea Bay (S. Wales) | 76.0 | 70.0 | Naylor, 1962 |
| Plymouth (S. England) | 86.0 | - | Carlisle, 1957 |

In the catch of 1982-1983, there were only nine individuals out of 1725 males that exceeded 70 mm. This represents only 0.5%. Out of 3054 females only 31 individuals exceeded 60.0 mm (c. 1%). In contrast to crabs from other localities as the table above shows, it is clear that although crabs inhabit much lower salinity areas than those in Swansea Bay, it does not correlate with size. Animals from Plymouth reach a much bigger size than crabs from both other localities, which could be due to the warm water in the south.

### III.2.4.1.5 Moulting season of males and females

Moulting in adult shore crabs has a double significance. It is not only the growth period, but the time when females can copulate (Broekhuysen, 1936). There is now considerable evidence that at least in N.W. Europe there is a well-marked main moulting period for the males in May and June and for females from July to September (Broekhuysen, 1936; Rasmussen, 1973). In the Burry Inlet, however, no soft crabs were caught throughout the survey. This was to be expected since the sampling method used was biased towards the active crabs only, so the inactive newly moulted crabs stayed away from the traps presumably in the sub-littoral. Although there were no direct records of soft crabs, there were some indicators to the moulting cycle and these are outlined below under the headings:

1. Copulation season
2. Carrying eggs
3. Changes in the population structure
4. Sex ratio
5. Body colour
6. Epizoites
7. Autotomy

### 1. Copulation season

It is generally recognised that copulation of C. maenas takes place just after the female moults (see Warner, 1977). Therefore, the presence of pairing crabs (in copulo awaiting moult) indicates the moulting season of females. In the Burry Inlet there is no adequate cover for mating crabs to hide intertidally, but a few were recorded at the level of HWNT at the sampling area for juvenile crabs (Section III.1) between July and October (Table III.2.2) which is in agreement with the copulation of crabs from Swansea Bay (Naylor, 1962) and Milford Haven (Crothers, 1966), and so serves as circumstantial evidence that the majority of the mature females mate at this time in the sub-littoral. In view of the continued high incidence of females in the mid-littoral traps throughout the summer, it must be presumed that they rapidly resume tidal migrating behaviour after mating.

### 2. Egg carrying

Results from different areas around the shores of Britain indicate that shore crabs breed throughout the year in the southern areas (Marine Biological Association, 1957) or one or two breeding seasons as reported by Crothers (1967). In Milford Haven, Crothers recorded two seasons for berried females, main (January-April) and subsidiary (August). Although the number of females carrying eggs would be underestimated due to the bait trapping method, a few berried females were recorded in the present study from April-July which suggests one season only and agrees with that of the population in Swansea Bay studied by Naylor (1962).

### 3. Changes in population structure

The rapid increase in the mean carapace width of males in early summer is probably not a result of immigration of large males to the area, but more likely due to their moulting and growth at that particular time. However, this does not necessarily mean that all males are restricted to moult in that period, but probably most of the surviving ones do. The evidnece for this is the extent of the rapid growth in spring and early summer (see Figs. III.2.4b and III.2.9). At this time of the year there is no complication arising from recruitment and it is evidence that the mean size of males increased from 43.6 mm to 54.8 mm between March and June (1983). This represents an increment of 26% about the extent of increase in size expected in an individual suggesting that most male individuals in the population moulted at this time. This is also reflected in the large increase in the number of large ( > 55 mm) males (Fig. III.2.6a) which reached a peak in June 1983 and May 1982.

In the case of females, autumn was the only time when the mean carapace width of females exceeded that of males. Nevertheless, this did not entail an increase in mean size of adult female crabs. However, as Figure III.2.5b demonstrates, females with green abdomen showed a clear increase in the average of their carapace width in late summer starting from August.

The reduction of mean carapace width in summer for males and females caught in traps is certainly due to a number of factors. These include the merging of one year old crabs with the migrating stock, the death of older crabs in terminal anecdysis after their final breeding season (perhaps females in summer and males in winter?) and other factors. The rapid disappearance of the largest male crabs in summer is probably the result of their retreat to the sub-littoral to await receptive females.

It was not within the scope of the study to assess recruitment and death rate.

## 4. Sex-ratio

The later arrival of females than males at the beginning of the season (March/April, Fig. III.2.9) is possibly the result of the behaviour of ovigerous females which elsewhere have been observed to remain in the more stable conditions of deeper water (Broekhuysen, 1936; Rasmussen, 1973) although data on egg carrying (Table III.2.2) give little evidence of females releasing their eggs by April. The reduction in female numbers in late autumn is probably explained by their behaviour, also recorded elsewhere, of leaving the intertidal water before the males (Crothers, 1968; Atkinson and Parsons, 1973) to return to their winter habitat. Overall there was a bias towards females (1.8:1) reflected in most months of the year. The baited trapping method is not considered as a source of bias towards females since other methods gave similar results (see Section III.3). Similar dominance of females in summer as seen in the Burry Inlet has also been recorded among sub-littoral populations of the shore crab in other areas such as Mumbles, Swansea (Atkinson and Parsons, 1973), the Yealm estuary, Plymouth (Mcvean and Findlay, 1979) and amongst intertidal populations at Lufkins in North America (Ropes, 1968). In the Swansea area it was concluded to be a local phenomenon to the crab population, while in the Yealm estuary it was related to the new recruits which were heavily biased towards the females. The present study showed that sex ratio in the case of juveniles was almost 50:50 (Section III.1).

Bennett (1974) working on the edible crab *Cancer pagurus* (L.) suggested that low catches of male crabs could be the result of intra-specific competition from females for food and space during approach and entry to pots. It is not likely to be so in the case of the present study of shore crabs since the pattern of male/female ratio changed throughout the season yet was observed to be consistent in the two years of the survey.

It is generally accepted that the majority of mature males moult in early summer (March-June), while females moult prior to copulation (where males still involved) in late summer and autumn. The inactive, newly moulted males would be expected to hide and avoid the traps (for about a week?) which might explain the increase of females in the population in early summer. After July, the largest male crabs disappeared from the tidally migrating population (Fig. III.2.9) presumably to wait in the sub-littoral for receptive females as mentioned previously. So the excess of females migrating tidally in summer could be a consequence of the absence of the moulted males. However, more study on the sub-littoral population is needed to understand that phenomenon.

### III.2.4.2 Subsidiary features of the population

#### III.2.4.2.1 Body colour

There appears to be no review of the significance of body colour of the adult shore crab in the literature. Colour change in juvenile crabs on the other hand had been studied quite extensively, for example, Powell (1962a and c) and Hogarth (1975 and 1978). The most detailed study of the significance of the colour of the adult shore crab was that of Crothers (1968) at Dale (South Wales). He collected crabs from different levels of the shore and demonstrated a predominance of red crabs sublittorally and a trend towards predominantly green crabs at higher levels on the shore. He suggested that there might be a correlation between the colour of the crabs and that of their habitat at different shore levels. He went on to suggest that colour may be actually determined by the environment through control of carotenoid pigments mediated through hormonal control via eye stalk.

The present study was, of course, carried out entirely at mid-tide level. No sampling of the sub-littoral population was carried out. Nevertheless both red and green crabs were caught at this level. Marked changes were found in the percentages of each body colour throughout the season and these changes were different in the two sexes and in crabs of different size (see results section for details).

The following hypothesis is offered to explain these facts:

1. Colour change appears to be correlated to moult cycle. The tendency is to be green after moult and gradually change to red before next moult or in final anecdysis.
2. Since larger crabs were more likely to be red and the small ones were mainly green, a progressive trend with age towards red colour is apparent. This may be partly explained by the decrease of moulting rate and final cessation of moulting in progressively older crabs.
3. Colour therefore appears not to be genetically controlled, ie. it is not a case of polymorphism but a reflection of the state of the moult cycle.

This simple concept seems not to have been suggested previously. The evidence for this is the seasonal increase in green crabs at about the time of moulting. In the case of males for which it is well-established that they moult in the spring, this increase in green occurs in April to June. In females (which moult in summer) the increase in green is from July to October. Obviously, this explanation is open to laboratory testing (see Addendum, page 69).

Circumstantial support for this explanation comes from the study of epizoites and autotomy. The percentage of crabs bearing epifauna (Fig. III.2.14) and missing limbs (Fig. III.2.12) is always higher amongst crabs with red abdomen. This also suggests that crabs in a late stage of intermoult are more likely to be red than green. It is probable that crabs at different stages of the moult cycle behave differently. As Crothers (1968) says large red crabs with an epifauna or the parasite Sacculina are typcial of the sub-littoral, while healthy green crabs with no encrusting growth are intertidal.

### III.2.4.2.2 Epizoites

A crab that bears algae and/or epifauna on the integument indicates that the animal has not moulted recently. A heavily affected crab may be in terminal anecdysis. Newly moulted crabs appear unusually clean, ie. no associates on their exoskelton. The two species of barnacles observed in the study, the lower shore Balanus crenatus as well as the widely zoned Australian species Elminius modestus are familiar to the estuarine habitat. These two species were also recorded as associates on crabs in North Wales (Heath, 1976). The bryozoa Conopeum reticulum and the hydroid Sertularia cupressina seem to be a new record as associates on the shore crab. Neither Crothers (1968) nor Ingle (1983) reported these epifauna as associates on the exoskelton of C. maenas.

The percentage of crabs bearing epizoites increased throughout the season to reach a maximum in late summer (July to September). The sharp overall drop by October corresponds to the drop in females (rather than males) bearing epifauna (females predominate at that time). This in turn reflects the fact that most females can be expected to moult in that period as mentioned earlier. Throughout the period, except in October, the percentage of females bearing epizoites was higher than that of males, presumably due to their late moulting season which allowed more organisms to settle on their exoskelton.

### III.2.4.2.3 Autotomy

As in any other decapod crustacea, C. maenas is able to shed any of its ten limbs. In the two years of study in the Burry Inlet the data in Table III.2.3 show the highest incidence of autotomy occurred in 1983. This time coincides with the fact that more crabs were caught in 1983 than 1982 (Fig. III.2.3). The possibility of encounters and interference between crabs increases with higher density and particularly in an area where only a few hiding places are present.

In general there were more crabs with missing chelae than walking limbs, which agrees with what Mcvean and Findlay (1979) recorded in a population of shore crabs in the Yealm estuary. They explained it as the result of the crabs' defence behaviour in using their chelae which make them more vulnerable to damage than the walking legs.

### III.2.4.2.4 Parasites

During the survey, crabs were examined for the occurrence of one parasite only, Sacculina carcini Thompson. It is worthwhile to record here that around 5500 crabs were examined and no single sacculinised crab was recorded. In Dale, Crothers (1968) recorded higher incidence of sacculinised crabs amongst the sub-littoral population. However, in the present study no sub-littoral survey was attempted.

The complex series of events recorded and discussed in this section can be recorded as a table:

1. Winter (December-February)
   Crabs mostly stay at sub-littoral level. A few move to the shore at high tide on mild days.

2. Early spring (March-April)
   As the sea water temperature rises, crabs begin to get active and appear on the sand flats. Males predominate presumably because some females are still carrying eggs and stay sub-littorally. Majority of females are red coloured.

3. Late spring and early summer (May-June)
   Most crabs tidally migrating to the Inlet. Maximum growth of males. Females predominate probably because males moulting and therefore stay in deeper water while soft. Berried females still present. Recruitment to the adult population due to previous year settlers joining the tidal migration.

4. Late summer (July-August)
   Maximum growth of epizoites. Females still predominate intertidally. Fewer large crabs perhaps because oldest crabs dying off and also because mating crabs stay sub-littorally.

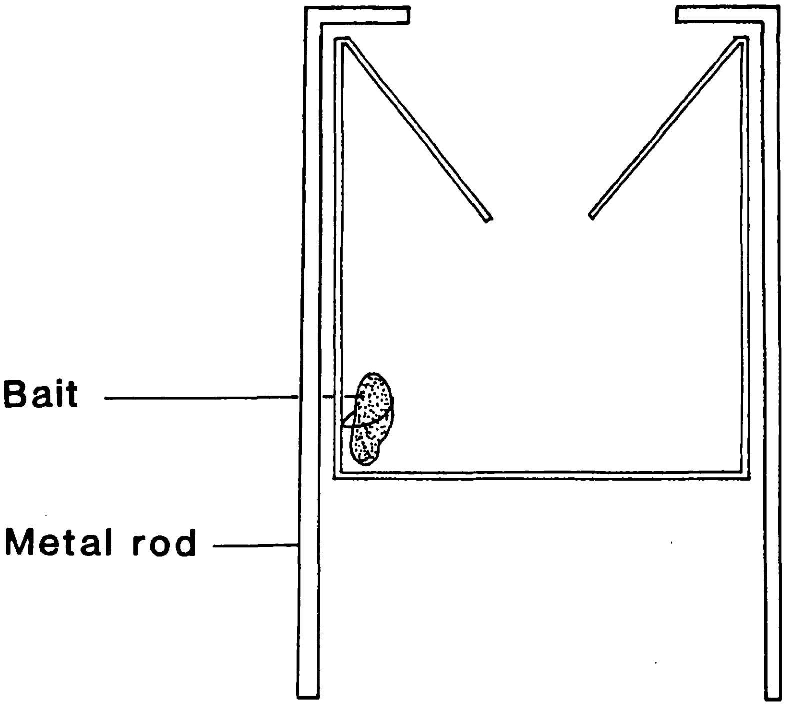
5. Autumn (September-November)
   Main moulting period of females, more mating crabs. Mean carapace width of intertidal females exceeds that of males. Majority of females are green in colour and have minimum growth of epizoites. The onset of winter retreat migration, females precede males, therefore sex ratio returns to 50:50 before all leave intertidal area.

# ADDENDUM

At a late stage in the study, a small experiment was conducted. Eight medium sized (carapace width 50-60 mm) red male crabs were confined individually in aquarium conditions. This experiment was started in December 1984. Temperature varied around 11-13°C. Food was presented occasionally. On 2 February 1985 one of these red crabs moulted. The new skeleton was a pale yellow-green. Twelve weeks after moulting, the colour of that crab became darker and slightly red. On 1 May 1985 another one moulted and the new exoskeleton was again pale greenish in colour. Although a very small sample, this experiment clearly supports the hypothesis advanced earlier in the section.

Fig. III.2.1 Shape of the baited pot.

(a) Side view



(b) Top view

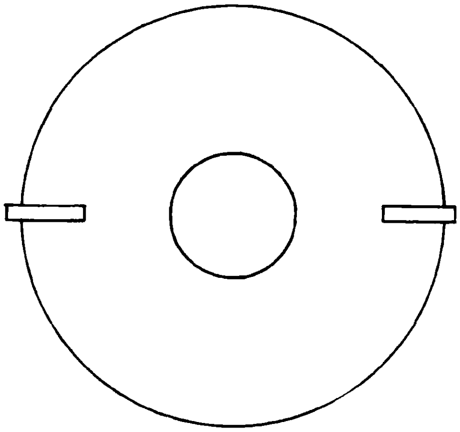


Fig. III.2.2 Size-frequency distribution of adult crab population during period from July 1981 to January 1984

NC No catch

β

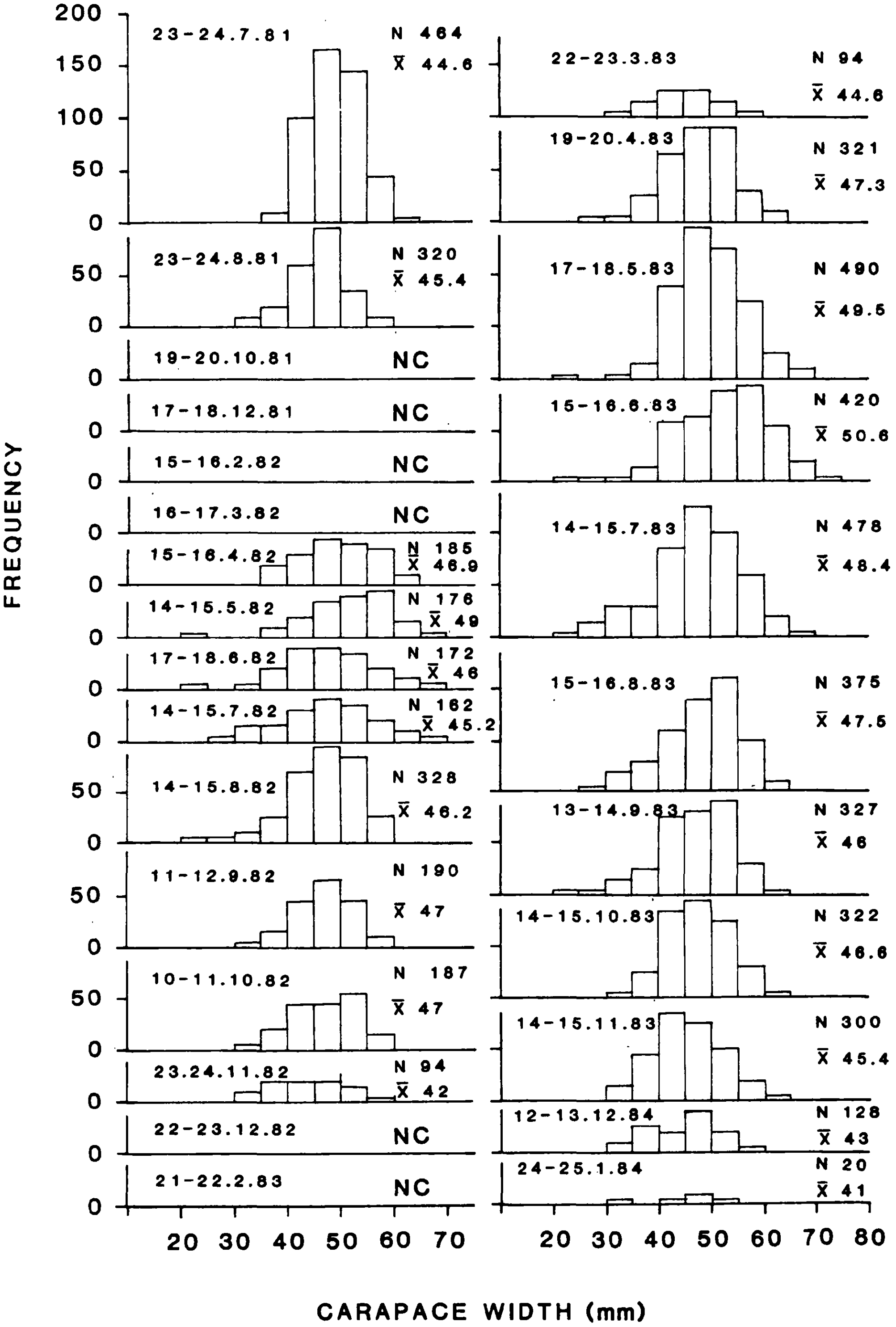
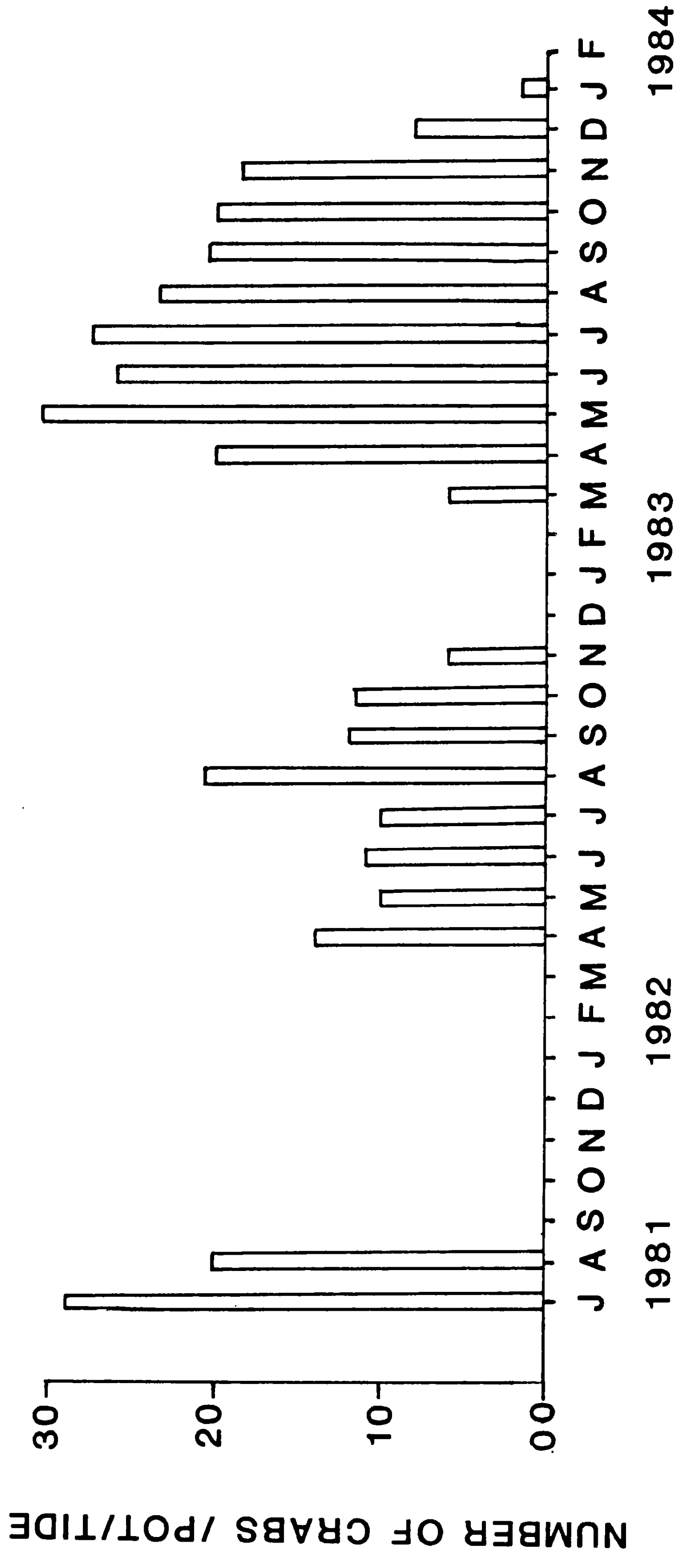

FREQUENCY
200
150
100
50
0
23-24.7.81
N 464
X̄ 44.6
23-24.8.81
N 320
X̄ 45.4
19-20.10.81
NC
17-18.12.81
NC
15-16.2.82
NC
16-17.3.82
NC
15-16.4.82
N 185
X̄ 46.9
14-15.5.82
N 176
X̄ 49
17-18.6.82
N 172
X̄ 46
14-15.7.82
N 162
X̄ 45.2
14-15.8.82
N 328
X̄ 46.2
11-12.9.82
N 190
X̄ 47
10-11.10.82
N 187
X̄ 47
23.24.11.82
N 94
X̄ 42
22-23.12.82
NC
21-22.2.83
NC
22-23.3.83
N 94
X̄ 44.6
19-20.4.83
N 321
X̄ 47.3
17-18.5.83
N 490
X̄ 49.5
15-16.6.83
N 420
X̄ 50.6
14-15.7.83
N 478
X̄ 48.4
15-16.8.83
N 375
X̄ 47.5
13-14.9.83
N 327
X̄ 46
14-15.10.83
N 322
X̄ 46.6
14-15.11.83
N 300
X̄ 45.4
12-13.12.84
N 128
X̄ 43
24-25.1.84
N 20
X̄ 41
20 30 40 50 60 70
20 30 40 50 60 70 80
CARAPACE WIDTH (mm)

Fig. III.2.3 Monthly catch of crabs per pot per tide


NUMBER OF CRABS /POT/TIDE
0.0
10
20
30
J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F
1981
1982
1983
1984

(MLW-LWNT)

Fig. III.2.4 Monthly variations of mean carapace width of migratory crabs.

a. All crabs
b. Males
c. Females

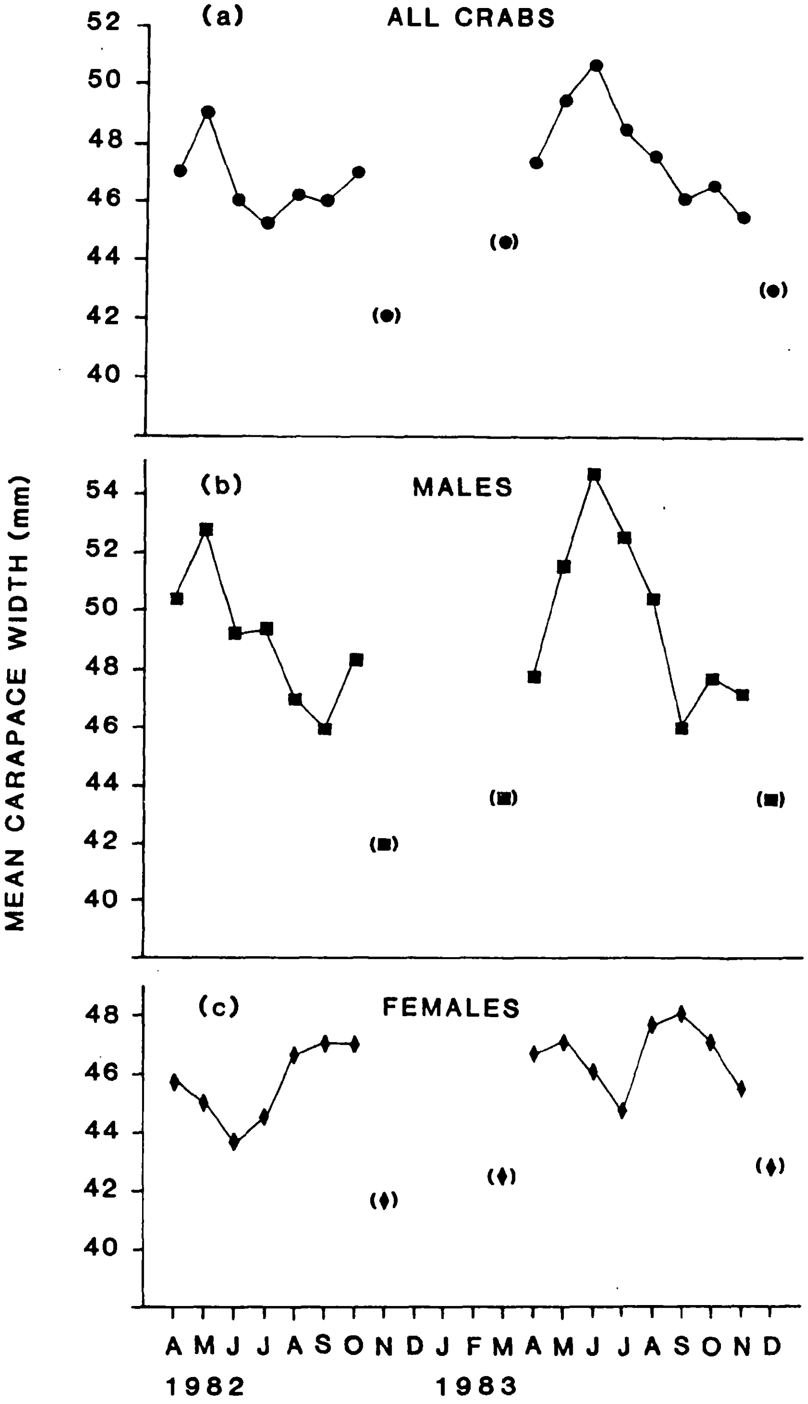

(a)
ALL CRABS
(b)
MALES
(c)
FEMALES
MEAN CARAPACE WIDTH (mm)
52
50
48
46
44
42
40
54
52
50
48
46
44
42
40
48
46
44
42
40
A M J J A S O N D J F M A M J J A S O N D
1982
1983

Fig. III.2.5 Monthly variations of mean carapace width of crabs with green and red abdomen

a. Males

b. Females

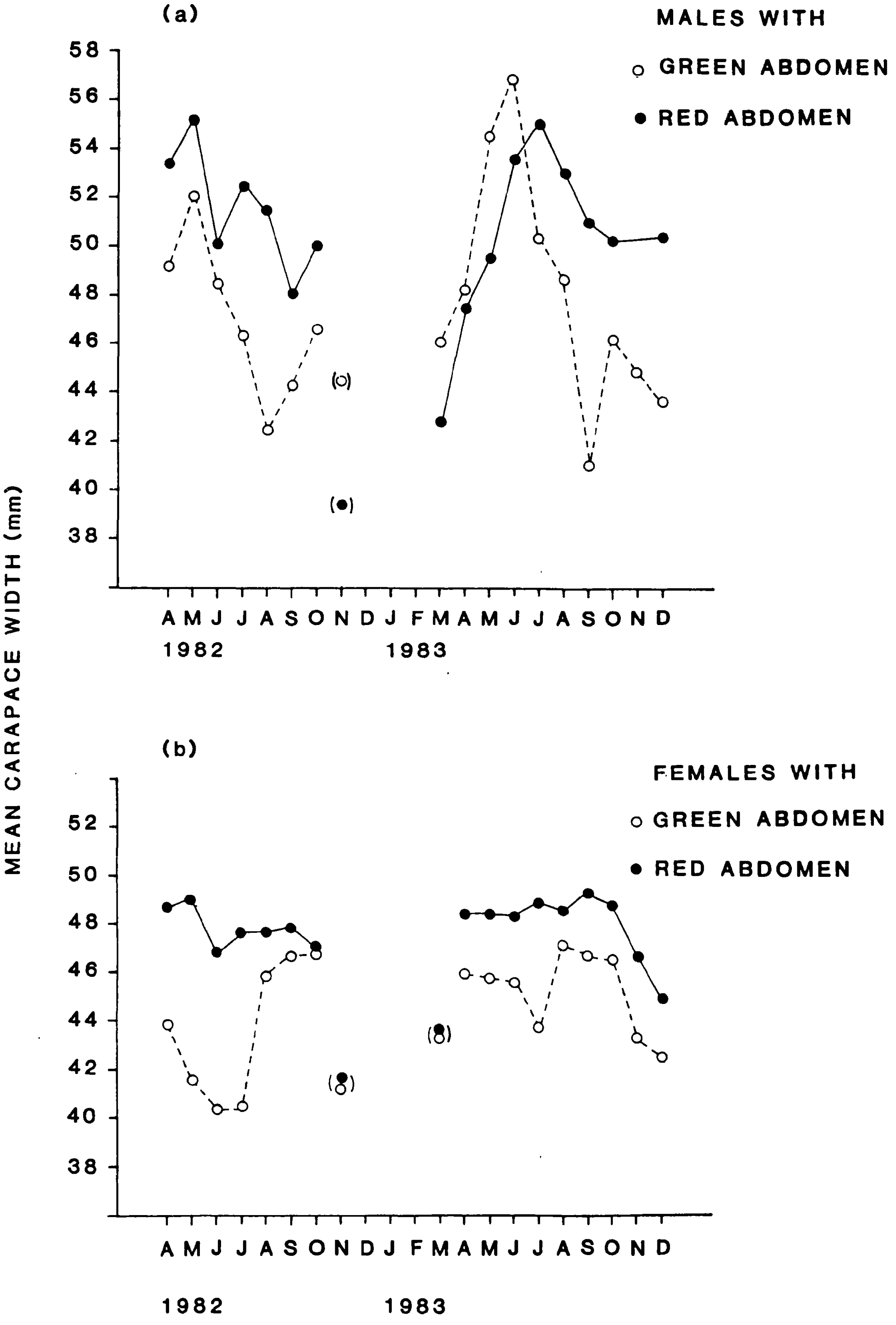
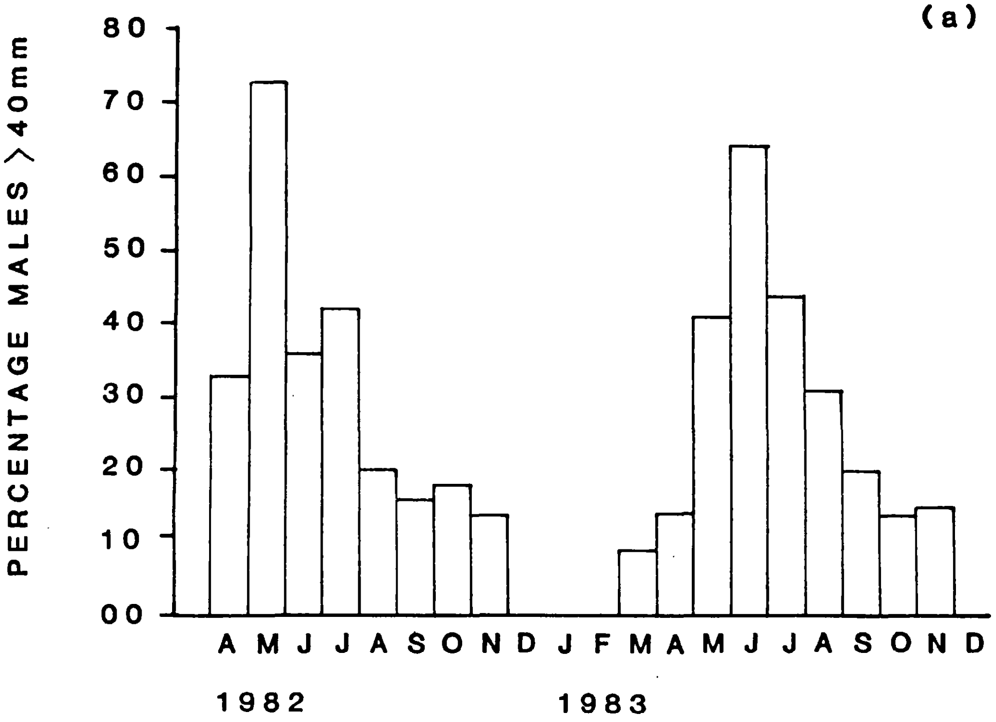

(a)
MALES WITH
○ GREEN ABDOMEN
● RED ABDOMEN
58
56
54
52
50
48
46
44
42
40
38
A M J J A S O N D J F M A M J J A S O N D
1982
1983
MEAN CARAPACE WIDTH (mm)
(b)
FEMALES WITH
○ GREEN ABDOMEN
● RED ABDOMEN
52
50
48
46
44
42
40
38
A M J J A S O N D J F M A M J J A S O N D
1982
1983

Fig. III.2.6 Monthly variations in the percentage of crabs > 55 mm CW

a. Males
b. Females


(a)
PERCENTAGE MALES > 40mm
80
70
60
50
40
30
20
10
00
A M J J A S O N D J F M A M J J A S O N D
1982
1983

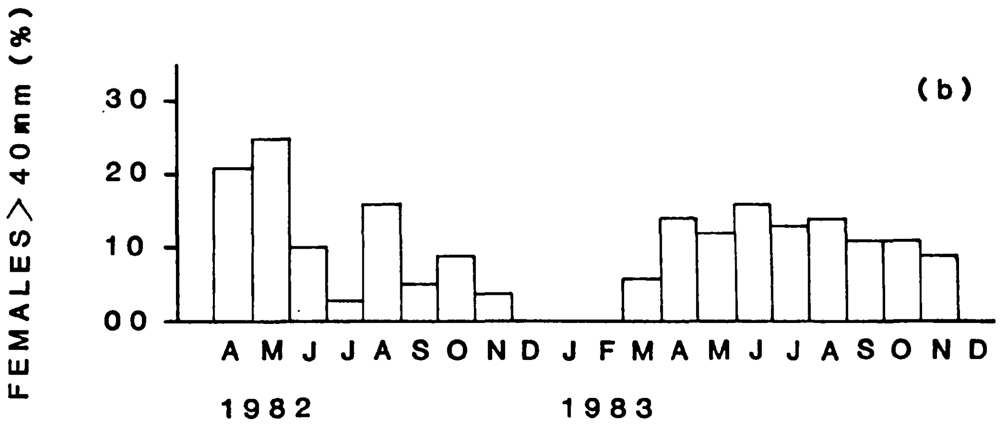

(b)
FEMALES > 40mm (%)
30
20
10
00
A M J J A S O N D J F M A M J J A S O N D
1982
1983

Fig. III.2.7 Monthly variations in the percentage of crabs < 35 mm CW caught in the traps. (Crabs based on small samples at ends of seasons omitted.)

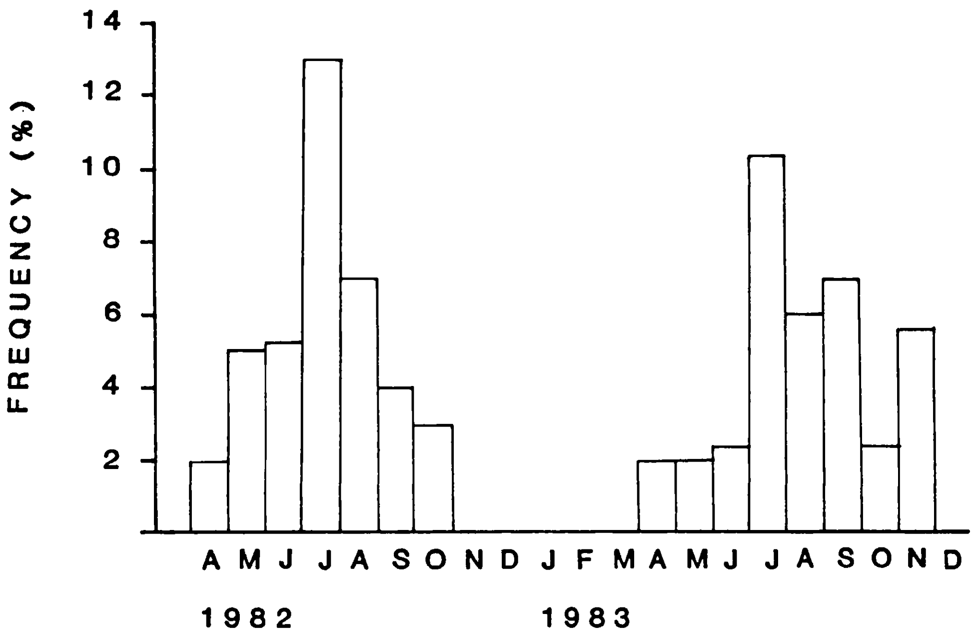

FREQUENCY (%)
14
12
10
8
6
4
2
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
1982
1983

Fig. III.2.8  Monthly variations in sex ratio

FEMALE SHORE CRABS CAUGHT IN THE TRAPS

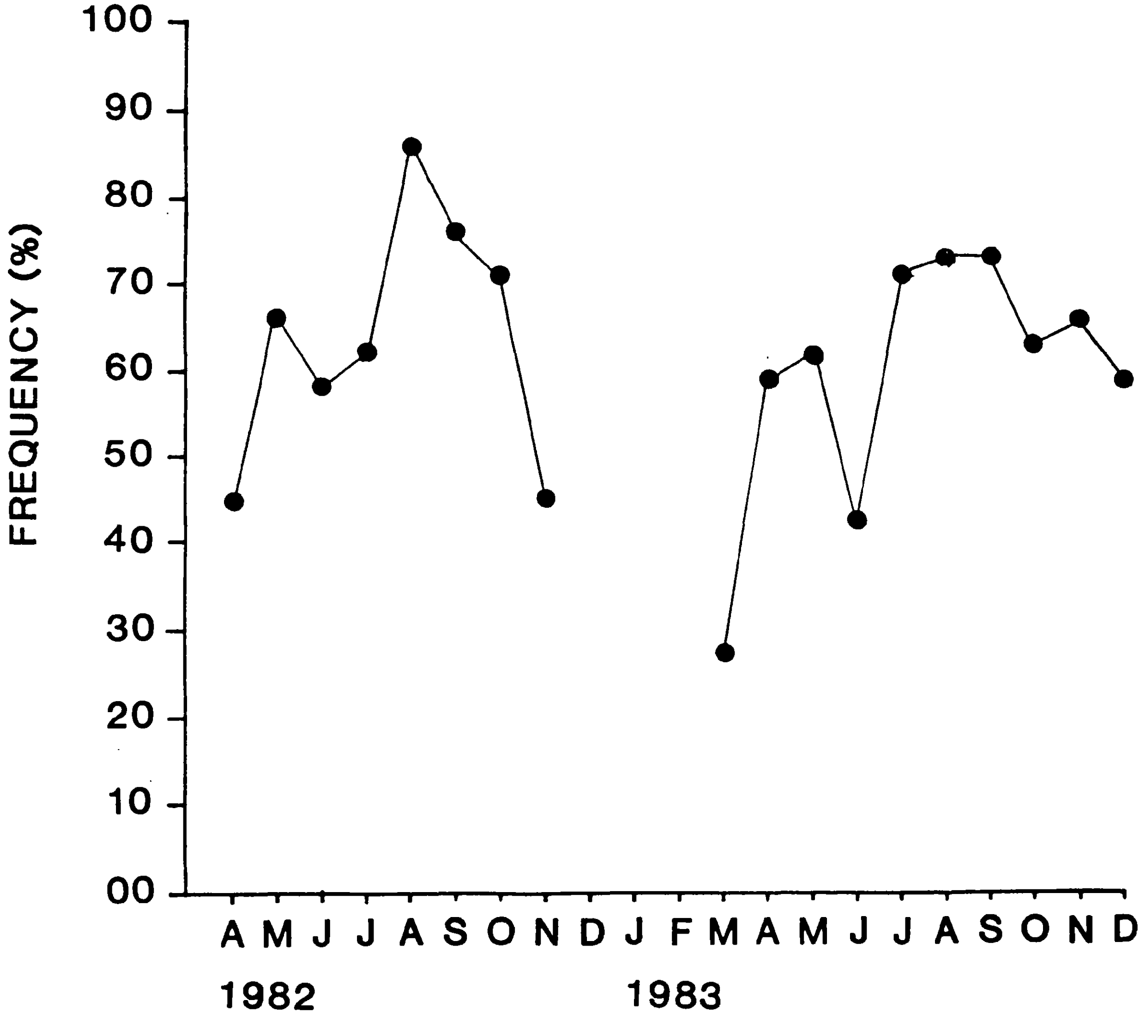


Fig. III.2.9 Monthly variations of different size groups for ● males and ○ females *C. maenas*

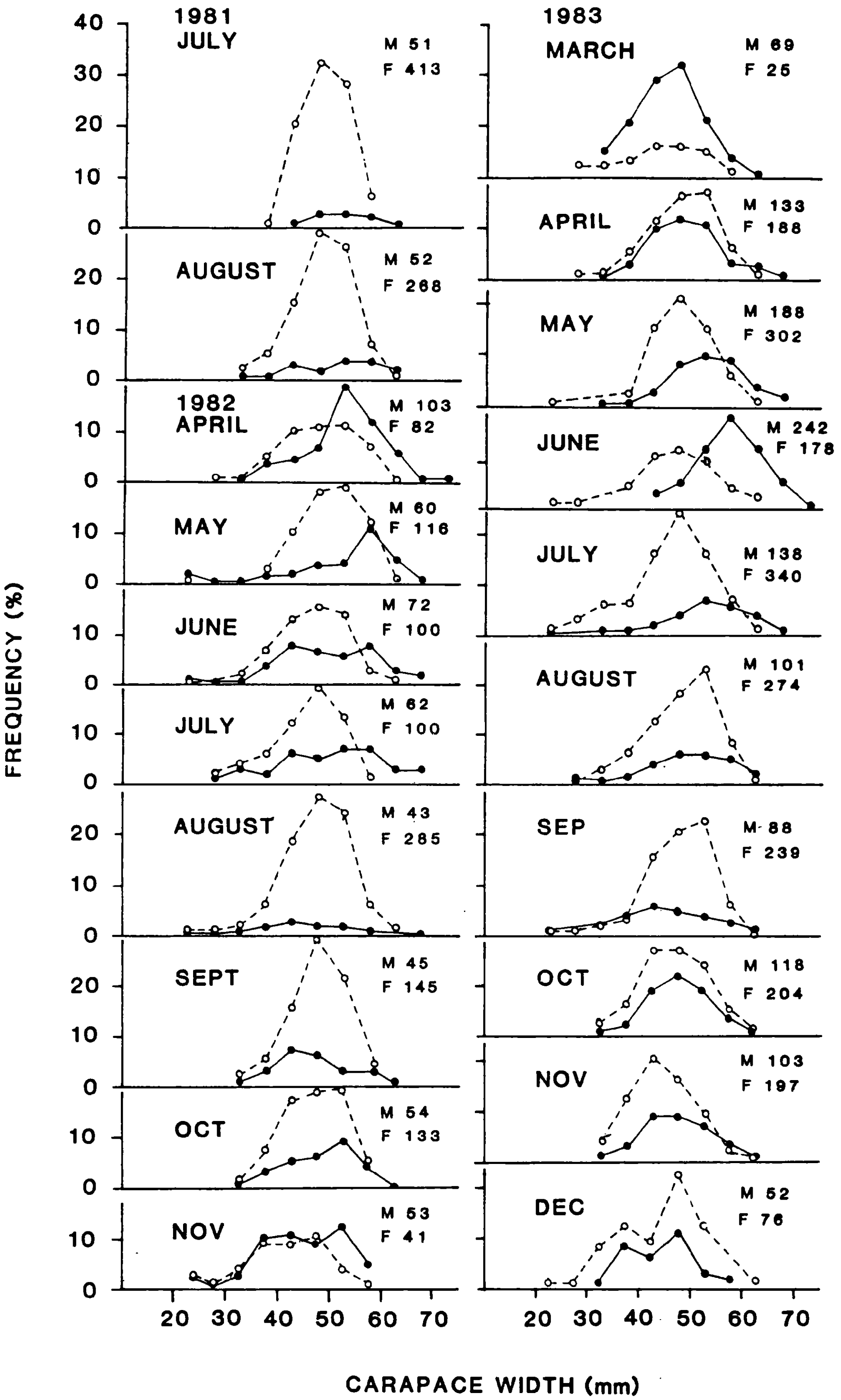

1981
JULY
M 51
F 413
AUGUST
M 52
F 268
1982
APRIL
M 103
F 82
MAY
M 60
F 116
JUNE
M 72
F 100
JULY
M 62
F 100
AUGUST
M 43
F 285
SEPT
M 45
F 145
OCT
M 54
F 133
NOV
M 53
F 41
1983
MARCH
M 69
F 25
APRIL
M 133
F 188
MAY
M 188
F 302
JUNE
M 242
F 178
JULY
M 138
F 340
AUGUST
M 101
F 274
SEP
M 88
F 239
OCT
M 118
F 204
NOV
M 103
F 197
DEC
M 52
F 76
40
30
20
10
0
FREQUENCY (%)
20 30 40 50 60 70
20 30 40 50 60 70
CARAPACE WIDTH (mm)

Fig. III.2.10a Changes in the number of crabs with green abdomen during the seasons

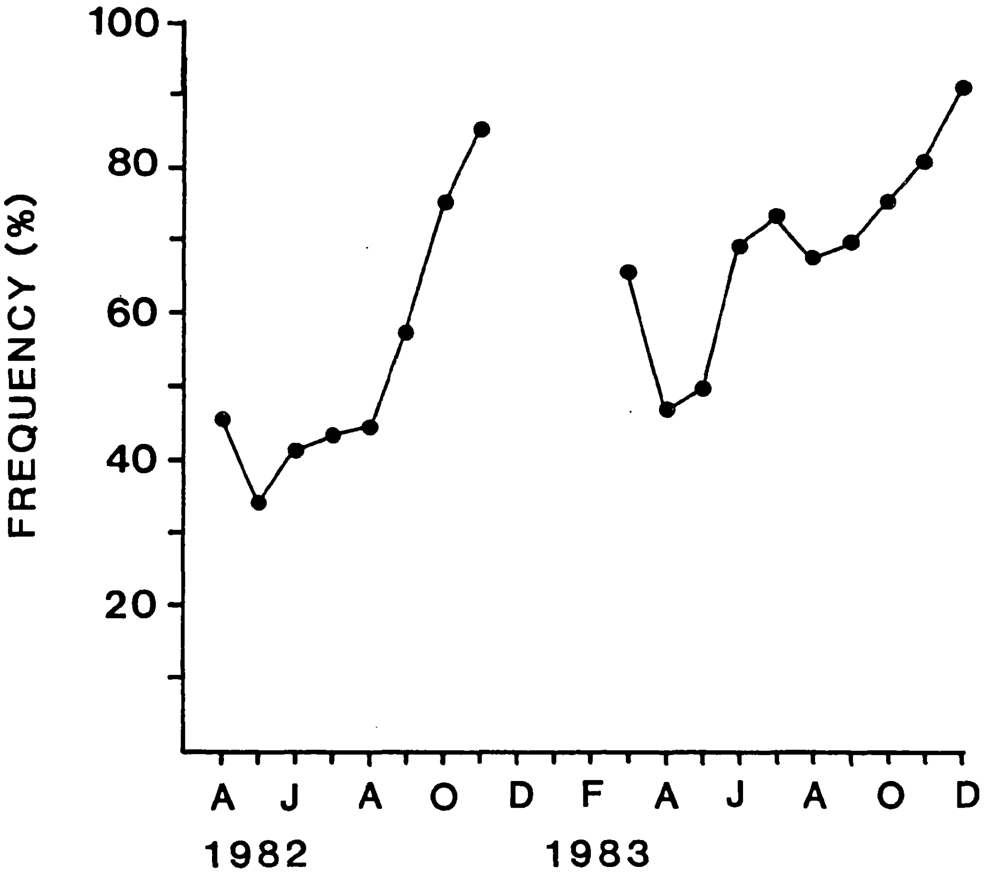
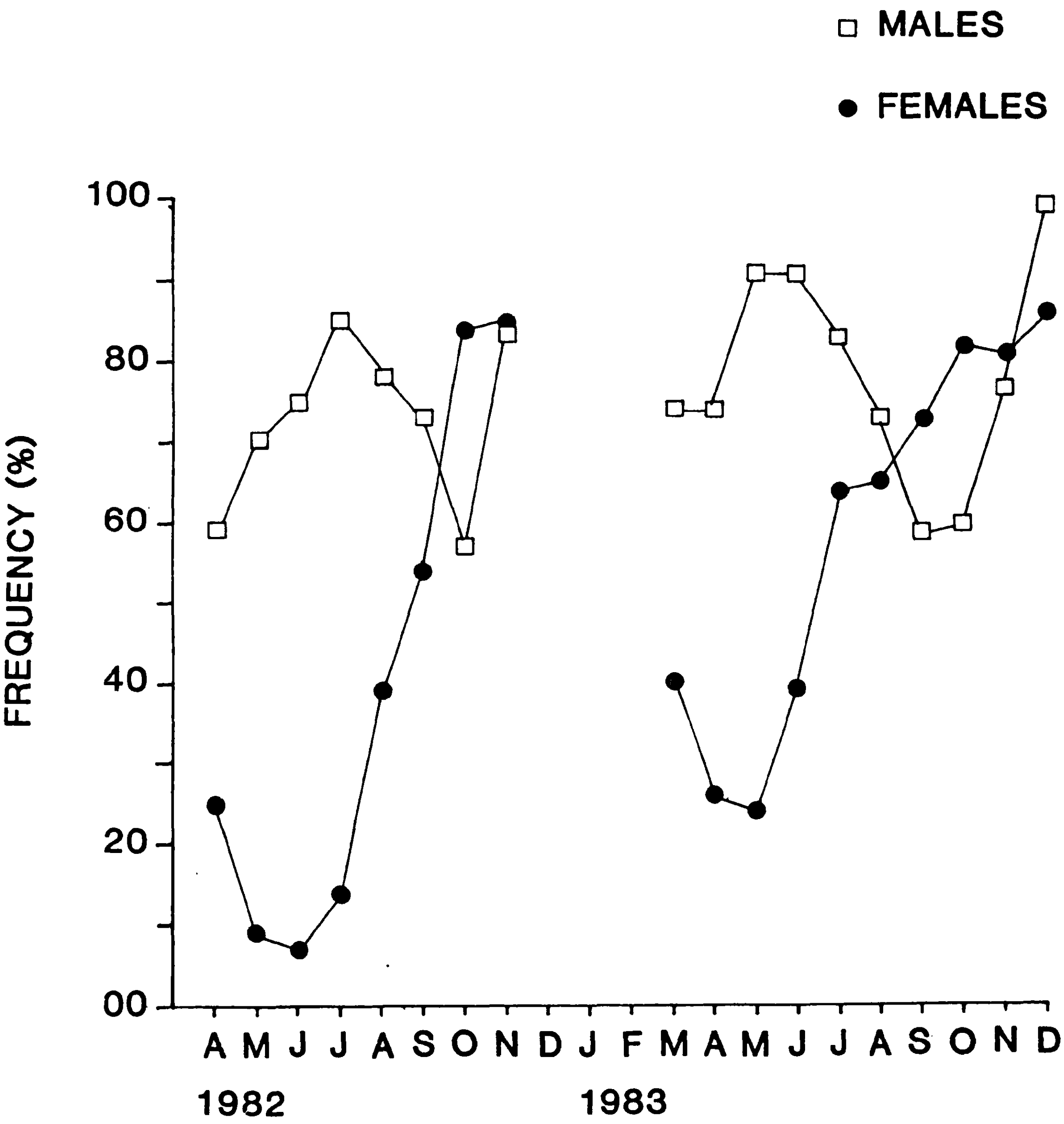

100
80
60
40
20
FREQUENCY (%)
A
J
A
O
D
F
A
J
A
O
D
1982
1983

Fig. III.2.10b Changes in the number of male and female crabs with green abdomen during the seasons



□ MALES
● FEMALES
FREQUENCY (%)
100
80
60
40
20
00
A M J J A S O N D J F M A M J J A S O N D
1982
1983

Fig. III.2.11 Relation between crab size and body colour from three size groups of crab with green abdomen

▲ Crabs with < 40 mm CW

■ Crabs with 40-50 mm CW

● Crabs with > 50 mm CW

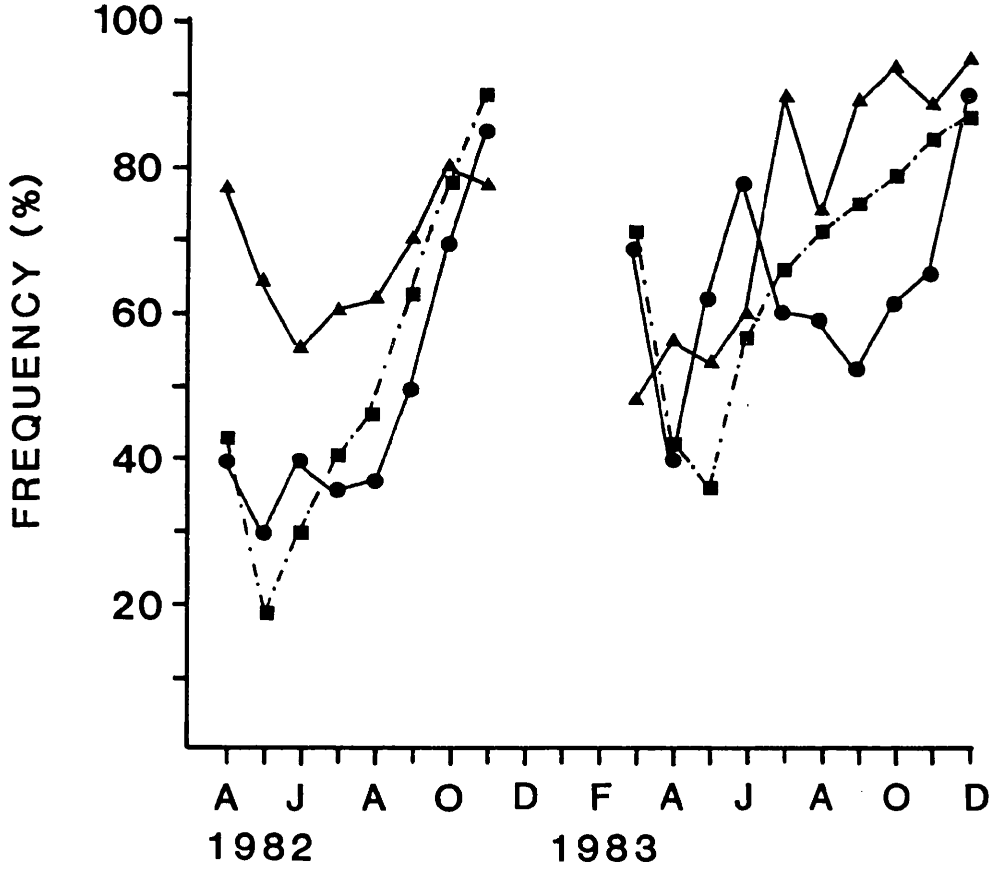

100
80
60
40
20
FREQUENCY (%)
A
J
A
O
D
F
A
J
A
O
D
1982
1983

Fig. III.2.12 Percentage of crabs with missing appendages

○ Crabs with green abdomen

● Crabs with red abdomen

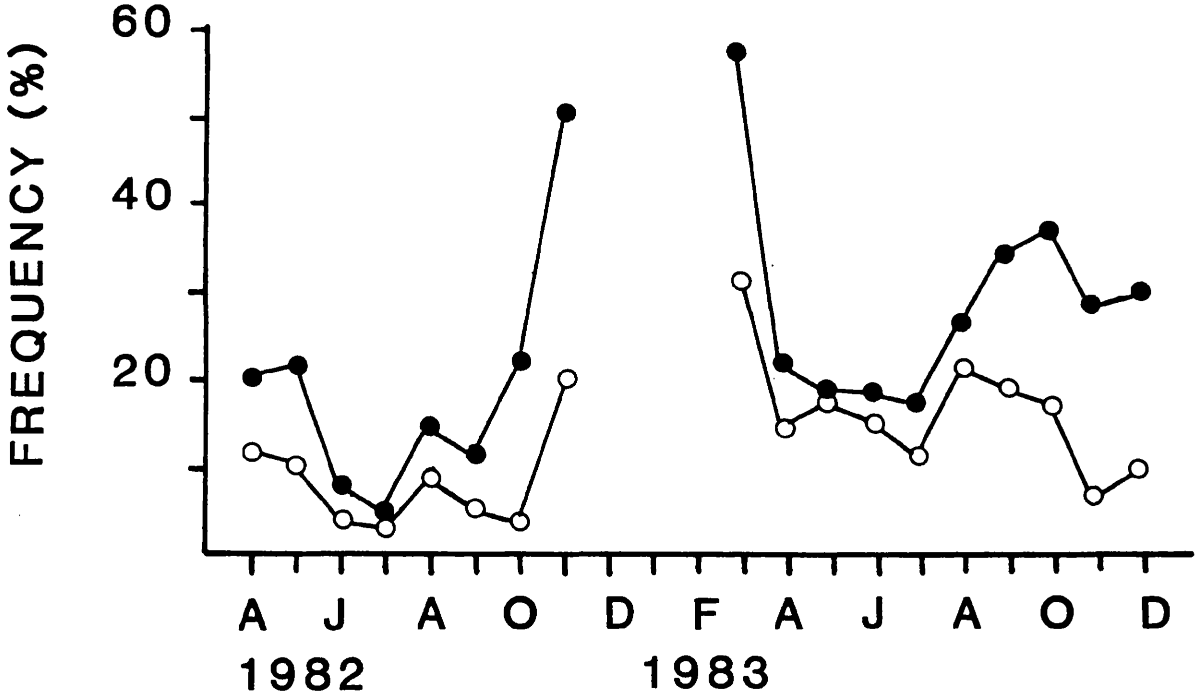

FREQUENCY (%)
60
40
20
A
J
A
O
D
F
A
J
A
O
D
1982
1983

Fig. III.2.13 Seasonal variation in the presence of epifauna (barnacles and hydroids) on adult C. maenas for each sex separately and in total

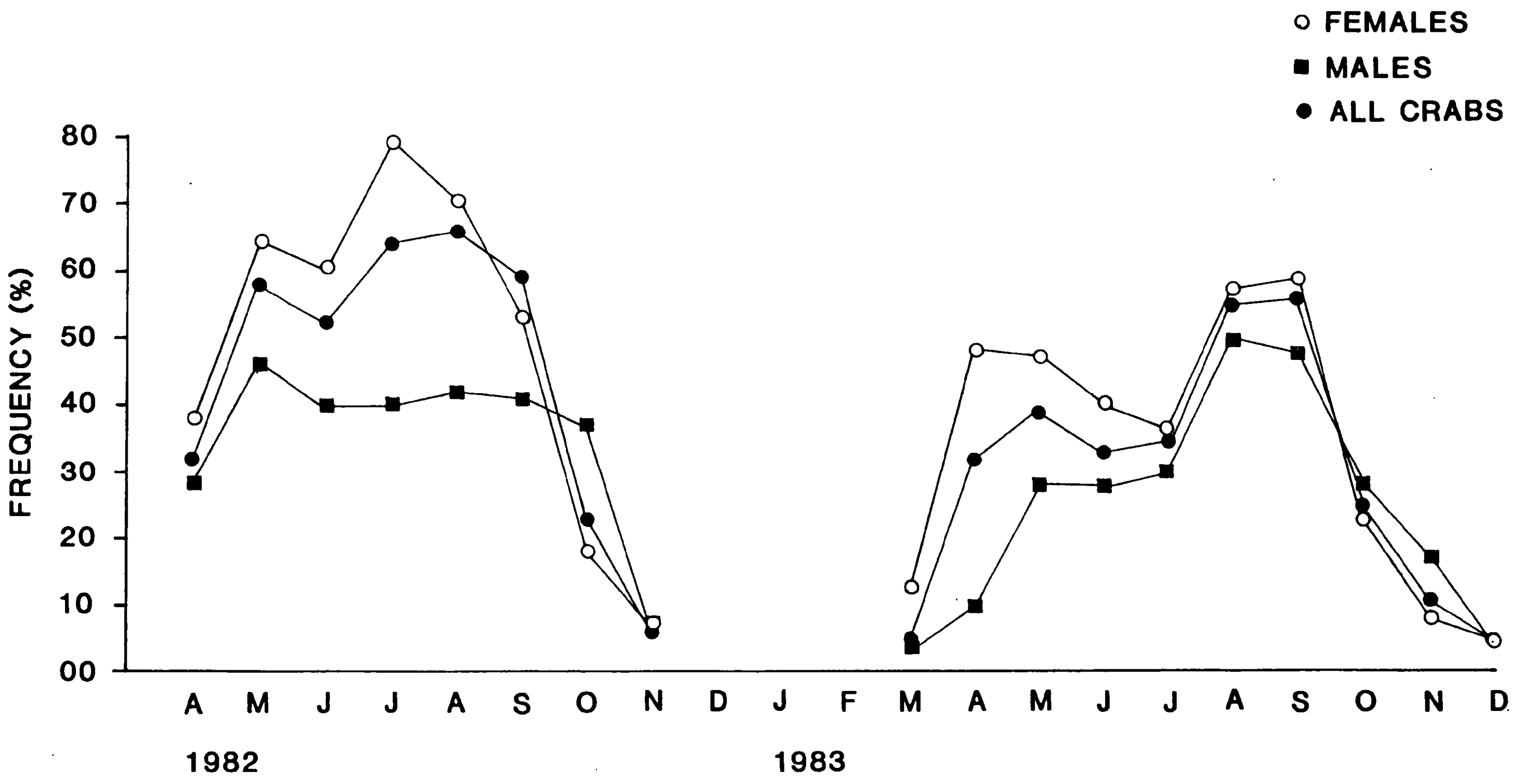

○ FEMALES
■ MALES
● ALL CRABS
FREQUENCY (%)
80
70
60
50
40
30
20
10
00
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
1982
1983

Fig. III.2.14 Percentage of crabs bearing epifauna (barnacles and hydroids)

○ Crabs with green abdomen
● Crabs with red abdomen

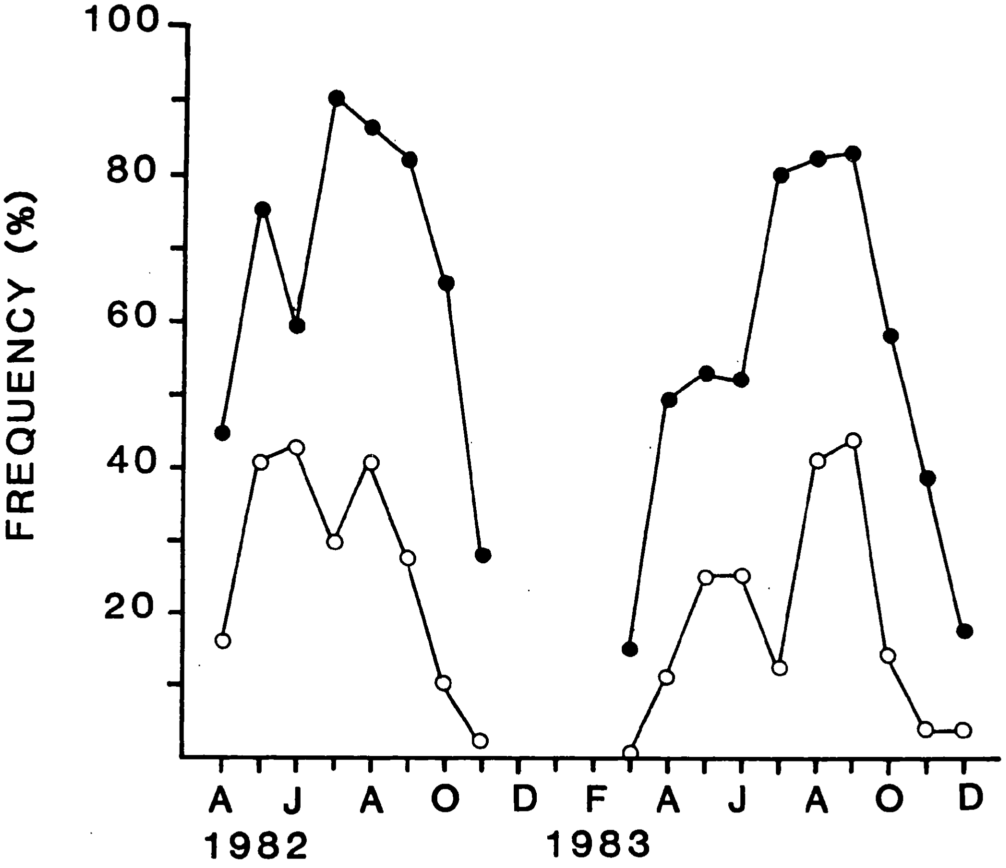

100
80
60
40
20
FREQUENCY (%)
A
J
A
O
D
F
A
J
A
O
D
1982
1983

Plate III.2.1 The four baited pots in position at 10 metre intervals. Remains of the 'training wall' are visible in the background

Table III.2.1 Night and day catch of adult C. maenas in the Burry Inlet

| Date | Total catch | | Ratio N/D catch |
|---|---|---|---|
| | Night | Day | |
| 1981 | | | |
| 23-24 July | 202 | 262 | 0.77 |
| 23-24 August | 185 | 135 | 1.37 |
| 1982 | | | |
| 15-16 April | 139 | 46 | 3.0 |
| 14-15 May | 93 | 83 | 1.1 |
| 17-18 June | 116 | 56 | 2.07 |
| 14-15 July | 84 | 78 | 1.07 |
| 14-15 August | 180 | 148 | 1.21 |
| 11-12 September | 118 | 72 | 1.64 |
| 10-11 October | 81 | 106 | 0.76 |
| 23-24 November | 52 | 42 | 1.23 |
| 1983 | | | |
| 22-23 March | 74 | 20 | 3.7 |
| 19-20 April | 208 | 113 | 1.84 |
| 17-18 May | 328 | 162 | 2.02 |
| 15-16 June | 328 | 92 | 3.56 |
| 14-15 July | 258 | 220 | 1.17 |
| 15-16 August | 251 | 124 | 2.02 |
| 13-14 September | 138 | 189 | 0.73 |
| 14-15 October | 186 | 136 | 1.36 |
| 14-15 November | 175 | 125 | 1.40 |
| 12-13 December | 84 | 44 | 1.90 |
| 1984 | | | |
| 24-25 January | 11 | 9 | 1.22 |
| TOTALS | 3291 | 2262 | 1.45 |

Table III.2.2 Number of berried females (in traps) and pairing crabs (in juvenile area) at Salthouse Point from 1981-1983.

| Month | Berried females | | Pairing crabs | |
|---|---|---|---|---|
| | 1982 | 1983 | 1981 | 1982 |
| January | NS | NS | 0 | 0 |
| February | - | - | 0 | 0 |
| March | - | 0 | 0 | 0 |
| April | 1 | 2 | 0 | 0 |
| May | 2 | 1 | 0 | 0 |
| June | 1 | 4 | 0 | 0 |
| July | 0 | 1 | 0 | 1 |
| August | 0 | 0 | 2 | 2 |
| September | 0 | 0 | 4 | 2 |
| October | 0 | 0 | 2 | 3 |
| November | 0 | 0 | 0 | 0 |
| December | - | 0 | 0 | 0 |

| | |
|---|---|
| - | No crabs caught |
| 0 | Crabs caught but none berrried/paired |
| NS | No sampling |

Table III.2.3 Percentage of crabs missing chelae, walking legs or both in the Burry Inlet from July 1981 to January 1984

| Date | No of intact crabs | No of crabs with missing limbs | % of crabs missing | | | All autotomised crabs (%) |
|---|---|---|---|---|---|---|
| | | | chelae | walking legs | both | |
| 1981 | | | | | | |
| July | 406 | 58 | 9 | 2.2 | 1.3 | 12.5 |
| August | 234 | 86 | 15 | 6 | 6 | 27 |
| 1982 | | | | | | |
| April | 155 | 30 | 10 | 6 | - | 16 |
| May | 164 | 12 | 6.2 | 0.6 | - | 6.8 |
| June | 163 | 9 | 5.2 | - | - | 5.2 |
| July | 149 | 13 | 8 | - | - | 8 |
| August | 295 | 33 | 10 | - | - | 10 |
| September | 175 | 15 | 7.8 | - | - | 7.8 |
| October | 172 | 15 | 8 | - | - | 8 |
| November | 70 | 24 | 25.5 | - | - | 25.5 |
| TOTAL | 1343 | 151 | 9.3 | 0.8 | | 10 |
| 1983 | | | | | | |
| March | 56 | 38 | 29 | 3 | 8 | 40 |
| April | 263 | 58 | 13 | 3 | 2 | 18 |
| May | 402 | 88 | 13 | 2 | 3 | 18 |
| June | 353 | 67 | 11 | 3 | 2 | 16 |
| July | 416 | 62 | 10 | 1 | 2 | 13 |
| August | 285 | 90 | 16 | 3 | 5 | 24 |
| September | 249 | 78 | 19 | 2 | 3 | 24 |
| October | 251 | 71 | 13 | 5 | 4 | 22 |
| November | 267 | 33 | 6 | 3 | 2 | 11 |
| December | 110 | 18 | 6 | 3 | 5 | 14 |
| TOTAL | 2652 | 603 | 12.8 | 2.6 | 3.0 | 18.4 |
| 1984 | | | | | | |
| January | 16 | 4 | 10 | 5 | 5 | 20 |

# SECTION III.3

# ASSESSMENT OF CRAB DENSITY IN THE BURRY INLET

## III.3.1 INTRODUCTION

The behaviour of moving up and down the shore by adult C. maenas makes it a difficult task for workers to estimate accurately crab density. Many methods have been used to assess the population size of the shore crab at such intertidal and sub-littoral sites.

In an estuary in south-east England, in the county of Essex, Hancock and Urquhart (1965) sampled them by using trawling and dredging. They managed to catch up to 84 adult crabs in summer at the cockle bed in 30 minutes with a 12 foot beam trawl. This method was considered by the same workers as impracticable in the Burry Inlet because of the presence of many posts, beacons and the shallow water.

Direct observation, in which the number of crabs feeding in an area is monitored by sub-aqua divers, is usually applicable only in areas where the visibility is good enough to see and record their numbers. In an area near Tal-y-foel in the Menai Straits, North Wales, divers using 0.5 $m^2$ quadrats and hand capture, managed to achieve a mean crab capture rate of 1.85 $m^{-2}$ (Dare and Edwards, 1981).

Use of baited traps is a well-known method for catching shore crabs. Different bait and traps have been used. Naylor (1962) and Atkinson and Parsons (1973) used the creels, while Crothers (1968) preferred the Leaky 'Universal' trap, and Welch (1968) used a specially designed trap for the same purpose.

The catch per unit effort (CPUE) is considered by many workers as an index of abundance. It was used for the shore crab (Welch, 1968), and for the British commercial crabs, Cancer pagurus (Brown and Bennett, 1980), and Maja squinado Herbst (Rodhouse, 1984).

Some of the main disadvantages of using the baited trap method is the underestimation of the population where only the active crabs will be attracted by the bait. Crothers (1968) suggested that the newly moulted crabs, the paired crabs, parasitised crabs and berried females are unlikely to enter traps and those represent more than 20% of the population. Other things are involved when using baited traps such as the type of the bait, whether to leave it exposed or in a perforated bag, the mesh size, the presence or absence of a collar at the mouth of the cage to reduce escape of the crabs, and the immersion time of the trap. In the study of two crab species, Cancer productus Randall and Cancer magister Dana, by using exposed bait, fitting a collar at the mouth of the trap and by decreasing the time of trap immersion, Miller (1978) found that the catch was increased up to five times.

An unbaited funnel trap was used by Dare and Edwards (1981), together with an underwater television system to monitor the crabs on their movement up and down the shore in North Wales.

The mark, release, recapture method has also been used to estimate the stock of crabs, mainly commercial ones. In order to mark the edible crab Cancer pagurus, Mason (1965) used the claw tag, while Edwards (1965) tried the suture tag which has the advantage of remaining on the animal even after moulting. For small animals such as C. maenas, Edwards (1958) chipped the marginal teeth of their carapace to mark them for the study of their tidal movement.

Gaskell and Parr (1966), using the quadrat procedure method, estimated that the total population of crabs occurring at low tide on the shore of Cliff Cottages at Dale, South Wales (500 x 70 yards), to be around 250,000.

To emphasise the pressure of the shore crab as predator on the infaunal bivalves in the Burry Inlet, it was necessary to assess their density in the area. In order to apply any method of measuring the density, many difficulties were presented in the area making it a difficult decision to select the proper method. Some of the special difficulties are: the large size of the Inlet with an area of approximately 45 $km^2$, the long distance from low water to high water level, many sand banks, the large and small gullies draining in different directions, turbidity of water and the presence of many posts and beacons as mentioned earlier. Finally the uneven distribution of prey species is probably reflected in the abundance of the predators.

All these problems made it difficult to rely on a specific method for measuring the crab density, and therefore, four different methods were employed: baited traps; unbaited funnel trap; sub-aqua diving and mark, release, recapture.

## III.3.2 MATERIALS AND METHODS

In order to assess the population density of adult C. maenas in the area, four different methods were used: baited trapping, unbaited funnel trap, sub-aqua diving, and mark, release, recapture.

### 1. Baited traps

Six of the same sort of traps as described in Section III.2 were used. The experiment was carried out at Salthouse Point at the same site as usually used for studying the crab population. The traps were set up at different distance intervals, and the catches over two successive tides were collected separately. The interval between traps was 10 metres at the beginning of the experiment. After two tides, the interval was reduced to only 2 metres, and after another two tides, the traps were left adjacent to each other, while finally they were reset again 10 metres apart.

### 2. Unbaited funnel trap

Plate III.3.1 shows the trap located in the field. A funnel mouth of 5 metres faced the advancing tide, while the other mouth was directed toward the shore. Three guide walls made of rigid 'netlon', each 20 cm high, and 5 metres long were inserted into 45 cm high polythene sheet (Fig. III.3.1a). 15 cm of the guide wall was erected on the sand surface, while 5 cm of the 'netlon' and the rest of the polythene sheet (30 cm) was buried in the sand. Metal rods were used in order to support the guide wall and prevent it being washed away by the tide. The guide walls led in two opposite directions to two unidirectional cages which each measured 90 x 60 x 30 cm (see Fig. III.3.1b). The cages were covered by a 5.0 mm mesh to retain the small crabs as well as the large ones. A curtain made of the same fine mesh was fixed on the cage mouth in a way to allow crabs to enter the cage, but not leave it. The rear panel of the cage was held closed by pieces of wire which made it easy to open and collect the catch.

The funnel trap was set up in the same area as the baited pots. After a single tide, all the crabs caught in both cages were collected, and the trap was left again for the next incoming tide.

### 3. Sub-aqua diving

Five different sites in the area were chosen for examination according to the presence of four different bivalve species. They were as follows:

Site a - mainly small *Cerastoderma edule*
Site b - mainly *Scrobicularia plana*
Site c - mainly *Macoma balthica*
Site d - mainly *Mya arenaria*
Site e - no bivalves

At each site a 10 $m^2$ transect was made, 1 metre wide and 10 metres long. It was marked by using two 10 metre parallel white strings fixed in position by metal rods during a low tide period (see Plate III.3.2). The string was left approximately 10 cm above the sand surface, so as not to be buried at the rising tide. At each transect a buoy was positioned to mark the site to the diver. By diving at high tide the number of crabs present at the transect area was monitored at that particular time. An inflatable boat with outboard engine was used to travel from one site to another, while care was taken to keep the boat away from the site so as not to disturb the animals.

### 4. Mark, Release, Recapture

Some trials made in the laboratory, showed that paint (nail varnish) remained on the carapace of the crabs for more than two weeks.

One hundred adult crabs were used in the experiment. They were trapped in the usual way. After cleaning and drying the carapace with tissue soaked in alcohol in the field, a nail varnish was used as a marker. The paint was left to dry before the animals were released in the main river. After two tides, to allow enough time for them to mix with the rest of the population, four baited traps were set up at the usual site in order to catch any of the marked specimens. The traps were set up at two successive tides.

## III.3.3 RESULTS

### 1. Baited traps

When the distance between baited traps decreased the number of crabs caught in the pots decreased. Catch per pot per tide will be used as an index of crab abundance. In Table III.3.1 the average number of crabs caught per pot per tide declined from 31.2 when the pots were 10 metres apart to only 20.9 at 2 metre intervals, and finally the catch was 11.6 crabs per pot per tide when the pots were attached together. When the traps were reset again at 10 metre intervals the catch increased to 26.7 crabs pot$^{-1}$ tide$^{-1}$.

Table III.3.2 shows that, in most cases, the pots which were at the middle (nos. 3 and 4) caught fewer crabs than the ones at the margin and particularly those at the very far end (nos. 1 and 6).

### 2. Funnel trap (see Table III.3.3)

When the unbaited funnel trap was used with a 5 metres wide mouth, more crabs were caught on their way down the shore (on the outgoing tide) than coming up the shore (on the incoming tide). More crabs were caught in June than May. For the two occasions the average catch per metre of tide line was 1.25 for the incoming and 6.7 for the outgoing crabs. It is shown in the same table that catch was higher at night (16 and 76 compared to 9 and 58 in both trials).

### 3. Diver Monitoring

Results of recording the number of adult crabs by diving is shown in Table III.3.4. More crabs were found at the area where abundant small cockles were present. No crabs were found at the diving time in the area where only properly buried large *Mya arenaria* were present, while

0.35 crabs per $m^2$ were observed foraging in an area full of cockle spat. The overall average of crabs was 0.15 per $m^2$ at day time.

### 4. Mark, Release, Recapture

The result of this method was negative, since no marked crabs were captured in any of the four baited traps which were set up at two successive tides.

## III.3.4 DISCUSSION

Table III.3.1 indicates substantial numbers of crabs in the area which reached a maximum CPUE of 31.2 crabs. Although this indicates that large numbers of crabs invade the intertidal zone to feed, it does not give an easy answer to the problem of how many crabs invade the whole Inlet during the high tide.

When the baited pots were set up at different intervals, it showed a direct relationship between the catch and the distance separating the pots suggesting that crabs were attracted over a great distance by the bait. To what extent the relationship goes is not that clear.

Although the unbaited funnel trap does not suffer the problems of the baited trap, the decision of where to locate the trap was not easy. Trenches had to be dug to bury the guide walls of the funnel. This could bring bivalves to the surface where these could act as unwanted bait. A decision was made to site the trap on a sand bank with little buried fauna. Nevertheless, many polychaetes were brought to the surface when establishing the troughs. A variation of this way of assessing the crab density on a mud flat area was used by Dare and Edwards (1981). They related the number of crabs caught to the tide line and expressed it as number of crabs present per metre of tide line. An estimation of the number of adult shore crabs was given by the same authors as an average of 84 crabs per metre of tide line. In contrast to that, the present study showed a maximum of only 6.7 crabs per metre of tide line (less than one-tenth of the North Wales figures). The large differences in the results could be related to the type of the shore line. In North Wales, it was simple and evenly sloping. In the Burry Inlet the 'shore' is an elaborate shape so the pathways of individual crabs may be different. The two situations are certainly not easily comparable. However, the large difference between numbers of incoming and outgoing crabs suggests that crabs may enter one 'sand bank' area by several routes and leave by different routes. The movement of the crabs is not clear but it is possible that crabs use mainly channels and streams at their flood movement, but when the water leaves the sand flat they more likely move down the slope.

It was noticed that because of the poor visibility, the diver needed to be very close to the transect area in order to see the crabs (about 0.5 metres). This may have caused many crabs to escape and not to be counted. A mean crab capture rate of 0.35 per $m^2$ was achieved at the site where plenty of small cockles were available. However, the capture rate in the Inlet seems to be small in contrast to 1.85 per $m^2$ (about five times as many) on Tal-y-foel mud flat (Dare and Edwards, 1981).

A rough estimate of the number of crabs invading the whole Inlet (45 $km^2$) based on the diving result would give a value of $6.75 \times 10^6$ crabs if evenly spread throughout the estuary at an average density of 0.15 per $m^2$. However, approximately 16 $km^2$ of the Inlet is now Spartina dominated and it is unlikely that crabs invade this area to any extent. Furthermore, the value of 0.15 is based on an average of five types of area which are not in fact equally represented.

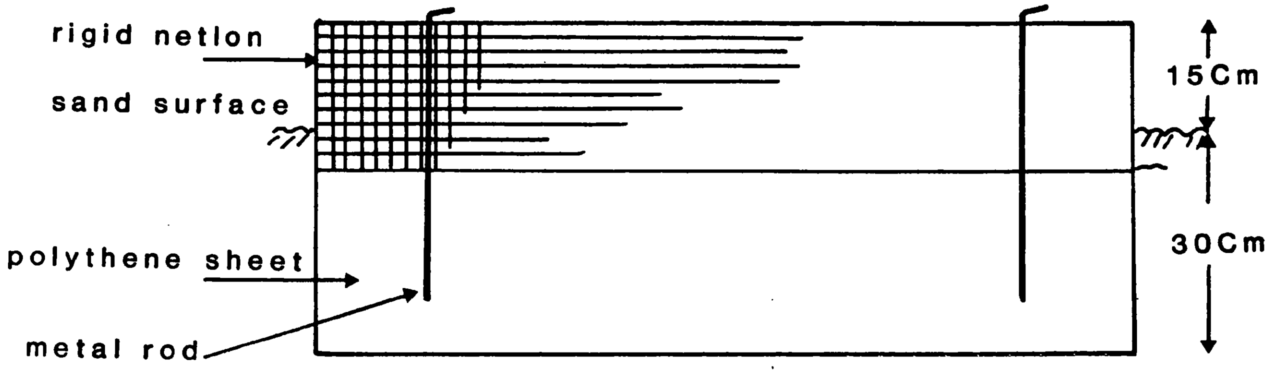
It is worthwhile recording here that three different trapping methods gave more or less similar results about male/female ratio in summer months (see Table III.3.5). It appears that the majority of females in summer is not the result of bias towards females because of the use of any particular trapping method but the data here give support to the suggestion offered in Section III.2 in relation to the crabs' behaviour.

The total failure of the mark, release, recapture experiment reported in the results section of this report is interesting. A number of points need to be made. Firstly, it is thought unlikely that the paint washed off. Painted crabs in the laboratory did not lose their marks. Nor is it likely that the crabs all moulted during that short time. It is possible that the marked crabs became more conspicuous and were predated by fish or birds, but this seems unlikely. More possible is that their behaviour changed. In a laboratory experiment it was observed that paint damaged the exoskeleton. Solvent may have had an effect on metabolism causing crabs to stay sub-littoral. Nevertheless, it is also possible that failure to recapture any is a reflection of the large size of the population which needed more animals to be marked.

In general all methods used indicated directly or indirectly that a large number of crabs move to the intertidal zone under the cover of water in the Burry Inlet, but it is difficult to determine accurately the density of such adult crabs feeding in the area.

Figure III.3.1a The guide wall of the funnel trap

Figure III.3.1b Diagram shows the construction of the cage


rigid netlon
sand surface
polythene sheet
metal rod
15Cm
30Cm

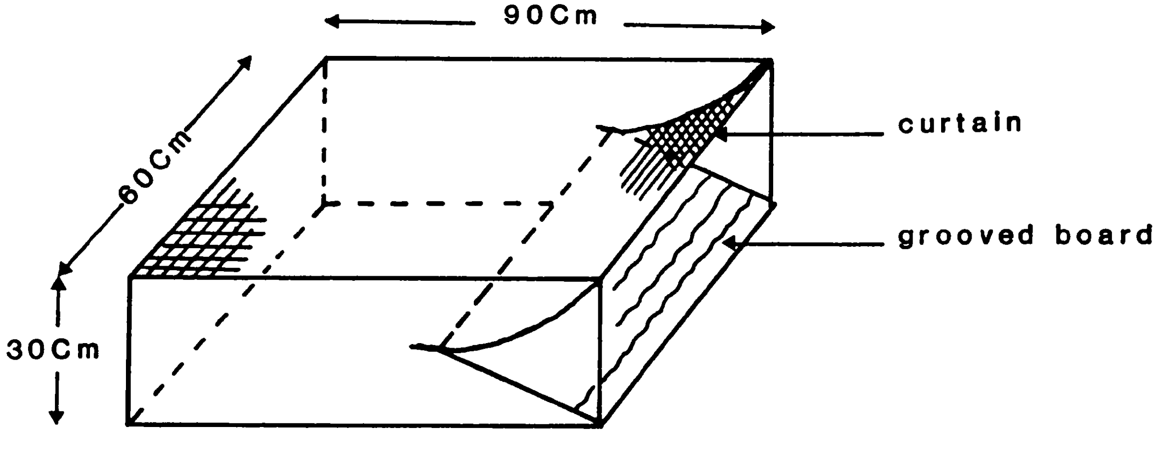

90Cm
60Cm
30Cm
curtain
grooved board

Table III.3.1 Relation between catch and intervals between pots

| | Intervals between pots (m) | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Number of the pot | 10 metres | | 2 metres | | pots attached | | 10 metres | |
| | 1st tide | 2nd tide | 1st tide | 2nd tide | 1st tide | 2nd tide | 1st tide | 2nd tide |
| 1 | 46 | 29 | 15 | 17 | 11 | 7 | 26 | 24 |
| 2 | 42 | 34 | 11 | 29 | 3 | 5 | 36 | 16 |
| 3 | 32 | 13 | 19 | 13 | 17 | 9 | 22 | 32 |
| 4 | 30 | 19 | 19 | 24 | 5 | 7 | 24 | 25 |
| 5 | 41 | 25 | 13 | 27 | 15 | 12 | 20 | 19 |
| 6 | 37 | 27 | 35 | 29 | 8 | 40 | 37 | 40 |
| All pots | 228 | 147 | 112 | 139 | 59 | 80 | 165 | 156 |
| Total catch | 375 | | 251 | | 139 | | 321 | |
| Number of crabs pot$^{-1}$ tide$^{-1}$ | 31.2 | | 20.9 | | 11.6 | | 26.7 | |

Table III.3.2 Comparison between catch of marginal pots (1 and 6), the middle ones (3 and 4), and the others (2 and 5) at different intervals

| Interval between pots (m) | The marginal (1 and 6) | The middle (3 and 4) | The others (2 and 5) |
|---|---|---|---|
| 10 | 139 | 94 | 142 |
| 2 | 96 | 75 | 80 |
| None | 66 | 38 | 35 |
| 10 | 127 | 103 | 91 |
| Total catch | 428 | 310 | 348 |

Table III.3.3 Number of incoming and outgoing adult shore crabs caught in the unbaited funnel trap. For each catch, crabs $m^{-1}$ of tide line is in parenthesis

| Type of crabs | 14.5.1982 | | 3.6.1982 | | Total | Total | Average of crabs $m^{-1}$ of tide line |
|---|---|---|---|---|---|---|---|
| | day | night | day | night | (day) | (night) | |
| Incoming | 3 (0.6) | 5 (1) | 6 (1.2) | 11 (2.2) | 9 (0.9) | 16 (1.6) | 1.25 |
| Outgoing | 18 (3.6) | 26 (5.2) | 40 (8) | 50 (10) | 58 (5.8) | 76 (7.6) | 6.7 |

Table III.3.4 Number of adult crabs caught by diving at five different sites

a - mainly *C.edule*
b - mainly *M. balthica*
c - mainly *S. plana*
d - mainly *M. arenaria*
e - no bivalves

| Site | Number of crabs | | Total | Number of crabs per $m^2$ |
|---|---|---|---|---|
| | 27.7.82 | 28.7.82 | | |
| a | 3 | 4 | 7 | 0.35 |
| b | 2 | 2 | 4 | 0.2 |
| c | 2 | 1 | 3 | 0.15 |
| d | 0 | 0 | 0 | 0.0 |
| e | 1 | 0 | 1 | 0.05 |
| Total | 8 | 7 | 15 | 0.75 |
| Average | 1.6 | 1.4 | 3 | 0.15 |

Table III.3.5 Male/female ratio of shore crabs caught by three methods: the baited trap, unbaited funnel trap, and diving

| Date | Type of trap | male/female ratio |
|---|---|---|
| May 1982 | Funnel trap | 0.62 |
| | Baited trap | 0.52 |
| June 1982 | Funnel trap | 0.69 |
| | Baited trap | 0.72 |
| July 1982 | Diving | 0.58 |
| | Baited trap | 0.62 |

Plate III.3.1 The funnel trap in position

Plate III.3.2 Transect of 10 $m^2$ area at low tide shows where diving took place to record the number of adult crabs

# CONCLUSION

Preceeding chapters were concerned with crabs as predators of intertidal bivalves. Therefore, it is not intended or possible to give a comprehensive account of the population structure and dynamics of the crabs. Nevertheless, considerable information was gathered of direct bearing to predation and a number of incidental matters recorded. The main points of relevance to predation can be summarised.

1. Adult crabs invade the intertidal area starting from spring and retreat to the sub-littoral in late autumn-early winter.
2. More crabs were found to move to the area under cover of water at night.
3. Crabs are abundant in the Inlet, but their uneven distribution and the complexity of their movement make it difficult to give an accurate estimation of their density.
4. Diving results suggested that more crabs were found feeding on an area where small cockles were abundant, and an average of 0.35 crabs per $m^2$ was recorded.

# SECTION IV

# NATURAL DIET OF THE SHORE CRAB IN THE INLET

## IV.1 INTRODUCTION

As mentioned earlier, the shore crab C. maenas feeds on a wide variety of organisms, but appears to be principally a predatory carnivore. A considerable body of published accounts documents this predation, for instance Crothers (1968), Perkins and Penfound (1969). The standard method of determining the diet of given crabs (and many other animals) is to examine stomach contents. However, this does present problems in the case of Carcinus. When feeding, the mouth parts usually tear up the food into small fragments and further mastication by the gastric mill in the cardiac stomach makes it difficult to identify the resulting particles. Special studies of the diet of adult and juvenile shore crabs based on stomach content analysis have been made for populations living in different habitats (see Ropes, 1968; Elner, 1977 and 1981; Pihl, 1985)

Two methods have been widely used in the measurement of the relative importance of different items in the crab's stomach contents. The first method is used to determine the percentage occurrence of each food species (see Ropes, 1968; Hill, 1976; Elner, 1977; Gotshall, 1977). The second is a point method of determining the absolute abundance and volume or weight of each type of food (Hartnoll, 1963). However, in recent studies, some workers have used both methods (Elner, 1981; Paul, 1981; Jewett and Feder, 1982). Although both methods had been criticised because of their bias (Hynes, 1950), in a comparative study by Williams (1981) on the natural diet of four species of portunid crabs, she recommended the use of the percentage occurrence method when a broad description of the types of food eaten by crabs is required. In a more detailed technique, Stevens et al (1982) used the 'Index of Relative Importance' to determine the diet of Cancer magister by combining measures of frequency of occurrence, percentage of total prey numbers and percentage of total prey biomass or volume. This method is usually applied when it is possible to count the number of prey items in the stomach contents, which is clearly not possible in the case of *Carcinus*.

The percentage occurrence method was used in the present study to determine the relative importance of each type of food eaten by shore crabs in the Burry Inlet.

A feature of the study reported in this section is the statistical technique used. This was conducted by F.M. Al-Boutiahi from the Department of Management Science and Statistics.

## IV.2 MATERIALS AND METHODS

From the catch of the baited trap experiment (see Section III.2), 30 adult crabs of each sex (carapace width not less than 30 mm) were taken monthly for stomach content analysis during the period from March to December 1983. The specimens were taken equally from day and night catches to reduce any variation in the diet related to tide time.

At the same period another 30 juvenile crabs ( <20 mm CW) were collected by hand from the nearby nursery area (see Section III.1) at low tide. These numbers were in line with the work of Williams (1981). She said that the sample size necessary to include most food and stabilise percentage occurrence for common food types was determined as ≈ 30 gastric mills. Only intact and not newly moulted crabs were used in the survey.

Within two hours of collection, specimens were preserved in 4% sea water formalin, and then the top of each crab's carapace was pulled away to reveal the stomach sac. Each of these was then removed carefully and place in 70% alcohol in individual vials. Each stomach was opened and its contents rinsed into a glass dish for identification under a binocular dissecting microscope. The occurrence of each food item was recorded on a presence or absence basis, and its percentage frequency of occurrence was obtained from the pooled data. Empty stomachs were omitted from the calculations.

Contents were identified to the lowest taxon possible. Visual estimates were made of the amount of food in stomachs based on five scale points (nearly full, 75%, 50%, 25% and empty stomachs). Furthermore, the nature of the food was categorised into three groups: soft tissues and hard parts of food; soft tissue only and hard parts or shell fragments.

Results from each crab group were compared to determine the influence of size, sex and seasonal variations on diet.

In order to examine the null hypothesis that different crab groups had the same diet, chi-square ($\chi^2$) contingency table was used. In this case it was based on method of randomisation (Bradley, 1968) to permit the use of the test in dependent observations. Due to the large number of combinations in arranging the data (which were $C^{60}_{30}$ combinations in the case of male/female and $C^{180}_{60}$ when the diet of crabs in three seasons was tested), it was decided to use Monte Carlo tests which allowed the selection of 1000 samples. The $\chi^2$ values (R) were calculated from each sample and arranged in ascending order. The test was conducted at two levels of significance, 5% and 1%. The values of chi-square from the actual data (Q) were compared to R values and on that basis it was concluded whether Q belongs to the rejection region or not.

## IV.3 RESULTS

More than 80% of shore crabs examined during this survey had identifiable material in the fore-gut. Only 18% of the stomachs examined had only soft tissues (unidentifiable), while 4% of them had only hard shell fragments or exoskeleton and the highest (78%) had both soft tissues and hard remains (Fig. IV.1).

Usually, hard skeletal structures were used to identify food. However, owing to the form and fragmented nature of the remains, it was not always possible to classify the food item to a definite species, but it could usually be categorised into more general taxonomic groups.

Mollusc remains were most readily identified food items. Bivalve species such as Cerastoderma edule, Macoma balthica and Mytilus edulis could be recognised by their shell features, colour and the intact hinge structure (see Palte IV.1a). Because of their fragment occurrence in the stomachs, the species C. edule and M. balthica were separated in the analysis while other species of buried bivalves such as M. arenaria and S. plana were combined in one group 'other buried bivalves'. Gastropods mainly Hydrobia ulvae (Pennant) and in less number Littorina sp. formed another main food item identifiable from shell fragments and operculi. Polychaetes, mostly Nereidae were identified by their jaws and cirri. Crutaceans could rarely be identified to species, but were separated into two main groups:

1. Barnacles, identified from the white shells (see Plate IV.1b)
2. Other crustacean, such as Corophium sp. and Crangon sp. identified from their light brown flattened exoskeletal plates and eyes.

Items such as various eggs and fish, recognised by their vertebrae or scales were not present in sufficient numbers to form separate categories and were therefore placed in one common group 'other animals'. Only two plant foods, cord grass (Spartina) and algae were identified. The latter were separated into reds and greens where possible. Inorganic materials such as mud or sand grains, nylon strings, etc. were uncommon but form a separate group. Many stomachs contained food remains that were classified as unidentifiable tissues.

The amount of food present in stomachs varied from nearly full stomachs to empty ones. Few of them were nearly full (100%), while most of them ranged between 25% and 50% (Fig. IV.2). In the case of juvenile crabs (see Fig. IV.3) the frequency of crabs with empty stomachs changed throughout the season. Fewer crabs with empty stomachs were found in summer.

Fig. IV.4 shows that buried bivalves (mainly M. balthica and C. edule) represent the most important item in the diet of adult shore crabs which reached 58%, followed by gastropods (40%) and then crustaceans (17%) which were mainly Crangon sp.. No significant difference was recorded in the diet of males and females (March, max. $R = 27.390$, $Q = 5.983$, $P > 0.05$; August, max. $R = 24.529$, $Q = 5.983$, $P > 0.05$; November, max. $R = 17.223$, $Q = 7.473$, $P > 0.05$). On the other hand, a high significant difference was found between the diet of juvenile and adult crabs of both sex (max. $R = 15.913$, $Q = 28.741$, $P < 0.01$) as shown clearly in Fig. IV.5. The most important food items in the diet of juvenile crabs are gastropods (45%), followed by polychaetes (28%) and then crustaceans (19%) which were mainly Corophium sp.. The buried bivalves were found in lower numbers and were present in only 9% of the stomachs examined. Plant materials were less important than animal matter for both adults and juveniles.

Seasonal variations in the fore-gut contents were examined for adult crabs by comparing the results of three months of the year, March, August and November (Fig. IV.6) which represent the three seasons in which crabs are present in the area. The diet of the crabs is significantly different from one month to another (max R = 22.191, Q = 129.822, $P < 0.01$). The monthly variations in the occurrence of five important food items are shown for adults (Fig. IV.7) and juveniles (Fig. IV.8). In spring and early summer, adult crabs feed mainly on gastropods, M. balthica and crustaceans (mainly Crangon sp.) while in summer, cockles represent the most important food item for them. These increased progressively in their diet to reach a maximum (64%) in September and then decreased toward the end of autumn to a minimum of 4% in December. During summer months, gastropods and Macoma occurred in low numbers, but increased again in the diet of adult crabs after August and September respectively. However, no clear change was recorded for polychaetes throughout the season.

Figure IV.8 shows that gastropods, polychaetes and crustaceans (mainly Corophium sp.) represent the most important food items in the diet of juveniles throughout the seasons. However, in autumn fewer crustaceans occurred in their diet. The buried bivalves, M. balthica and C. edule occurred in low percentages in some months only, particularly in summer.

## IV.4 DISCUSSION

The analysis of stomach contents of adult shore crabs from the Burry Inlet shows that they are predators of sessile or slow moving benthic macro-invertebrates, mainly molluscs. Their diet comprised chiefly of burrowing bivalves such as C. edule and M. balthica from which it can be inferred that C. maenas is an efficient burrower. The other main groups are gastropods and crustaceans. Of lesser extent in their diet are polychaetes and plant materials such as algae and Spartina. This is in contrast to Elner's (1977) finding that shore crabs from Menai Bridge in North Wales relied most strongly on algae, crustacea, polychaetes and less strongly on molluscs. The variation in diet between crabs in these two areas presumably reflects the prey availability in each habitat. The presence of plant items in the stomach contents does not itself indicate the ability of crabs to digest them. However, since carbohydrases have been detected in their stomach fluid (Hylleberg-Kristensen, 1972) they probably do.

Although females have relatively smaller and weaker chelae than males, this is not reflected in their natural diet as demonstrated in the population from North Wales (Elner, 1977). However, a difference in diet between males and females was recorded by Ropes (1968) for crabs from Plum Island River in North America. In the present study, the comparison between the diet of both sexes confirmed that of Elner.

Juveniles' stomach contents revealed that gastropods (mainly Hydrobia ulvae) are the most important food item, followed by polychaetes and crustaceans (mainly Corophium sp.), and of less importance are the burrowing bivalves. The difference in the diet composition of adults and juveniles presumably results from the change in their foraging behaviour due to the strength of their chelipeds. The small and weak claws of juveniles prevent them feeding on relativley strong bivalves, and they probably experience difficulties in gaining access to buried ones. Diet differences in shore crabs of different size groups have been recorded in other areas (Ropes, 1968 and Elner, 1977).

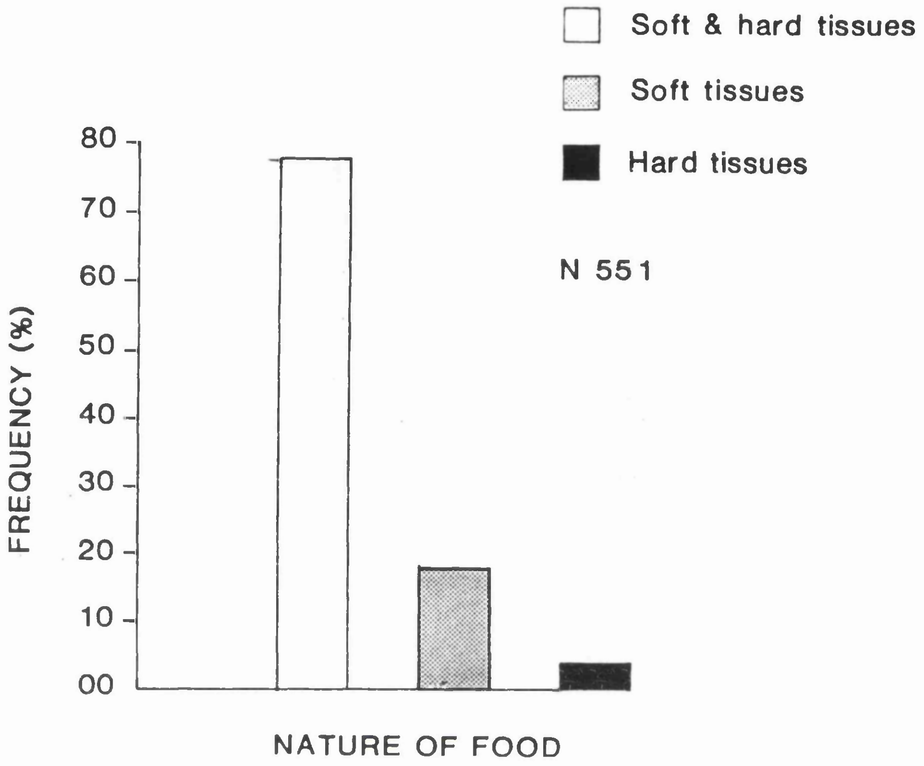
Seasonal variations in the diet of shore crab as demonstrated in the present study are presumably due to the changes in the availability of prey organisms throughout the seasons. Relative abundance of different prey is the most important reason for generalist predators (such as *Carcinus*) to exhibit prey shifting (Cornell, 1976). The peak of abundance of cockles in the crab diet in late summer coincides with the attainment of a preferred size by cockles. These had settled in early summer, as reported by Franklin and Picket (1979). The difference in prey availability was reported in other areas as the main cause behind variation in natural diet of *Carcinus* (Elner, 1981) and other crab species (Paul, 1981; Stevens *et al*, 1982).

In any case, the study of stomach contents demonstrates that crabs in the Burry Inlet do indeed (as expected) feed on the commercially important bivalves. However, it would be interesting to see whether the area of trapping does affect the diet composition of the crabs or not since the distribution and abundance of bivalves and other fauna varies from one site to another in the estuary.

Figure IV.1 Nature of food in the adult crab stomach expressed as a percentage of each type of food

Figure IV.2 Amount of food present in the crab stomach based on five point scale:

a - Nearly full
b - 75%
c - 50%
d - 25%
e - Empty


Soft & hard tissues
Soft tissues
Hard tissues
N 551
FREQUENCY (%)
80
70
60
50
40
30
20
10
00
NATURE OF FOOD

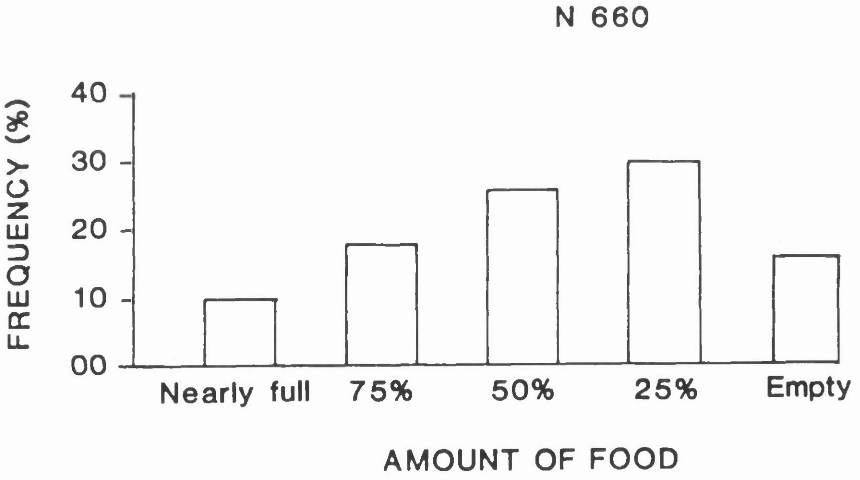

N 660
FREQUENCY (%)
40
30
20
10
00
Nearly full
75%
50%
25%
Empty
AMOUNT OF FOOD

Figure IV.3 Monthly variations in the number of juvenile crabs with empty stomachs

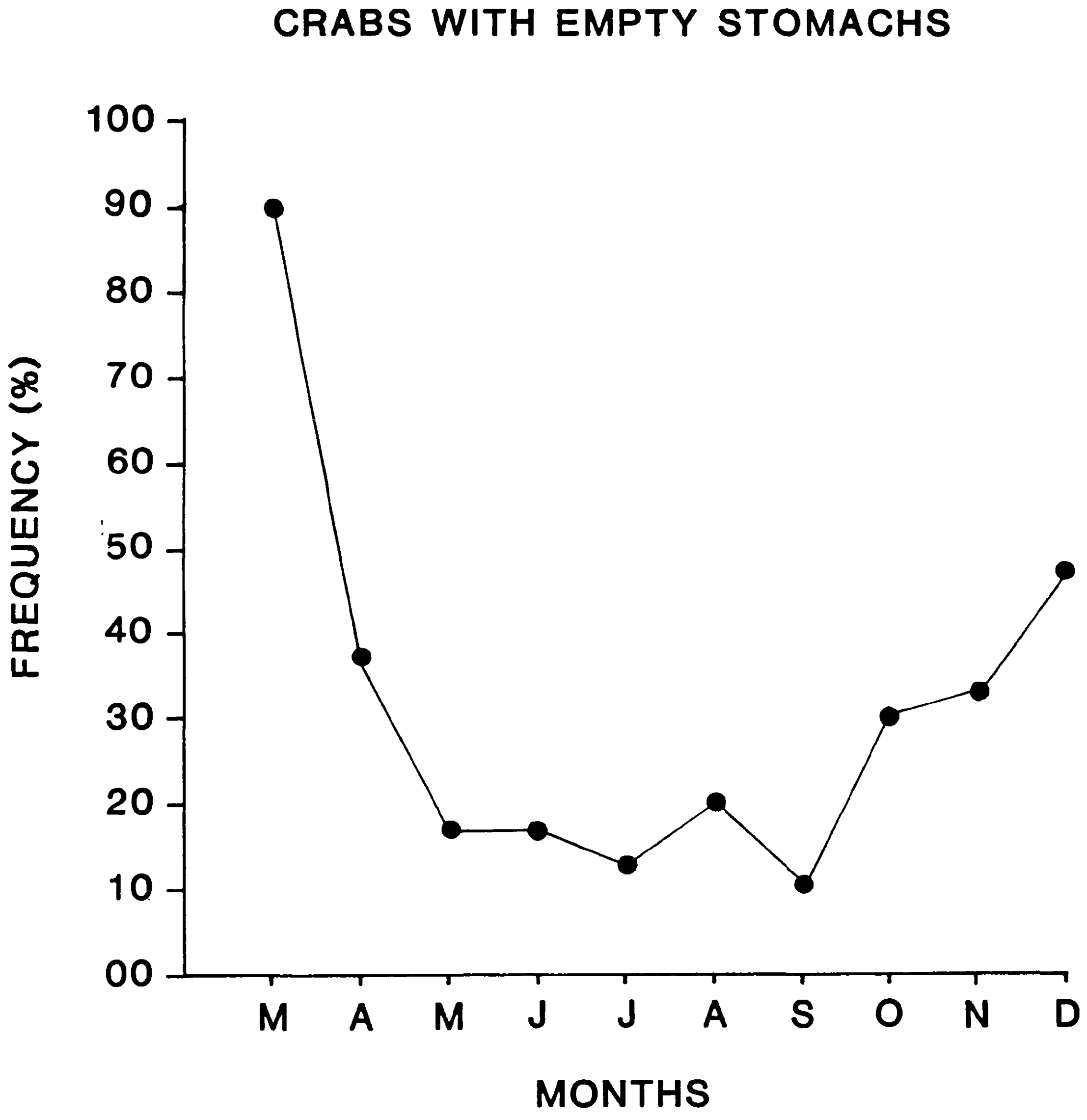

CRABS WITH EMPTY STOMACHS
FREQUENCY (%)
100
90
80
70
60
50
40
30
20
10
00
M
A
M
J
J
A
S
O
N
D
MONTHS

Figure IV.4 The relative importance of foods analysed by the percentage frequency of occurrence for adult crabs

ADULTS N 551

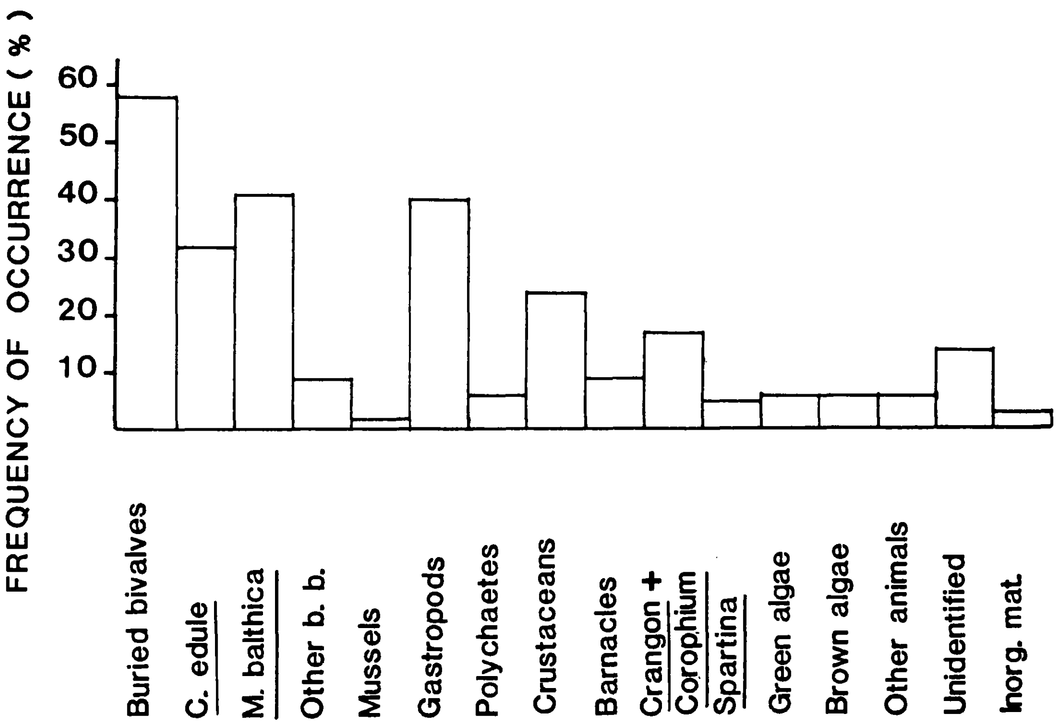

FREQUENCY OF OCCURRENCE ( % )
60
50
40
30
20
10
Buried bivalves
C. edule
M. balthica
Other b. b.
Mussels
Gastropods
Polychaetes
Crustaceans
Barnacles
Crangon +
Corophium
Spartina
Green algae
Brown algae
Other animals
Unidentified
Inorg. mat.

Figure IV.5 The relative importance of foods analysed by the percentage frequency of occurrence for adult males and females and juvenile crabs

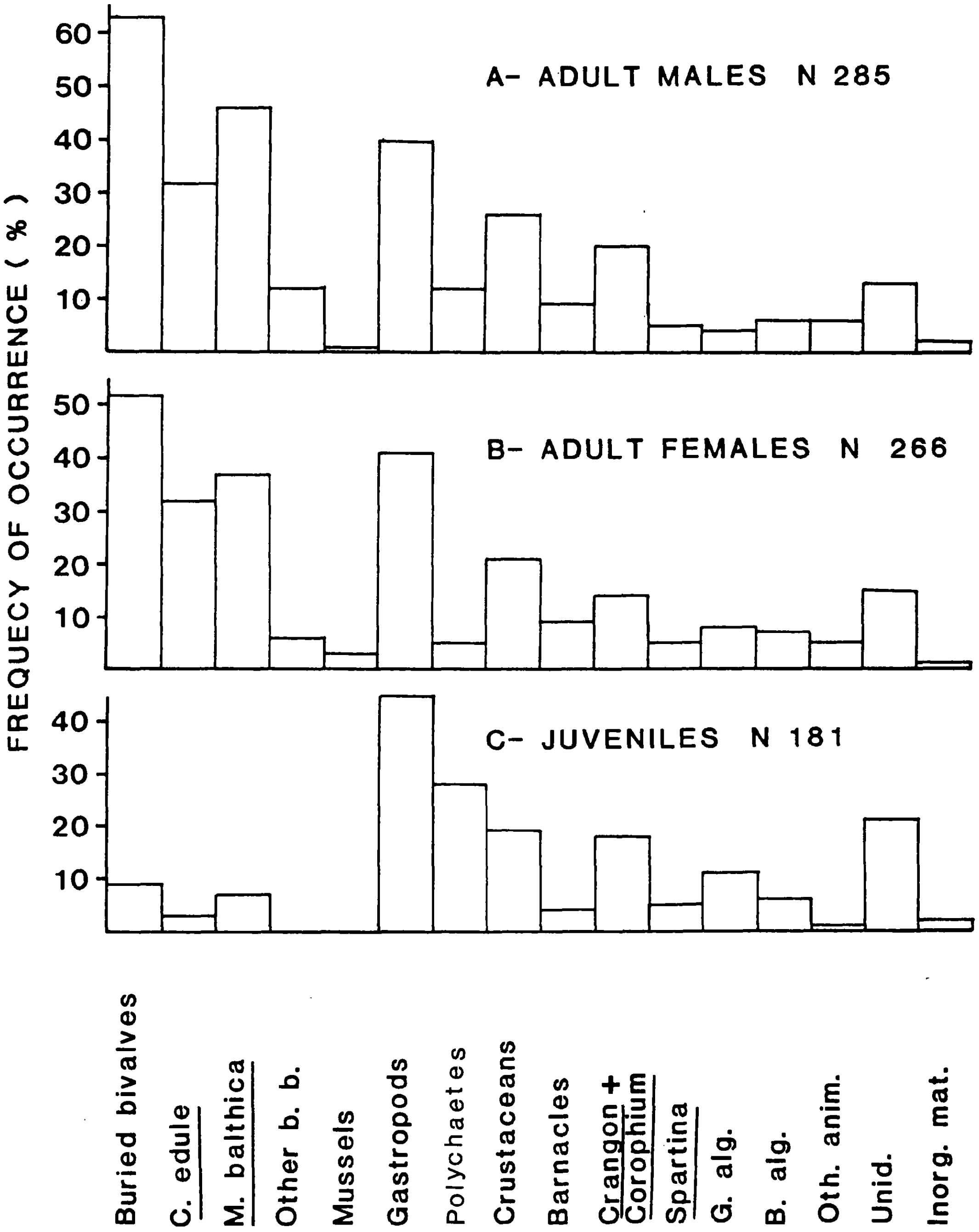

FREQUECY OF OCCURRENCE ( % )
A- ADULT MALES N 285
60
50
40
30
20
10
B- ADULT FEMALES N 266
50
40
30
20
10
C- JUVENILES N 181
40
30
20
10
Buried bivalves
C. edule
M. balthica
Other b. b.
Mussels
Gastropods
Polychaetes
Crustaceans
Barnacles
Crangon + Corophium
Spartina
G. alg.
B. alg.
Oth. anim.
Unid.
Inorg. mat.

Figure IV.6 The relative importance of foods analysed by the percentage frequency of occurrence for adult crabs caught in three different months (March, August, November)

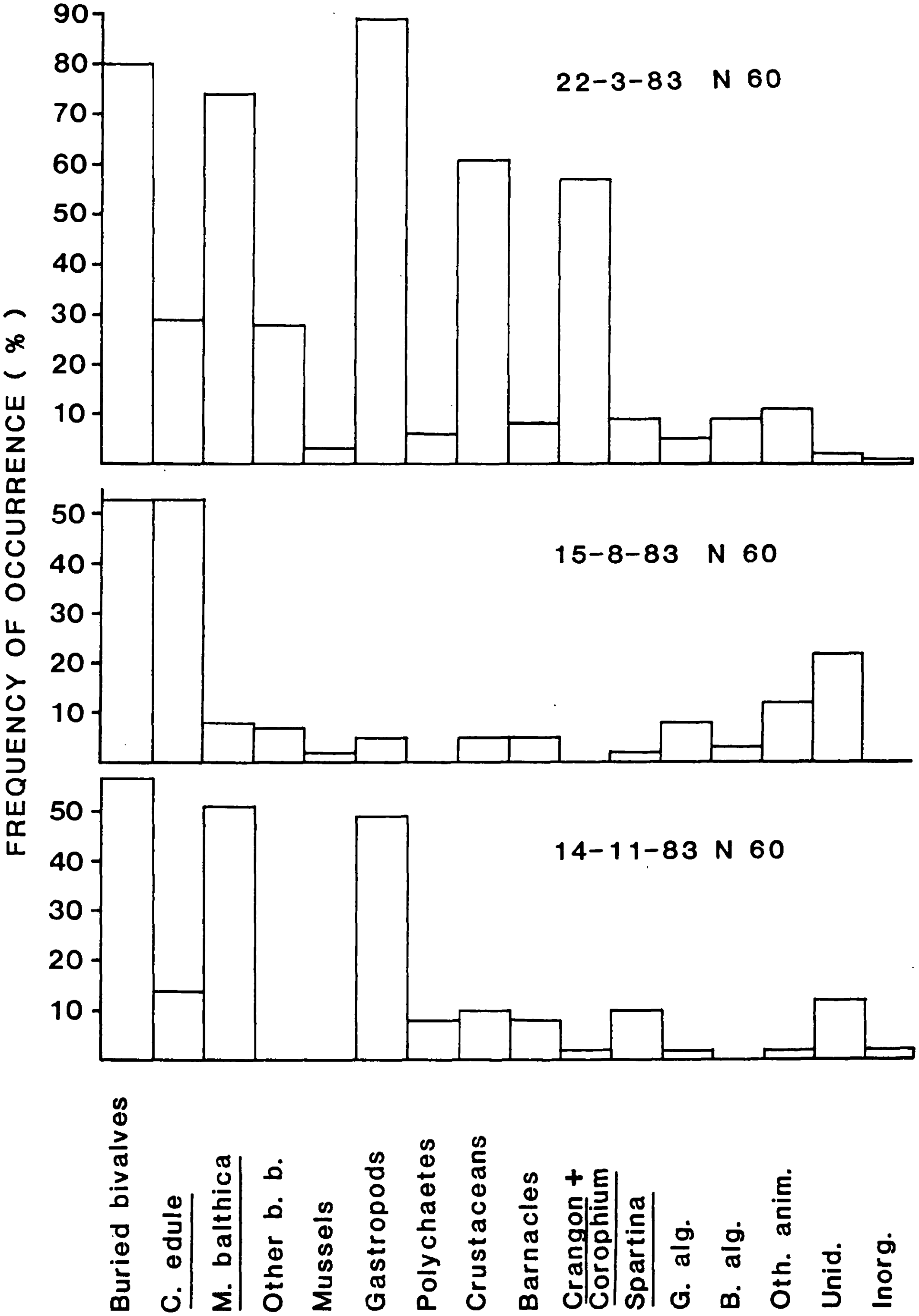

FREQUENCY OF OCCURRENCE ( % )
90
80
70
60
50
40
30
20
10
22-3-83 N 60
50
40
30
20
10
15-8-83 N 60
50
40
30
20
10
14-11-83 N 60
Buried bivalves
C. edule
M. balthica
Other b. b.
Mussels
Gastropods
Polychaetes
Crustaceans
Barnacles
Crangon + Corophium
Spartina
G. alg.
B. alg.
Oth. anim.
Unid.
Inorg.

Figure IV.7 Monthly variations in the percentage of occurrence of five food items in the stomach contents of adult crabs from March to December 1983

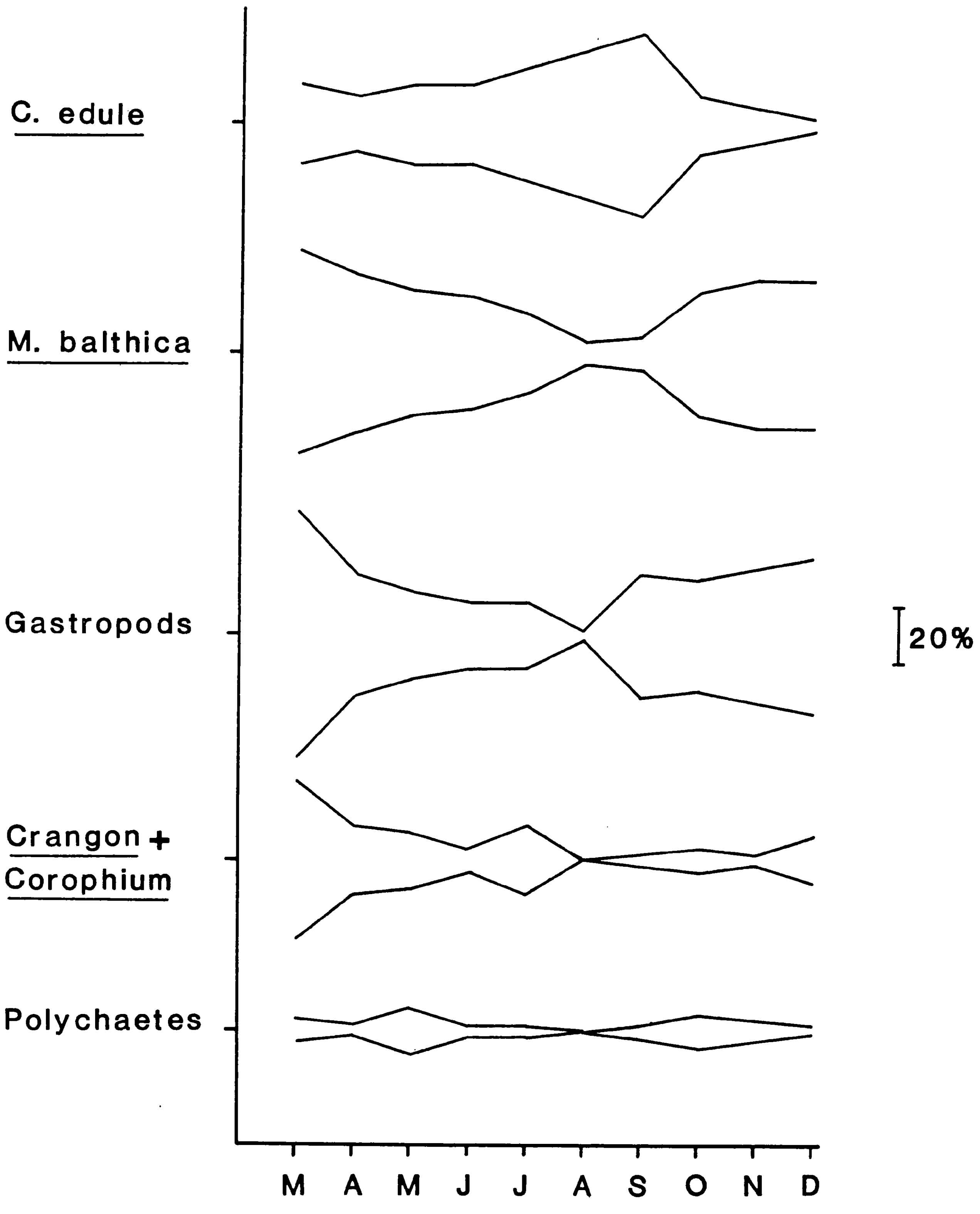

C. edule
M. balthica
Gastropods
Crangon + Corophium
Polychaetes
20%
M
A
M
J
J
A
S
O
N
D

Figure IV.8 Monthly variations in the percentage of occurrence of five food items in the stomach contents of juvenile crabs from March to December 1983

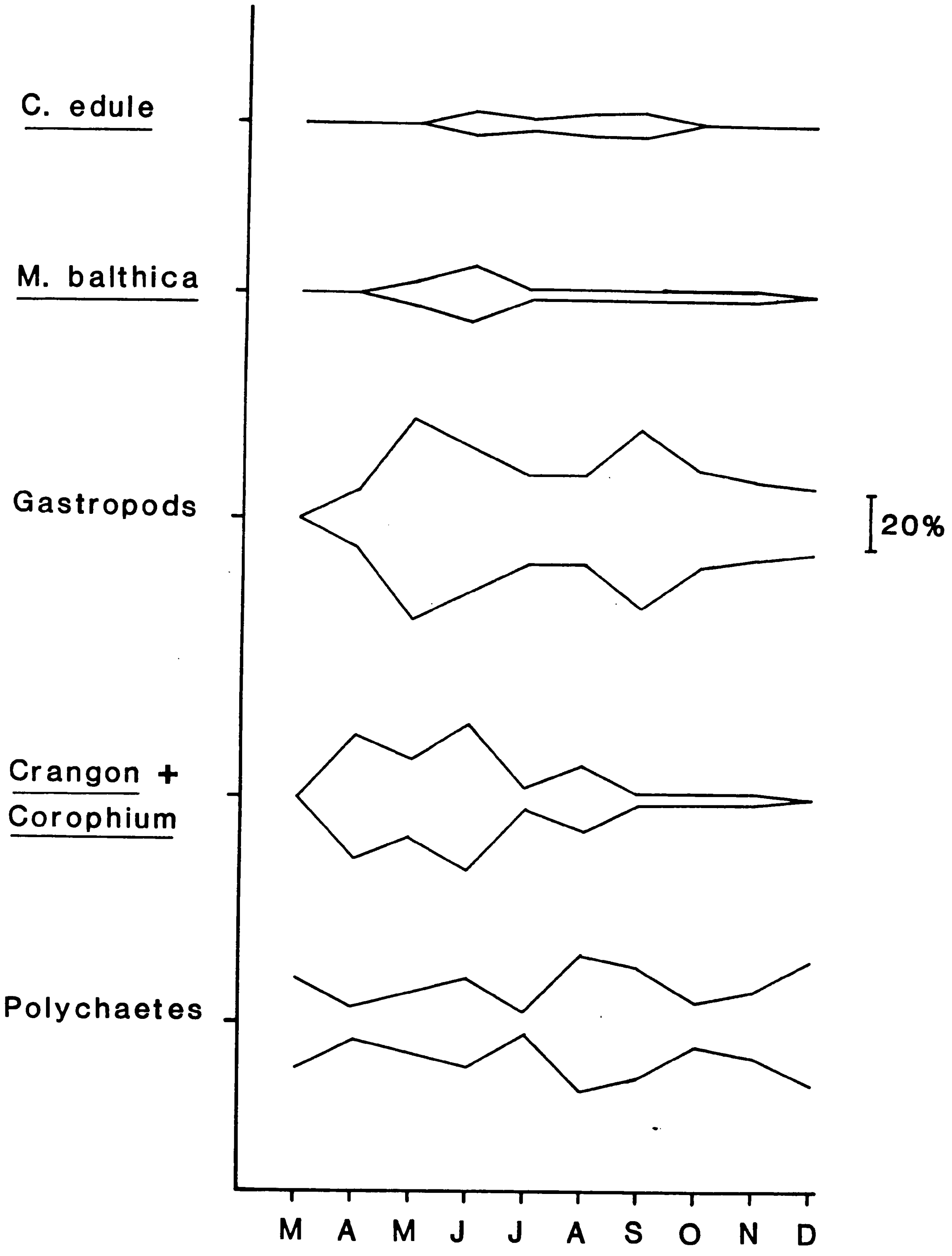
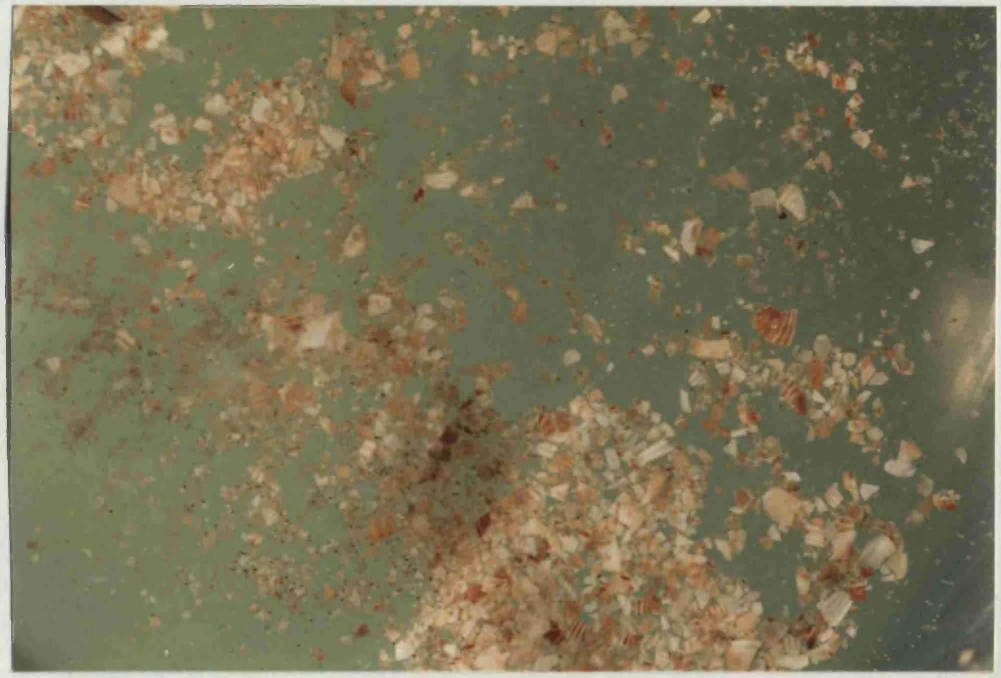

C. edule
M. balthica
Gastropods
Crangon + Corophium
Polychaetes
20%
M
A
M
J
J
A
S
O
N
D

Plate IV.1 Remains of food from the stomachs of adult shore crabs

a - Cockles x 2
b - Barnacles and some bivalves x 10



# SECTION V

# LABORATORY EXPERIMENTS ON PREDATION OF INFAUNAL BIVALVES BY THE SHORE CRAB

## 1

## MECHANICS OF SHELL OPENING

## V.1.1 INTRODUCTION

Crabs employ different techniques to open bivalve shells. Breaking the shell and chipping the edge of the valves are the most common methods reported for many crab species, such as *Carcinus maenas* (Elner, 1978); *Scylla serrata* (Williams, 1978); *Callinectes sapidus* (Seed, 1982); *Cancer productus*, *Cancer magister*, *Pugettia productus* and *Hemigrapsus oregonensis* (Boulding, 1984); *Ovalipes punctatus* (Du Preez, 1984). In all previous studies, a direct relation between the opening method and the bivalve size was recorded. Shore crabs from the Menai Straits, North Wales, used five distinct opening methods when they preyed upon mussels (Elner, 1978).

As in many other decapods, the chelae of adult shore crabs are morphologically dissimilar 'hetrochelous'. The larger chela 'master' or 'major' is big and well adapted to crush prey whilst the smaller one 'minor' or 'cutter' is thinner and acts to hold and manipulate prey. The differences are less marked in female shore crabs where both chelae are more 'cutter-like'. Warner *et al* (1982) showed the difference in chela structure and chela closer-muscle between master and minor chelae of *Carcinus maenas*. Previous experiments mostly used only male specimens in laboratory tests.

The main objective of this part is firstly to examine the specific techniques used by crabs to open the four different species of studied bivalves; secondly, to record the 'critical size' (*sensu* Vermeij, 1976) at which prey are no longer vulnerable to crabs; and thirdly the mechanical properties of the different bivalve shells.

## V.1.2 MATERIAL AND METHODS

### V.1.2.1 Bivalve opening methods

Adult shore crabs were caught in the Burry Inlet using baited traps. Healthy male crabs were chosen for the experiments in order to avoid potential bias caused by sexual differences in morphology and predatory behaviour.

Carapace width of the crabs was measured to the nearest 0.1 mm, only three categories were selected from the large numbers of crabs available namely: 40 ± 2.0, 50 ± 2.0, and 60 ± 2.0 mm. Each size class was represented by four individuals and each animal was maintained in a separate aquarium measuring 55 x 35 x 18 cm with circulating sea water at 15 ± 1°C.

Four different infaunal bivalve species were used as prey, *Cerastoderma edule*, *Macoma balthica*, *Scrobicularia plana* and *Mya arenaria*. They were collected from the Burry Inlet near Salthouse Point by sieving sand in the field. The bivalves were measured according to their shell length by using Vernier calipers to the nearest 0.1 mm and again different size categories were selected. During experiments, the bivalves were kept as stock in separate aquaria with running sea water and fed frequently on cultured algae to keep them in a healthy condition.

Experiments were conducted in aquaria (polypropylene) devoid of sand. Each crab was offered prey specimens of one size group, one at a time. After the specimen was consumed another was offered and this was repeated five times in that manner except for *Mya arenaria* of which only limited numbers were available. When the crab succeeded in opening at least one specimen of a particular prey size, a larger size bivalve was offered and so on. Shell fragments were collected after each successful attack to aid in the interpretation and description of the observed opening techniques.

The critical size of bivalve for each size class of crab was considered to be reached when the prey were left undamaged in the aquarium for two successive days.

### V.1.2.2 The strength of bivalve shells

The load needed to break various sizes of bivalve shells was obtained by using a Triaxial Compression Machine with 100 lb proving ring (Plate V.1.1). A piece of perspex was sharpened to be similar to the tip of the crab's claw (see Plate V.1.2). This was fixed to the pressing bar. Specimens were placed in chambers of the right size made of perspex, and held in position with a little 'Blue tac' (silicon putty) before force was applied. Care was taken to keep the shells wet before conducting the experiment to resemble the natural situation, since dryness makes the shell slightly stronger (Currey, 1976).

## V.1.3 RESULTS

### V.1.3.1 Bivalve opening methods

In the following pages, methods to open each of the four species will be reported on separately.

1. Methods used by shore crabs to open Cerastoderma edule.

Four different methods were recorded for crabs fed on cockles.

a. Simple crushing

This method was used by crabs to open comparatively small cockles. The prey was held, usually (but not always) by the small chela, and then the master chela crushed the shell indiscriminately before passing it to the mouth parts. Cockles required only a single closing of the chela to break them open.

Crabs of 40 mm CW managed to open cockles of only 8.0 mm SL (the smallest size used in the experiment) while the largest crab size group (60 mm CW) opened up to 14 mm SL cockles by this method (as shown in Table V.1.1).

b. Umbone breaking

This was the main method used by the shore crab to open C. edule (see Table V.1.1). With the assistance of the anterior walking limbs and the mouth parts, the small chela held the prey in position making it easier for the large chela to apply force and break the shell at the most convex portion of the valves near the umbone area (Plate V.1.3).

The capability of opening larger cockles by this method increased with crab size (Fig. V.1.1).

### c. Prying the valves apart

This was a rare method used by crabs to open comparatively large cockles, usually when the umbone breaking method had failed. When cockles close their valves, a little gape is left at the posterior end of the shell (at the siphons area). Some crabs, especially those of 40.0 mm CW were able to insert the tips of their chelae in that gape and pull apart the valves damaging the adductor muscle. This left the valves wide open.

### d. Hinge attack

This was an uncommon method used by differnt size classes of crabs to open considerably large cockles. With the lower dactylus of the large claw, a passage was forced between the valves at the hinge ligament and, by a sawing action, the adductor muscle was damaged and valves left wide apart. This method needed a long time and quite often crabs were found to give up and the prey was abandoned.

Table V.1.1. shows the frequency of using the different methods to open various sizes of cockles by three size classes of crabs. Transition from one technique to another is clear among the different crab sizes.

## 2. Methods used by shore crabs to open *Macoma balthica*

Four different methods were recorded (for crabs fed on *M. balthica*) which were in some respects different from those used for *C. edule*.

### a. Simple crushing

In a similar way to that used to open small cockles, crabs crush comparatively small *M. balthica* indiscriminately mainly by the master chela. By the help of the other chela, prey passed toward the mouth parts. Table V.1.2 shows the maximum size of *Macoma* which was opened by simple crushing method for three size classes of crabs.

### b. Umbone breaking

This is one of the main methods used by crabs to open a wide size range of M. balthica. The prey was treated in a similar manner to C. edule. By applying force at the umbone area, crabs of 40 mm CW opened prey of up to 12 mm SL, while 50 mm CW crabs opened up to 14 mm SL, and the large crabs (60 mm CW) succeeded in breaking open shells of up to 16 mm length. Fragments of M. balthica shells opened by the umbone breaking method are shown in Plate V.1.4.

### c. Edge chipping

Plate V.1.5 shows shell fragments of M. balthica opened by edge chipping, a method commonly used by crabs to open particularly large prey which were too strong to be opened by the previous methods.

In this case, maxillipeds of the crab, both chelae and the fore-limbs were all used to hold the prey in a vertical position. The hind limbs were used to keep the crab firm in position. However, sometimes crabs pressed the posterior of the carapace against the aquarium wall in order to get more support.

Pieces of the shell were chipped away from the ventral margin of the prey using the mandibles. Often crabs rotated the prey until they found a weak part to be chipped which allowed them to insert the dactylus between the valves and tear off parts of the shell enabling them to reach the flesh of their prey. Using this method crabs of 40 mm CW were enabled to open Macoma up to 14 mm SL and up to 16 mm for 50 mm crabs, while the 60 mm crabs opened the largest prey available (20 mm SL) as shown in Table V.1.2.

### d. Hinge attack

This is similar to the method used for opening large cockles. It is employed here to open large M. balthica when other methods proved fruitless. Usually it took longer than other methods, but enabled the large crabs to open the largest prey avialable.

Table V.1.2 shows the frequency of using the different methods to open M. balthica by the three size classes of crabs. A pattern of transition from one technique to another is apparent.

### 3. Methods used by shore crabs to open Scrobicularia plana

Three different techniques were used by shore crab to open S. plana.

#### a. Simple crushing

This is similar to that for other bivalves, but this method was used to open considerably bigger S. plana in contrast to M. balthica and C. edule. Using this method enabled 40 mm CW crabs to open up to 12 mm SL S. plana while 50 mm crabs opened up to 14 mm prey and up to 20 mm SL S. plana were crushed indiscriminately by crabs of 60 mm CW (see Table V.1.3).

#### b. Umbone breaking

This method was widely used by crabs to open the whole size range of S. plana. Even the 40 mm CW crabs succeeded in breaking open a prey of similar 40 mm SL size without much difficulty. Plate V.1.6 shows fragments of S. plana shells opened by umbone breaking methods.

#### c. Edge chipping

This method was used mainly by the smallest (40 mm CW) crabs to open particularly large S. plana. Crabs here used their master chelae to chip away small pieces of the valve's ventral margin, followed by tearing off bigger fragments to expose the prey's flesh. Shells opened by this method are shown in Plate V.1.7.

Table V.1.3 shows the frequency of using the three different methods for opening the full size range of S. plana by the three size classes of C. maenas.

### 4 Methods used by shore crabs to open Mya arenaria

Three different methods were used by crabs to open Mya arenaria shells which are characterised (in contrast to the other three bivalves) by the large size which exceeds 100 mm SL and the large permanent posterior gape.

#### a. Simple crushing

Crabs of 60 mm CW used simple crushing to open small M. arenaria up to 25 mm SL as described for the other bivalve species.

#### b. Umbone breaking

This is the most common method used by crabs to open medium size prey as shown in Table V.1.4. The umbone breaking method enabled the smallest crabs (40 mm CW) to open up to 30 mm prey and up to 40 mm SL for crabs of 50 mm CW and 60 mm CW. Fragments of M. arenaria shells opened by the umbone breaking method are shown in Plate V.1.8.

#### c. Edge chipping

This method was used by crabs to open large shells of M. arenaria. When other methods had failed to open the prey, crabs usually attacked the siphon, but Mya succeeded during all observations to withdraw their siphons safely. Thereafter, crabs started to attack the shell at the gape by chipping fragments of the shell. This was remarkably successful for opening comparatively large shells which reached up to 70 mm for crabs of 60 mm CW. On one occasion a 50 mm crab chipped the edge of the anterior side of a specimen measuring 50 mm SL by the chelae and succeeded in opening it. Crabs were not able to eat the siphons of prey $> 60$ mm SL.

The frequency of using the three methods is shown in Table V.1.4. The trend of technique transition is apparent.

### V.1.3.2 Critical size of bivalves

For *C. edule*, *M. balthica* and *M. arenaria* the critical size increased with crab size (see Table V.1.5). Critical size of both *C. edule* and *M. balthica* is similar for the different size of crabs but this is much smaller for *M. arenaria*. No critical size could be obtained by *M. balthica* against crabs of 60 mm CW, and no critical size was recorded for *S. plana* against all size classes of crabs.

### V.1.3.3 The strength of the bivalve shells

Failure load for bivalve shells increased with their length (see Fig. V.1.2). Analysis of the data showed that for any given size group, *M. balthica* has the strongest shell, followed by *C. edule* and then both *S. plana* and *M. arenaria* ($P < 0.05$). Nearly 11 kg was needed to break the shell of 20 mm *M. balthica* while it was only 5 kg for *C. edule* and only around 0.5 kg for *S. plana* and *M. arenaria*.

## V.1.4 DISCUSSION

Various methods were used by the shore crab to open different bivalve species. These methods vary with prey size and shell strength.

The simple crushing method was used by all size crabs to open small bivalves. Intermediate prey size needed more force to be applied by the crabs who centred their attacks mainly near the umbone area. Some shells were broken from the first attack, but quite often crabs were observed to adjust their claw force by trial and error to the right spot where the shells were weakest. These spots near the umbone area of the bivalve species in this study corresponded to the areas of other bivalves (Mytilus edulis) attacked by shore crab, which were referred to by Seed (1969) as thin and brittle.

The limit of using simple crushing and umbone breaking is related to the shell strength and its structure.

It was noticed that crabs used only the master chelae to break open the shells of different bivalves. Presumably this is because the master chelae pinch more strongly than minor chelae (Warner et al, 1982).

To open large and therefore strong bivalves, crabs shifted from using a quick method which relied upon their chelae strength, to adopting a slower and longer technique, either chipping the edge of the prey shell with their mouth parts (M. balthica) or with their claws (M. arenaria and S. plana). These methods are similar to those used by the Menai Straits' crabs preying on Mytilus edulis (Elner, 1978).

The structure of a bivalve shell influences the choice of the opening technique. Mya arenaria as a permanent gaper allowed easy access for the crab to chip the gaping edge and open large specimens even bigger than the crab itself. This attacking method has been recorded for other crabs such as Cancer productus and Cancer magister when fed on bivalves with permanent gape (Boulding, 1984). However, the same author found that shells with a gape are more vulnerable to crabs than clams of the same shell weight without a gape. On the other hand, the inflated shape of *C. edule* with the blunt and strong margin prevents crabs using the edge chipping method which usually enables them to open large prey.

The increase of critical size with crab size presumably results from an increase in chelae strength. Larger crabs have stronger claws. Elner (1978) found that the maximum load generated by shore crabs increased with the master chela height.

The difference between critical size among the four species is related directly to their shell strength. The less vulnerable bivalves to crab predation were both *C. edule* and *M. balthica* which have smaller critical size and the result of the compression machine tests demonstrated them as stronger than *M. arenaria* and *S. plana* which are more vulnerable to predation by having either larger critical size (*M. arenaria*) or no critical size was obtained (*S. plana*).

Figure V.1.1 Percentage using umbone breaking method to open different size groups of _C. edule_ by three size classes of shore crab

● Crabs of 40.0 mm CW

▲ Crabs of 50.0 mm CW

○ Crabs of 60.0 mm CW

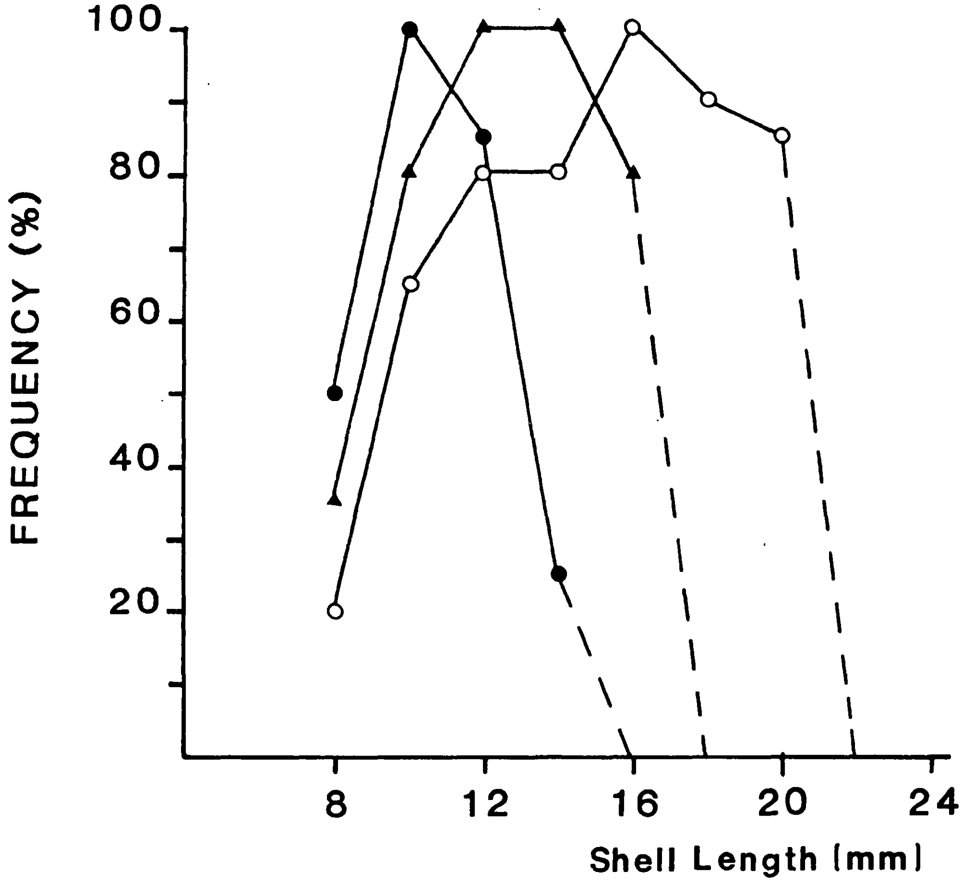

100
80
60
40
20
FREQUENCY (%)
8
12
16
20
24
Shell Length (mm)

Figure V.1.2 Load needed to break shells of four bivalve species plotted against their shell length. Curves are fitted according to the regression equations:

△ *M. balthica* $y = 10^{0.11\ SL\ +\ 1.84}$, $r = 0.94$

□ *C. edule* $y = 10^{0.098\ SL\ +\ 1.73}$, $r = 0.93$

● *S. plana* $y = 10^{0.067\ SL\ +\ 1.38}$, $r = 0.89$

▲ *M. arenaria* $y = 10^{0.074\ SL\ +\ 1.28}$, $r = 0.93$

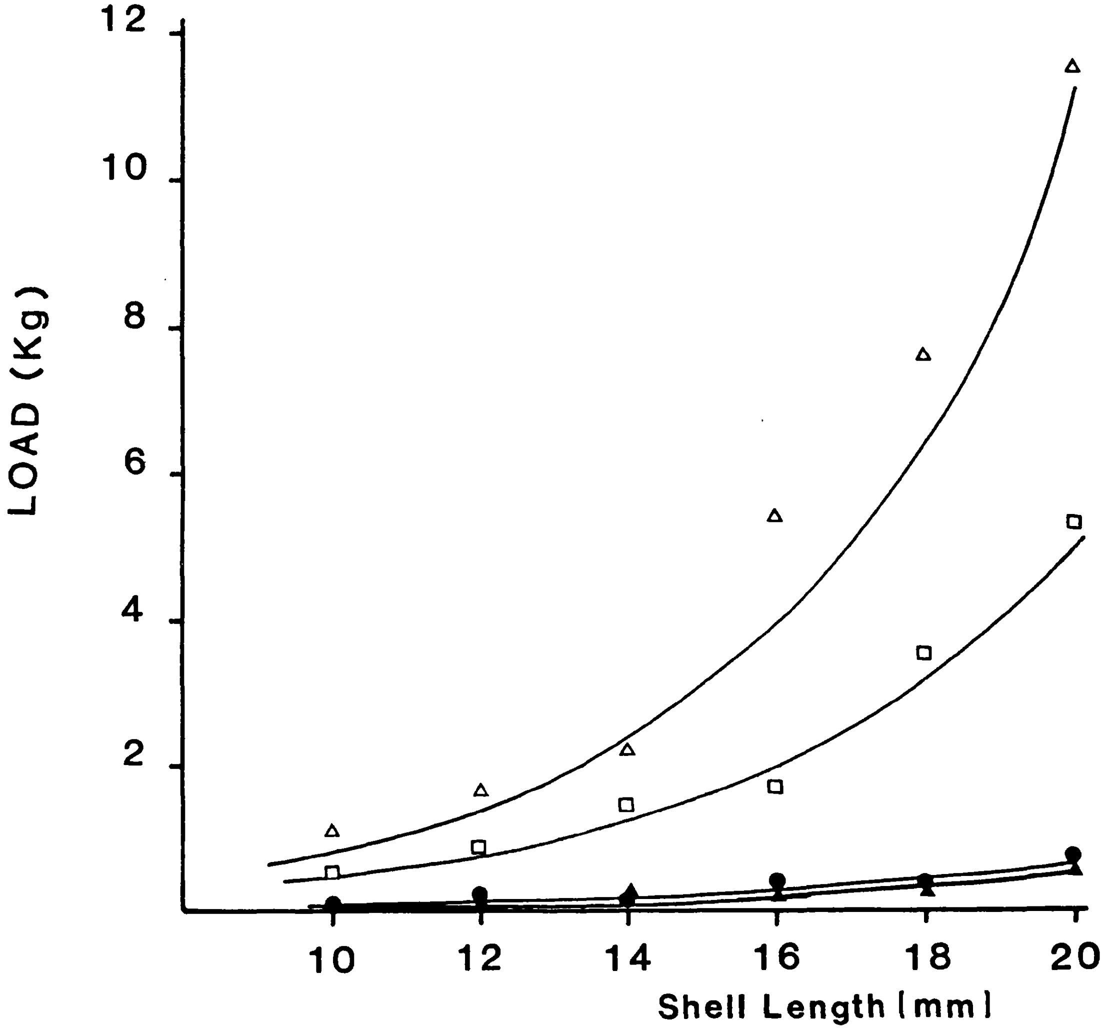

12
10
8
6
4
2
LOAD (Kg)
10
12
14
16
18
20
Shell Length (mm)

Table V.1.1 Frequency (%) of crabs using each opening method for three size classes of *C. maenas* fed on wide size range of *C. edule*

| | Carapace width (mm) | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *C. edule* | 40 | | | | 50 | | | | 60 | | | |
| SL (mm) | Opening method | | | | Opening method | | | | Opening method | | | |
| | SC | UB | HA | PV | SC | UB | HA | PV | SC | UB | HA | PV |
| 8 | 50 | 50 | - | - | 65 | 35 | - | - | 80 | 20 | - | - |
| 10 | - | 100 | - | - | 20 | 80 | - | - | 35 | 65 | - | - |
| 12 | - | 85 | - | 15 | - | 100 | - | - | 20 | 80 | - | - |
| 14 | -* | 25 | - | 75 | - | 100 | - | - | 20 | 80 | - | - |
| 16 | - | - | - | - | * | 80 | 5 | 15 | - | 100 | - | - |
| 18 | | | | | - | - | - | - | - | 90 | 10 | - |
| 20 | | | | | | | | | * | 85 | 15 | - |
| 22 | | | | | | | | | - | - | - | - |

SC = simple crushing

UB = umbone breaking

HA = hinge attack

PV = prying valves apart

* Not all crabs managed to open that prey size

Table V.1.2 Frequency (%) of crabs using each opening method for three size classes of C. maenas fed on wide size range of M. balthica

| | Carapace width (mm) | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| M. balthica SL (mm) | 40 | | | 50 | | | 60 | | | |
| | Opening method | | | Opening method | | | Opening method | | | |
| | SC | UB | EC | SC | UB | EC | SC | UB | EC | HA |
| 8 | 50 | 50 | | 50 | 50 | | 100 | - | | |
| 10 | - | 80 | 20 | 40 | 60 | | 80 | 20 | | |
| 12 | - | 30 | 70 | | 80 | 20 | 20 | 80 | | |
| 14 | -* | - | 100 | | 60 | 40 | - | 100 | - | |
| 16 | - | - | - | * | | 100 | | 70 | 30 | |
| 18 | | | | | | | | 20 | 80 | |
| 20 | | | | | | | * | - | 80 | 20 |

SC = simple crushing

UB = umbone breaking

EC = edge chipping

HA = hinge attack

* Not all crabs of that size managed to open the prey size

Table V.1.3 Frequency (%) of crabs using each opening method for three size classes of C. maenas fed on wide size range of S. plana

| | Carapace width (mm) | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| S. plana | 40 | | | 50 | | | 60 | | |
| SL (mm) | Opening method | | | Opening method | | | Opening method | | |
| | SC | UB | EC | SC | UB | EC | SC | UB | EC |
| 8 | 85 | 15 | - | 100 | - | - | 100 | - | - |
| 10 | 50 | 50 | - | 70 | 30 | - | 100 | - | - |
| 12 | 10 | 90 | - | 50 | 50 | - | 100 | - | - |
| 14 | - | 100 | - | 25 | 75 | - | 90 | 10 | - |
| 16 | - | 100 | - | - | 100 | - | 75 | 25 | - |
| 18 | - | 75 | 25 | - | 80 | 20 | 35 | 65 | - |
| 20 | - | 60 | 40 | - | 100 | - | 15 | 85 | - |
| 25 | - | 40 | 60 | - | 100 | - | - | 100 | - |
| 30 | - | 15 | 85 | - | 85 | 15 | - | 95 | 5 |
| 35 | - | 20 | 80 | - | 100 | - | - | 100 | - |
| 40 | * | 20 | 80 | - | 90 | 10 | - | 100 | - |

SC = simple crushing

UB = umbone breaking

EC = edge chipping

* Not all crabs of that size managed to open the prey size

Table V.1.4 Frequency (%) of crabs using each opening method for three size classes of *C. maenas* fed on wide size range of *M. arenaria*

| *M. arenaria* | Carapace width (mm) | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 40 | | | 50 | | | 60 | | |
| SL (mm) | Opening method | | | Opening method | | | Opening method | | |
| | SC | UB | EC | SC | UB | EC | SC | UB | EC |
| 15 | 10 | 90 | - | 30 | 70 | - | 70 | 30 | - |
| 20 | - | 80 | 20 | - | 100 | - | 30 | 70 | - |
| 25 | - | 90 | 10 | - | 100 | - | 10 | 90 | - |
| 30 | - | 20 | 80 | - | 80 | 20 | - | 100 | - |
| 35 | - | - | 100 | - | 70 | 30 | - | 90 | 10 |
| 40 | - | -* | 100 | - | 20 | 80 | - | 50 | 50 |
| 50 | - | - | - | - | - | 100 | - | - | 100 |
| 60 | | | | - | -* | 100 | - | - | 100 |
| 70 | | | | - | - | - | - | - | 100 |
| 80 | | | | | | | - | - | - |

SC = simple crushing

UB = umbone breaking

EC = edge chipping

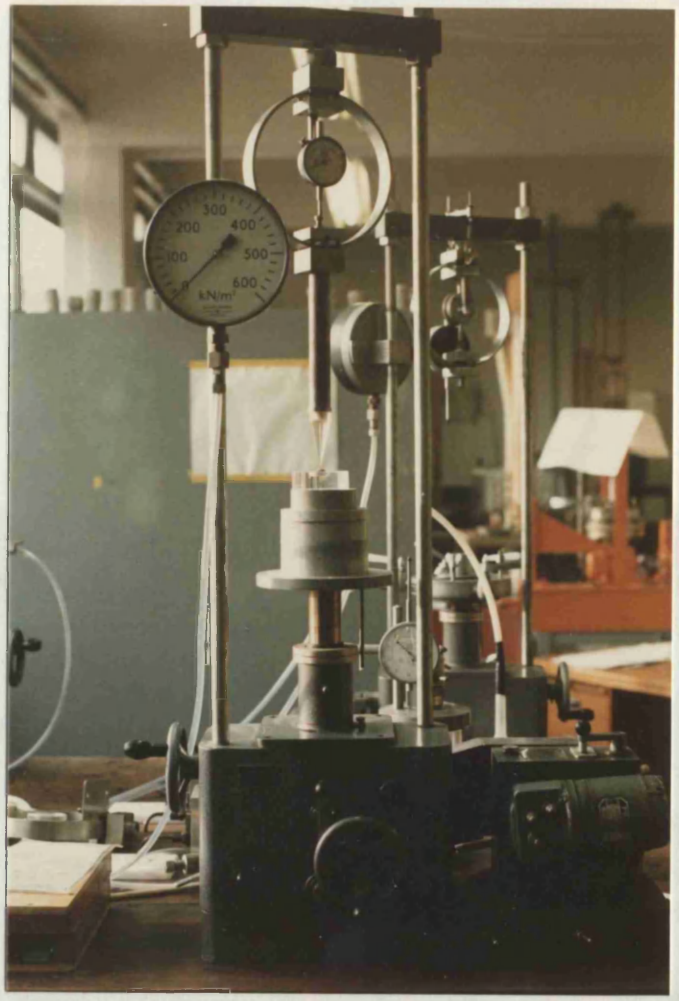
* Not all crabs of that size managed to open the prey size

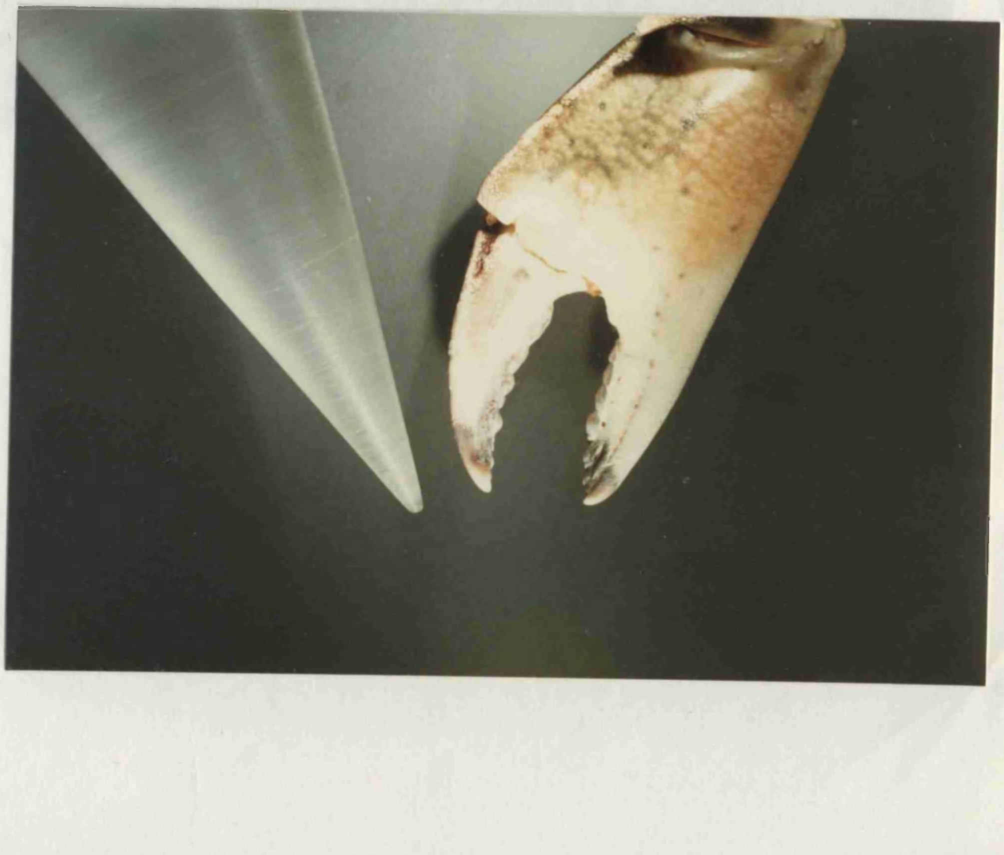
Table V.1.5 Critical size of four bivalves species for three size classes of crab, 40, 50 and 60 mm carapace width

| Prey type | Maximum size available | Crab carapace width (mm) | | |
|---|---|---|---|---|
| | | 40 | 50 | 60 |
| *C. edule* | 35 | 16 | 18 | 22 |
| *M. balthica* | 20 | 16 | 18 | - |
| *S. plana* | 40 | - | - | - |
| *M. arenaria* | 90 | 50 | 70 | 80 |

Plate V.1.1 Triaxial Compression Machine used to measure the bivalve shell strength. A specimen in the chamber is shown ready to be tested.

Plate V.1.2 The similarity between the tip of crab claw and perspex modal claw tip


100
200
300
400
500
600
kN/m²



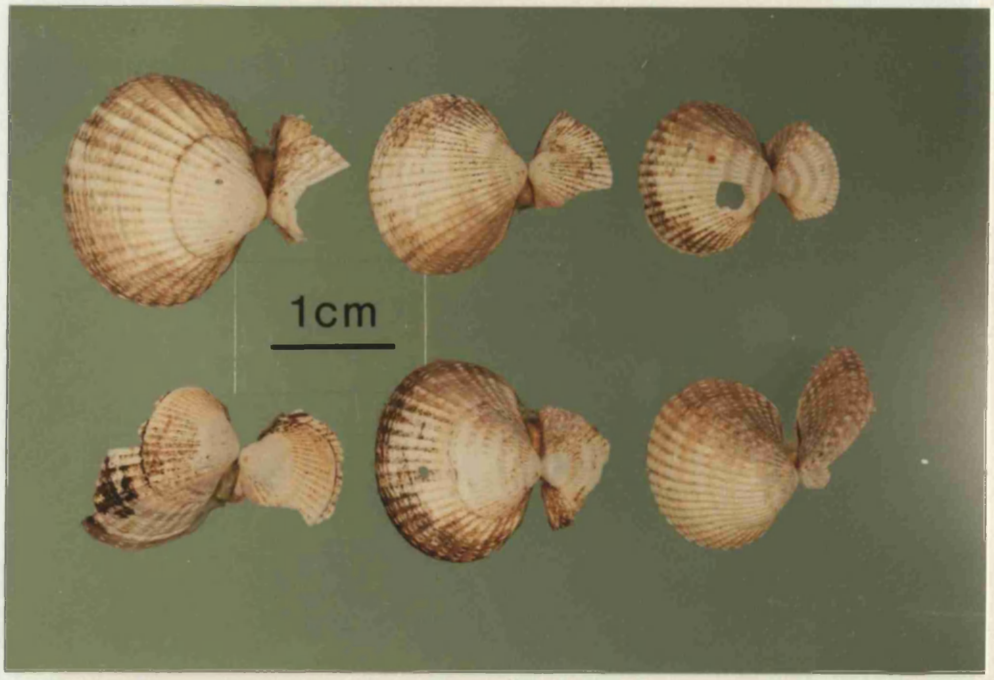


Plate V.1.3 Shell fragments of C. edule opened by umbone breaking method

Plate V.1.4 Shell fragments of *M. balthica* opened by umbone breaking method

Plate V.1.5 Shell fragments of *M. balthica* opened by edge chipping method


1cm


1cm

Plate V.1.6 Shell fragments of *S. plana* opened by umbone breaking method

Plate V.1.7 Shell fragments of S. *plana* opened by edge chipping method

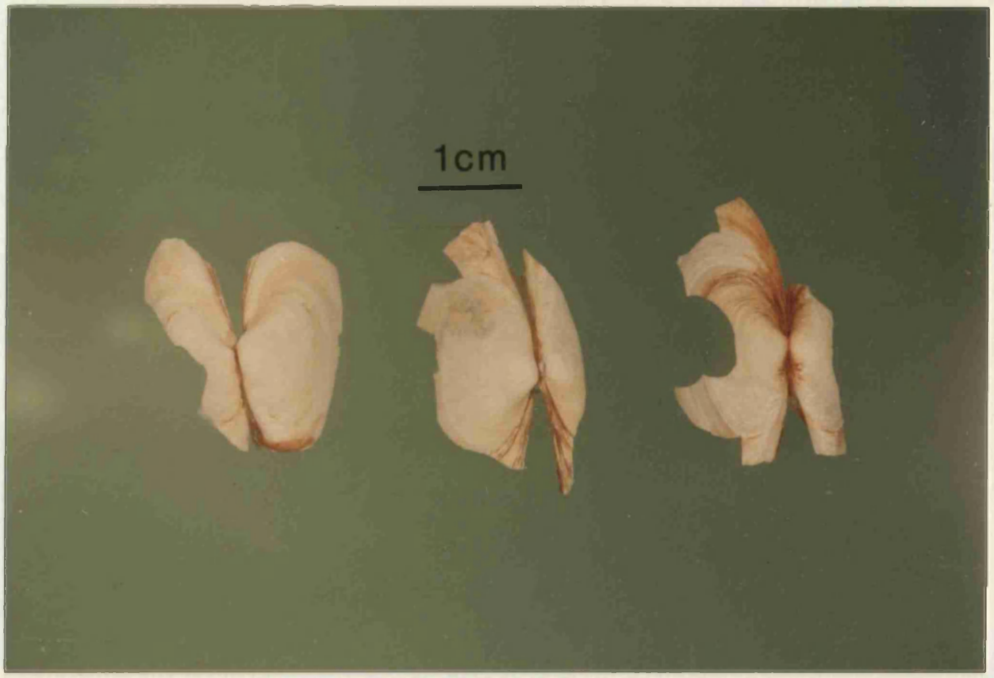


Plate V.1.8 Shell fragments of M. arenaria opened by umbone breaking method

## SECTION V.2

## DYNAMICS OF CRAB FEEDING BEHAVIOUR

## V.2.1 INTRODUCTION

Methods by which predators detect and select their prey have been described from many standpoints. One fashionable approach is that of optimal foraging theory (see reviews by Pyke *et al*, 1977; Krebs, 1978; Townsend and Hughes, 1981). According to that theory, if the predator is faced with a choice of alternative food items, or different size groups of any particular prey, the energy maximisation premise predicts that the predatory animal would select the diet with the maximum energy intake (the optimal diet). Application of the theory in the marine context was reviewed by Hughes (1980).

Elner and Hughes (1978) used the shore crab and epibenthic prey as examples. When the different size classes of *C. maenas* were presented with a wide size range of mussels on plain containers, they showed preference towards the most profitable size ie. they are energy maximisers.

The selection of optimum epifaunal prey by *C. maenas* was explained by Jubb *et al* (1983) according to two hypotheses. Firstly, 'Prey Evaluation', small prey rejected on the basis of size, while large ones often rejected on the basis of strength. Secondly, 'Relative Stimulus Hypothesis', which depends on the strength of chela stimulus relative to stimuli caused simultaneously by other prey touching the pereiopods. However, the authors concluded that both behavioural mechanisms would lead to maximising the energy intake of the crab.

Predator-prey interaction has been studied widely using crabs and epifaunal bivalves. In Britain, shore crab predation of edible mussels has been reported on by Walne and Dean (1972), Elner and Hughes (1978), Elner (1980), Jubb *et al* (1983) and Cunningham and Hughes (1984). On the west coast of the Atlantic, the blue crab *Callinectes sapidus* and mud crab *Panopeus herbstii* on ribbed mussel *Geukensia demissa* were studied by Seed (1980 and 1982) and Hughes and Seed (1981); the rock crab *Cancer irroratus* on sea scallops *Placopecten magellanicus* by Elner and Jamieson (1979) and Jamieson *et al* (1982).

In recent years, extensive studies have been conducted in North America on the pedatory behaviour of crabs on infaunal bivalves in the laboratory as well as the field. Species of crab studied in this way include *Callinectes sapidus* (Blundon and Kennedy, 1982a and b; Arnold, 1984), *Panopeus herbstii* (Whetstone and Eversole, 1978 and 1981), *Cancer productus* (Boulding, 1984; Boulding and Hay, 1984), *Cancer irroratus* and *Neopanope sayi* (Mackenzie, 1977).

Although it has long been known that the shore crab digs for buried clams (Dow and Wallace, 1952; Glude, 1955; Ropes, 1968; Warner, 1977), no study has been made of its foraging behaviour on infaunal bivalves apart from the work of Walne and Dean (1972) who studied its feeding upon the imported hard clam *Mercenaria mercenaria*.

It has been assumed by previous workers (Hancock and Urquhart, 1965) that crabs in the Burry Inlet were predators of the young cockles there. It was assumed at the start of the study that they were also predators of the other buried bivalves there. Subsequent studies of the stomach contents of *C. maenas* demonstrated this to be so (see Section IV).

The objectives of the study reported in this section were twofold: firstly, to record the relationship between predator and prey size on the time taken to handle prey and secondly to examine the factors involved in prey selection when the predator was presented with a choice of prey.

## V.2.2 MATERIALS AND METHODS

### V.2.2.1 Collection and preparation of animals for the study

The shore crabs were collected from the Inlet by using baited traps (see Section III.2.2). In all the feeding experiments only male crabs with all appendages intact were used to avoid any potential bias that might exist through sexual differences in chela size or through limb loss. Crab carapace width was measured to the nearest 0.1 mm with Vernier calipers. Three size classes only of crab were used: 40, 50 and 60 ± 2 mm CW, all intermediate size specimens were rejected.

The study concentrated on three different species of infaunal bivalves, *Cerastoderma edule*, *Macoma balthica* and *Scrobicularia plana*. Owing to the difficulty of finding sufficient small specimens of *Mya arenaria* in the field, this species was excluded from the feeding studies.

The experimental bivalves were all collected from the same general area at Salthouse Point, by sieving sand in the field through 4.0 mm mesh. By using Vernier calipers, the shell length of the bivalves was measured to the nearest 0.1 mm and sorted into different size groups: 8, 10, 12, 14, 16, 18 and 20 ± 0.2 mm, all the intermediate sizes were rejected. In the case of *S. plana* other size groups were used which will be mentioned later.

A stock of the experimental animals (crabs and bivalves) was kept in various suitable containers, each supplied with a continuous flow of sea water. In order to keep the bivalves in a healthy state for the experiments they were fed on cultured algae. *M. balthica* and *S. plana* were also provided with native sediment. Any crab showing signs of moulting or loosing appetite before or during the experiments was rejected and replaced by another.

All feeding experiments were carried out in polypropylene aquaria with dimensions of 55 x 35 x 18 cm with running sea water at 15 ± 2°C. To reduce any external disturbance and to prevent crabs escaping, the containers were covered by plastic netting during the experiments.

### V.2.2.2 Feeding process experiments

The time spent by a crab opening a bivalve shell, 'Breaking Time', is considered to start from the first physical contact with the prey to the first bite of the flesh (*sensu* Elner and Hughes, 1978), while 'Eating Time', is the time taken by the crab to eat all the flesh in the shell. 'Handling Time' is the sum of breaking and eating time.

Breaking and eating times were recorded for three size classes of crab (40, 50, 60 mm CW). Each class was represented by four individuals. The crabs were presented separately with a wide size range of *C. edule* (8, 10, 12, 14, 16, 18, 20 mm SL), each size group represented by five individuals. Each crab was offered specimens of one size group, one at a time. Similar experiments were conducted on the two other bivalves, *M. balthica* and *S. plana*. All experiments were conducted in aquaria devoid of sand.

### V.2.2.3 Dry weight and calorimetry of bivalves

The relation between size and dry weight of the bivalves was obtained by drying the flesh in an oven to constant weight at 60°C for 48 hours. To estimate the energy content, a specimen of ground dry flesh (500 mg) was burnt in a Ballistic Bomb Calorimeter CB-370 (Gallenkamp). This examination was carried out in summer-time when most of the bivalve size groups were available.

### V.2.2.4 Burrowing depth of the bivalves

Although the burrowing depth of bivalves such as *S. plana* and *M. balthica* has been studied elsewhere (Hughes, 1970; Reading and McGrorty, 1978) it was decided to examine the burrowing depth of the different size groups for the studied bivalves in the present study under laboratory conditions.

Different size groups of *C. edule*, *M. balthica* and *S. plana* were used. Each size group was represented by 10 individuals. Clams were allowed to reburrow in sand (brouhgt from the field and sieved through a mesh of 300 μm) They were left in position overnight before their depth was recorded. Sand was removed carefully and the distance from the sand surface to the uppermost edge of the shell was measured.

### V.2.2.5 Prey selection

#### 1. Size selection experiments

Selective predation among different size groups of *C. edule* was determined by presenting the three size classes of crab (each class represented by three individuals) with seven size groups of *C. edule* (8, 10, 12, 14, 16, 18, 20 mm SL), each group represented by 15 individuals. Similar experiments were conducted for *M. balthica* of similar size groups as *C. edule*, and different size groups of *S. plana* (10, 15, 20, 25 mm SL), each group represented by 10 individuals. Only two size classes of crab (40 and 60 mm CW) were used for experiments carried out on *S. plana*.

Experiments were first conducted in aquaria devoid of sediment (for *M. balthica* and *S. plana only*). Bivalves here were scattered randomly on the floor of the aquarium and then the crab was introduced. For all three bivalve species, experiments were then repeated with the presence of sand. The bottom of the aquarium was covered to a depth of 8 cm with native sand brought from the field and sieved through a mesh of 300 μm (to remove larger particles). The proper number of all size groups of the bivalves examined was allowed to burrow in sand before crabs were introduced. Each experiment lasted for 10 days during which time the number of bivalves eaten was monitored daily and replacement with the same size added to keep the prey availability constant. In experiments where sediment was present, the sand was carefully sieved daily through 2.0 mm mesh to the same purpose. Prior to each experiment, crabs were starved for 48 hours to standardise their level of hunger.

In order to examine the null hypothesis that crabs had eaten an equal number from each size group of the bivalves, the number of prey eaten from those groups was pooled for each crab size class in every experiment and tested using the G-test for goodness of fit (Zar, 1974).

### 2. Species selection experiments

Prey species preference was examined by presenting crabs of different size groups (40, 50, 60 mm CW), each represented by three individuals with a mixed prey of 10 mm SL *C. edule* and *M. balthica* (each species represented by 60 individuals). Experiments were conducted first using plain containers and then repeated by adding sand for the bivalves to burrow in. Similar experiments were carried out on one size class of crab (50 mm CW) represented by two individuals and presented with mixed prey species of five combinations:

1. *C. edule* and *M. balthica* (12 mm SL), 30 individuals of each;
2. *C. edule* and *M. balthica* (14 mm SL), 25 individuals of each;
3. *C. edule* and *S. plana* (14 mm SL), 25 individuals of each;
4. *M. balthica* and *S. plana* (14 mm SL), 25 individuals of each;
5. *M. balthica*, *S. plana* and *C. edule* (14 mm SL), 25 individuals of each.

Comparison between means was analysed using Student's t test. For more than two means F test was applied first and then significant results were analysed further using the Newman-Keuls multiple range test (Zar, 1974).

### V.2.2.6 Feeding rate and hunger experiments

The feeding rate was determined for three crab size classes (40, 50, 60 mm CW), each represented by three individuals and each crab was presented with bivalves as follows:

1. *C. edule* of 10 mm SL (n = 80)
2. *M. balthica* of 10 mm SL (n = 80)
3. *S. plana* of 10 mm SL (n = 80)
4. *S. plana* of 15 mm SL (n = 30)
5. *S. plana* of 20 mm SL (n = 20)

The five series of experiments were first conducted in plain aquaria, and then repeated with the addition of sand. The number of prey eaten in each experiment was monitored daily for five days, eaten animals were replaced by others of the same size.

Similar experiments were carried out for two individual crabs of the same size (50 mm CW) by presenting them with *M. balthica* (14 mm SL, n = 30; 16 mm SL, n = 20) and *C. edule* (14 mm SL, n = 30; 16 mm SL, n = 20).

Results were compared statistically using Student's t test.

The influence of the type of container surface on crab feeding rate was examined by using three sets of containers:

1. Pneumatic glass troughs which represent a smooth surface measuring 30 cm in diameter and 12.5 cm in height.
2. Similar to the first type but the surface was roughened by using gravel (2-3 mm in size) fixed on the surface by glue. A series of processes was conducted to ensure that the gravel was firmly

attached (containers left for two days to dry) and to reduce any effect on the animals of glue solvent leaching out, by soaking the troughs in tap water and then sea water for two days before starting the experiment.

3. Polypropylene containers used were similar to those in all the feeding experiments in the present study.

Eight crabs of 50 mm carapace width were each presented with 15 individuals of 14 mm SL *C. edule* in each container type. The number of cockles eaten was recorded at 30 minute intervals for two hours. Crabs were starved for two days prior to the experiments. Results were compared statistically by using F test.

Influence of hunger level on crab feeding rates was examined as follows: Six crabs of 50 mm CW were first fed on cockles until satiated. They were refed individually on *C. edule* (12 mm SL) after various intervals of starvation (1, 3, 6, 9, 12, 18, 24, 48, 72 and 96 hours) until resatiated. The number of cockles eaten by the crabs was recorded at each starvation period. Handling time was also recorded for each encountered prey.

Fore-gut clearance-rate was determined by feeding 27 male crabs (50-60 mm CW) on cockles till satiated. After various intervals similar to those mentioned earlier (except 96 hours), the stomachs of three crabs from the groups were removed and opened. The amount of food present was recorded and classified under binocular microscope as hard (shell fragments) and soft tissue.

Defaecation of the crabs after feeding was examined to record the time it takes a crab to defaecate the shell fragments of a bivalve prey. Three crabs of 50-55 mm CW were starved for one week and then fed on small cockles (10-14 mm SL) until satiated. The crabs were then removed and placed in clean containers with sea water. The presence of faeces was observed after various intervals (1, 3, 6, 12, 24, 36, 48, 72 and 96 hours). At each interval, faeces were collected carefully and examined under a binocular microscope to record the presence or absence of shell fragments. At the end of the experiment the stomachs of the crabs were opened to record any remains.

## V.2.3 RESULTS

### V.2.3.1 Feeding process experiments

The breaking time (Tb) and eating time (Te) for each of the three size classes of crab were plotted against the shell length of the three bivalves, C. edule (Figs. V.2.1 and V.2.2), M. balthica (Figs. V.2.3 and V.2.4) and S. plana (Figs. V.2.5 and V.2.6).

Variations in the Tb and Te amongst similar sized clams occurred both within and between crabs which could be due to variability in shell strength on the one hand and differences in crab hunger levels on the other. Curves were fitted according to the regression equations (see Figures V.2.1-6). Handling time (Th) increased with prey length. Tb increased in relation to shell strength and the increase of Te reflected the amount of flesh in the shell. Both breaking and eating time decreased with the increase in crab size. Figures indicated that values of Tb and Te were higher for both C. edule and M. balthica than those of S. plana of the same size group.

### V.2.3.2 Burrowing depth of the bivalves

As expected, within the same bivalve species, large size animals burrow deeper than the small ones (Table V.2.1). The depth that both M. balthica and S. plana (18-20 mm SL) reached ranged between 5-6 cm. The whole size range of cockles examined in this experiment burrowed not deeper than 1 cm. No significant difference was recorded between the burrowing depth of M. balthica and S. plana of the same size group ($P > 0.05$), while both burrow deeper than C. edule of similar size group ($P < 0.001$)

### V.2.3.3 Calorimetry and prey value

The dry weight of the bivalves increased according to the increase of shell length (Fig. V.2.7). There is more flesh in M. balthica and C. edule in contrast to S. plana of the same size. No significant difference was recorded between the energy value of the meat of the three species ($P > 0.05$). Table V.2.2 shows that 1 mg dry weight of C. edule contains 20.8 joules, while that of M. balthica, 23.94, and 23.43 joules for S. plana.

The relation between shell length and energy content for the three bivalves is shown in Table V.2.3. It shows that for any size group of the three species M. balthica contains the most energy content while S. plana contains the least.

Prey value for any particular prey is the energy content divided by the handling time (E/Th). In Figure V.2.8 prey value is plotted against prey length of C. edule, M. balthica and S. plana for three size classes of crab. Prey value reached a maximum at different prey size according to the size of the crab. Beyond the maximum it declined due to the increase in handling time. A similar pattern was observed in the three bivalve species. However, the curve is more flattened in the case of S. plana.

### V.2.3.4 Size selection results

Some general observations were made on the crabs' feeding behaviour when they were introduced to aquaria with bivalves buried in the sand. They usually covered themselves immediately after being introduced into the experimental container. The time lag spent in that position varied between crabs and from one occasion to another. However, following this initial acclimatisation period they soon started wandering on the sand surface. It was clearly evident that they used their walking legs to detect the prey. When a buried specimen was encountered, it was brought up to the surface by the anterior walking legs with the help of the chelae. It was then opened by the appropriate technique as described in Section V.1.

Large size prey (usually *C. edule*) were found sometimes left untouched on the sand surface which indicated that the crab had dug them up but failed to open them.

When crabs were presented with a mixture of different sized specimens of *C. edule* or *M. balthica*, they showed a preference for a certain size range (see Figure V.2.9 for *C. edule* and Figure V.2.10 for *M. balthica*). Crabs of 40 mm CW predated mainly on 8-12 mm SL *C. edule* with a peak at the 8 mm group. The crab showed a similar pattern of preference for *M. balthica* whether having been offered on plain aquarium or buried in sand. Crabs of 50 mm CW selected 8-14 mm SL of *C. edule* with peak at the 10 mm group. When that crab was offered mixed sized groups of *M. balthica* on plain aquarium, a clear selection was towards 10 and 12 mm SL prey with the 8 mm group being relatively neglected. The pattern was almost similar in the presence of sand, except that the 8 mm size was increased. For 60 mm CW crabs fed on *C. edule* the peak shifted to the 12 mm size group and the diet curve was widened. Here predation of the smaller size prey decreasd sharply in contrast to the results with smaller crabs. On plain aquarium, this size of crab predated mainly on the 10-14 mm size group of *M. balthica* with a peak at the 12 mm group. However, smaller individuals were included in the diet when they fed on *M. balthica* buried in the sand (see Table V.2.4).

When the experiments were conducted on *S. plana* a completely different result was obtained for size preference when the clams were allowed to burrow in the sand (Fig. V.2.11). Crabs of 40 mm CW showed no preference among different sized *S. plana* presented on plain aquarium

($P > 0.25$). However, when the bivalves were allowed to burrow in the sand, crabs predated only small sizes (10 and 15 mm SL). Crabs of 60 mm CW fed non-selectively on different sizes of S. plana scattered on the floor of the aquarium without sand ($P > 0.25$), while they heavily selected 10 and 15 mm SL (small) specimens when bivalves were buried in the sand ($P < 0.001$).

### V.2.3.5 Prey species preference results

When the crabs were presented with mixed prey of 10 mm SL M. balthica and C. edule on plain aquaria, they showed a preference towards C. edule ($P < 0.002$) and particularly the large crabs (60 mm CW) who consumed 41 ± 7 C. edule and only 21 ± 5 M. balthica as shown in Figure V.2.12. The corresponding figures for 50 mm CW crabs were 27 ± 5 C. edule and 19 ± 4 M. balthica and those for 40 mm CW crabs were 14 ± 3 C. edule and 10 ± 2 M. balthica. However, when the experiment was repeated allowing the prey to burrow in the sand, crabs of all size classes heavily predated C. edule ($P < 0.001$). Crabs of 40 mm CW ate 16 ± 3 C. edule and only 4 ± 2 M. balthica, crabs of 50 mm CW ate 29 ± 7 C. edule and 11 ± 3 M. balthica while 60 mm CW crabs ate 47 ± 9 C. edule and only 17 ± 5 M. balthica.

A similar experiment conducted on 50 mm CW crabs and mixed prey of 12 mm SL M. balthica and C. edule showed, as in Figure V.2.13, that the proportion of M. balthica in the diet of the crab was reduced when the bivalves were allowed to burrow in the sand ($P < 0.001$). The number of M. balthica eaten from mixed prey was reduced from 16 to only 7 when they were buried, however, only a slight increase was recorded in the consumption of cockles.

Figure V.2.14 shows that there was no preference for particular species of 14 mm SL bivalves when they were presented to crabs (50 mm CW) on plain aquarium ($P > 0.05$). On the other hand, crabs preferred cockles when they were presented with either one or two other bivalve species when they were all buried in sand ($P < 0.001$). However, no preference was recorded for crabs fed on a mixed prey of M. balthica and S. plana when they were both buried ($P > 0.1$).

### V.2.3.6 Feeding rates and level of hunger results

Not surprisingly, in all the feeding experiments, feeding rates increased according to the size of the crab ($P < 0.001$). Irrespective of the presence or absence of sand in the aquaria, larger crabs (60 mm CW) ate more bivalves than other crab classes and the medium size crab (50 mm CW) ate more bivalves than the small ones (40 mm CW).

No significant difference was recorded in the feeding rate of crabs when they were fed on cockles (10 mm SL) presented on plain aquaria or buried in sand ($P > 0.1$). Crabs of the three classes (60, 50, 40 mm CW) ate 60 ± 8, 39 ± 3 and 23 ± 4 cockles daily in plain aquaria and the figures for buried ones were 56 ± 8, 37 ± 4 and 21 ± 3, respectively (Fig. V.2.15).

The daily consumption of crabs was higher when they were presented with M. balthica (10 mm SL) on plain container than when the animals were allowed to burrow in sand ($P < 0.001$). In aquaria devoid of sand, crabs of 60 mm CW ate 54 ± 7 M. balthica. The corresponding figures for 50 and 40 mm CW crabs were 35 ± 6 and 19 ± 4 (see Figure V.2.16). On the other hand, when the bivalves were allowed to reburrow in sand, the daily feeding rates of all the crabs were reduced. A crab of 60 mm CW ate 42 ± 5 M. balthica, the figures for 50 and 40 mm CW crabs were 21 ± 4 and 11 ± 2 respectively.

Other experiments on different size groups of C. edule (Fig. V.2.17) and M. balthica (Fig. V.2.18) showed that daily consumption of crabs (50 mm CW) was not affected by allowing C. edule to burrow in sand ($P > 0.05$)

while all results for M. balthica showed that higher numbers of prey were eaten when they were presented to crabs in containers devoid of sand ($P < 0.001$).

In the case of S. plana, Figure V.2.19 shows that all size classes of crab ate more clams in plain aquaria ($P < 0.001$). Although, crabs of 40 mm CW ate 5 ± 2 S. plana (20 mm SL) when they were presented in plain aquarium, they failed to dig up that size when the clams were buried in sand.

Experiments on different types of aquaria (Table V.2.5) showed that crab feeding rate in type (A) was slightly higher than in the other two types, but no significant difference was recorded between the feeding rates of crabs fed in containers with differnt types of surfaces ($P > 0.05$). It is clear that in the three treatments, crabs consumed the majority of cockles in the first 30 minutes of the experiment.

The number of cockles (12 mm SL) required to satiate crabs increased according to the increase in starvation time in the first 24 hours (see Figure V.2.20). The average value increased from 4 ± 1 in the first hour after satiation to 28 ± 3.5 ( ≈320 mg dry wt or 6.6 kJ) within a 24 hour period of starvation. However, no significant increase was recorded afterwards by prolonging the starving interval ($P > 0.05$).

The mean of the handling time (Th) for the successive cockles encountered by the crabs decreased asymptotically to about 50% of the initial value after 9-11 cockles had been eaten (Fig. V.2.21). After 18-19 prey were eaten the handling time increased rapidly to reach more than the initial value by the time the crabs became satiated. Owing to the variation of handling time value during the experiment, the number of cockles consumed by the crabs varied as shown in Figure V.2.22. On the basis of 10 minute intervals throughout the experiment, the least number of cockles was eaten at the beginning and end of the experiment when the crabs reached satiation.

### V.2.3.7 Fore-gut clearance rate and defaecation results

Table V.2.6. shows that fullness of the stomach decreased progressively with starving time. A full stomach becomes empty after 24-36 hours of starvation. No soft tissues were found in the stomach after 18 hours of starving, while shell fragments were present 24 hours after the crab was fed.

Up to 6 hours after feeding, no defaecation was recorded for the crabs. However, it was after only 12 hours from the time the crab was fed that faeces with a few shell fragments were recorded. The greatest number of shell fragments were found in the faeces 24 hours after feeding. In time, their presence decreased and none was observed after 48 hours (see Table V.2.7).

## V.2.4 DISCUSSION

The results of predation experiments can be discussed from the viewpoint of the predator or prey. In the following pages the predator's standpoint will be considered first.

### V.2.4.1 Crab feeding frequency

It is evident from starvation and satiation experiments (Fig. V.2.20 and Table V.2.6) that food passes quickly through the gut and that crabs probably feed at every tide. A plateau corresponding to the total evacuation of the crab's stomach is attained after about 24 hours of starvation. The plateau indicates the number of cockles or the corresponding dry weight needed to satiate a crab with an initially empty stomach.

### V.2.4.2 Total food intake

It is possible to demonstrate a maximum level to the sustainable daily intake of bivalve food. For 50 mm CW crabs (the modal size of migrators) this amounts to about 40 cockles of 10 mm length (one of the preferred sizes) and correspondingly fewer of larger sizes. Values can similarly be put on numbers consumed of other bivalve species.

### V.2.4.3 Feeding strategies

Crabs required more time to open M. balthica and C. edule in contrast to S. plana which reflects the difference in shell strength among these species, demonstrated by the load experiment (see Section V.1).

Obviously, the positive correlation between eating time and bivalve shell length is mainly due to the amount of flesh in the shell which increases in relation to the size of the bivalves. However, the relation between eating time and shell length of the prey is not as simple as that since the gleaning process of the crabs was found to vary according to the prey size (Elner and Hughes, 1978). In contrast to C. edule and M. balthica, it took the crabs a shorter time to glean the flesh of S. plana which reflects the relatively small amount of flesh in the latter species as shown in Figure V.2.7.

When the crabs were offered successive prey, the handling time for each encountered cockle showed a decrease in the Th value to less than 50% of the initial one at the beginning of the experiment. This reduction could be due to the learning of predatory skills which leads to the decrease in breaking time and therefore in handling time. This is in line with what Cunningham and Hughes (1984) recorded as a reduction in the breaking time to about 30% of the initial value for shore crabs fed on successive mussels. However, in the present study, towards the end of the experiment the handling time increased to even more than its initial value. This is clearly not a matter of forgetting the opening technique, but is more likely a result of prolonging the eating time as the crab approached satiation.

As was the case in similar experiments reported by other workers, when offered an ad lib mixture of different sizes of single prey species, crabs select a range of sizes as food with a clear modal size being evidently preferred. The modal preferred size varies in a highly consistent pattern between crabs of different size separately fed on Cerastoderma edule and Macoma balthica. Exercise of choice, as reported by various other workers, was here being demonstrated to a high degree.

In such a study conducted on the soft shell clam, Mya arenaria, no size preference was recorded for the blue crab Callinectes sapidus (Blundon and Kennedy, 1982b). In a similar way, the present study showed no such preferred modal size when the crabs were fed on Scrobicularia plana. The thin shells of all size specimens of this species are apparently equally easy to open.

The similarity between the crab preference pattern and the prey value curves (Fig. V.2.23) indicates that crabs select the most profitable prey in order to maximise their energy intake. This sort of energy maximisation has frequently been observed before for crabs fed on epibenthic bivalves (Elner and Hughes, 1978; Du Preez , 1984).

### V.2.4.4 Prey species preference

The study by Elner and Raffaelli (1980) showed that shore crabs preyed more heavily on the gastropod with higher prey value when they were presented with a mixture of Littorina rudis and L. nigrolineata. The present study showed clearly that the prey value (E/Th) varied according to the bivalve species. For instance, for a 50 mm CW crab the prey value of 14 mm SL C. edule was 1.02 joule per second while it was 1.4 and 2.14 for the same size of M. balthica and S. plana. In this case and according to the optimal foraging theory the crab would be expected to select the prey with the highest prey value (ie. S. plana and M. balthica). However, in the present study the crabs showed no preference for a particular species when presented randomly as mixed prey on plain aquarium. They included even the one with low value in similar proportion and furthermore they ate more C. edule than M. balthica when they were presented with smaller sizes (10 mm SL). It is thought that this is not a matter of preferred taste. Throughout these experiments it has been observed that the ability of crabs to grasp and manipulate the prey varied among the three bivalve species. Unlike the cockles, it was not easy for them to pick up small S. plana or M. balthica due to their flattened shells which slipped away when they tried to grasp them. The reason for including C. edule with the others could be the result of properties related to the shell shape and texture rather than the energy intake. More investigation is needed to study the influence of factors other than energy intake in choosing the prey.

Different results were observed when the experiments were conducted under conditions designed to stimulate more closely those in the field, ie. when the prey were allowed to burrow in sand.

In the present study it was clear that the burrowing behaviour of bivalves decreased the proportion of large size prey in contrast to that in plain aquarium. Crabs chose more individuals of the small size group M. balthica when a wide size range of them were allowed to burrow in sand. Furthermore, in the case of buried S. plana, crabs of 40 mm CW excluded the largest (deepest) specimens and predated heavily on small individuals living near the sand surface.

Obviously, the presence of sand introduced a new component in the handling time, which is the time the crab spends digging for prey (digging time). This presumably would lead to prolonging the handling time budget and therefore decrease the value of the deeper prey. It was not possible to record the digging time in the present study, however, it would be interesting to see whether crabs increased their energy intake by feeding on smaller individuals which occur near the sand surface.

It was apparent in the present study that crabs chose the species which occur near the surface of the sediment when mixed prey of more than one species were allowed to burrow in sand before introducing the crabs. In all the mixed prey experiments using small bivalves (10-14 mm SL) crabs fed heavily on cockles rather than either of the other bivalve species.

Finally, from the predator's viewpoint, a perplexing observation needs to be mentioned. In the present series of experiments it is shown that when crabs are fed bivalves in a plain aquarium, they consistently consume more than when offered buried food. And this is in spite of the extra effort (and therefore energy) required to obtain buried food. It would be interesting to observe, over a longer term experiment, whether the excess energy intake in plain aquaria resulted in faster growth or whether it was dissipated in some other way (perhaps partly lost in faeces).

### V.2.4.5 Bivalve defence against predation

It is generally recognised that some bivalve species adopt different strategies to reduce their vulnerability to predators. For instance, having strong shells (particularly epifaunal species, see Stanley (1970)) or living in habitats that are not easily accessible to predators (eg. Mytilus escape the gastropod Thais lapillus on very exposed shores, Menge (1978)). However, the clumping behaviour of the mussels also reduces their vulnerability to crab predation (Cunningham, 1983). The burrowing behaviour of some bivalve species is reported to be effective in reducing the feeding rate of predators (see for example Walne and Dean 1972; Doering, 1982; Arnold, 1984). The present study showed a significant reduction in the feeding rate of crabs when they were fed on buried prey. That was apparent in the case of both M. balthica and S. plana which showed the ability to burrow deep in the sediment. The shallow burrower C. edule, on the other hand, has a comparatively strong shell. The ribs and the inflated shape of the shell are other features which probably decrease its vulnerability to crabs. In the Burry Inlet, the deepest such burrowers are Mya arenaria which clearly avoid predators in this way when adult. However, in the laboratory, crabs attacked even the very large specimens at the siphonal gape and often succeeded in opening the shell and possibly that would be the case in the field if, for some reason, these clams were not deeply buried.

In addition to 'critical size' (see Section V.1), another concept can be developed. The results of these experiments demonstrate what may be termed an 'effective critical size' for Scrobicularia plana. This size corresponds to a burrowing depth that takes the bivalves beyond the digging depth of the largest crabs. Available observations on Mya arenaria suggest that this bivalve also has an effective critical size. Actual values were not measured but the table below gives estimates based on various observations.

| Bivalve species | Critical size (mm) | Effective critical size (mm) |
|---|---|---|
| Cerastoderma edule | 22 | 22 |
| Macoma balthica | - | - |
| Scrobicularia plana | - | 30 |
| Mya arenaria | 80 | 30 |

Bivalves above these critical or effective critical sizes are not vulnerable to crab predation under natural conditions. It is interesting to note that Macoma does not achieve a critical or effective critical size so far as largest crabs are concerned. In contrast Cerastoderma over 22 mm SL are not subject to crab predation.

Figure V.2.1 Breaking times of C. edule (sec.) plotted against their shell length for three crab size groups

● Crabs 40 mm CW, $y = 10^{0.183\ SL\ -\ 0.26}$, $r = 0.98$

▲ Crabs 50 mm CW, $y = 10^{0.19\ SL\ -\ 0.62}$ , $r = 0.94$

○ Crabs 60 mm CW, $y = 10^{0.15\ SL\ -\ 0.45}$ , $r = 0.97$

Figure V.2.2 Eating times of C. edule (sec.) plotted against their shell length for three crab size groups

● Crabs 40 mm CW, $y = 10^{0.095\ SL\ +\ 1.19}$, $r = 0.99$

▲ Crabs 50 mm CW, $y = 10^{0.093\ SL\ +\ 1.15}$, $r = 0.99$

○ Crabs 60 mm CW, $y = 10^{0.069\ SL\ +\ 1.27}$, $r = 0.98$

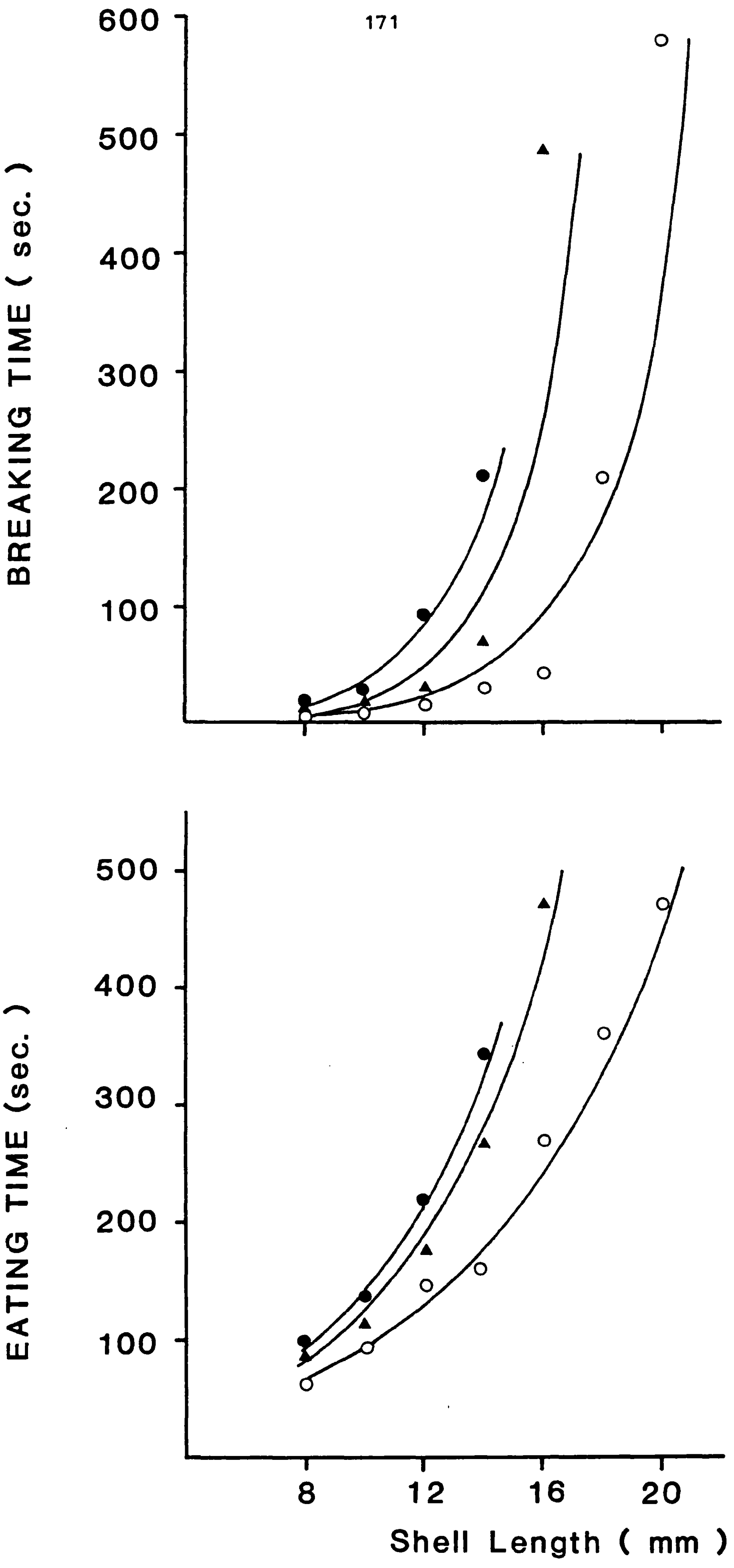

600
500
400
300
200
100
BREAKING TIME ( sec. )
500
400
300
200
100
EATING TIME (sec. )
8
12
16
20
Shell Length ( mm )

Figure V.2.3 Breaking times of M. *balthica* (sec.) plotted against their shell length for three crab size groups

● Crabs 40 mm CW, $y = 10^{0.18\ SL - 0.21}$, $r = 0.99$

▲ Crabs 50 mm CW, $y = 10^{0.16\ SL - 0.15}$, $r = 0.96$

○ Crabs 60 mm CW, $y = 10^{0.13\ SL - 0.07}$, $r = 0.98$

Figure V.2.4 Eating times of *M. balthica* (sec.) plotted against their shell length for three crab size groups

● Crabs 40 mm CW, $y = 10^{0.078\ SL + 1.23}$, $r = 0.99$

▲ Crabs 50 mm CW, $y = 10^{0.11\ SL + 0.85}$, $r = 0.98$

○ Crabs 60 mm CW, $y = 10^{0.085\ SL + 0.98}$, $r = 0.99$

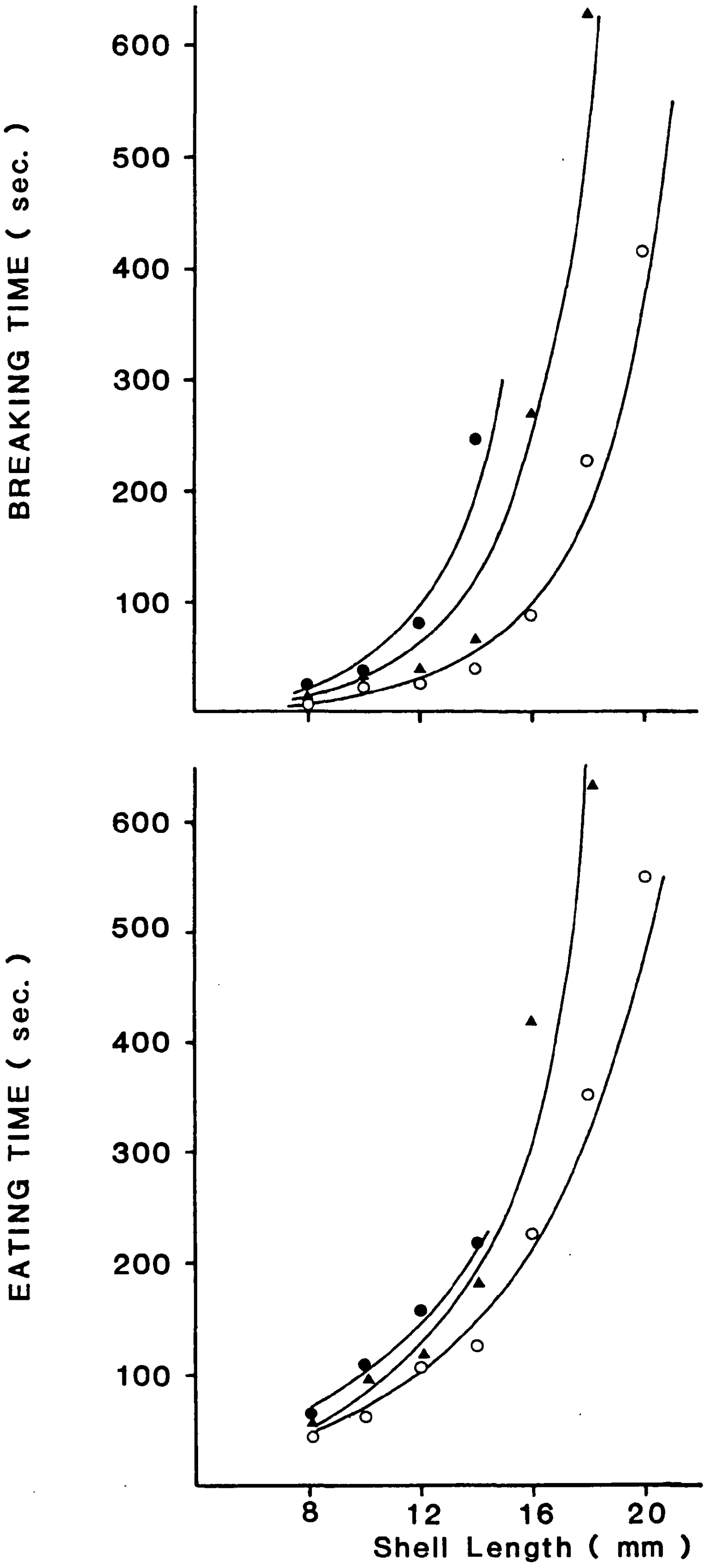

BREAKING TIME ( sec. )
600
500
400
300
200
100
EATING TIME ( sec. )
600
500
400
300
200
100
8
12
16
20
Shell Length ( mm )

Figure V.2.5 Breaking times of *S. plana* (sec.) plotted against their shell length for three crab size groups

● Crabs 40 mm CW, $y = 10^{0.08\ SL + 0.59}$, $r = 0.99$

▲ Crabs 50 mm CW, $y = 10^{0.048\ SL + 0.81}$, $r = 0.94$

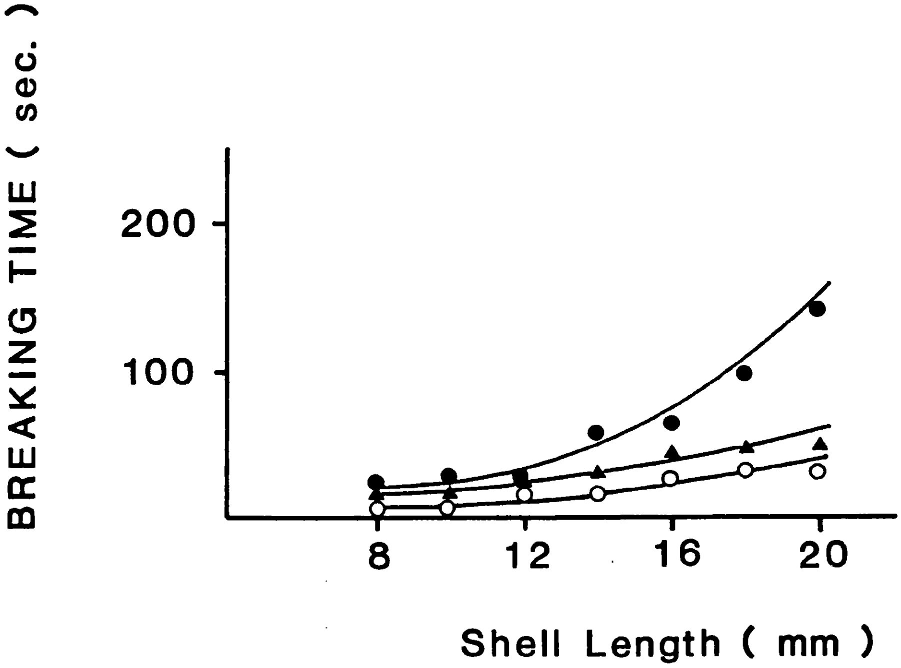
○ Crabs 60 mm CW, $y = 10^{0.06\ SL + 0.40}$, $r = 0.98$

Figure V.2.6 Eating times of *S. plana* (sec.) plotted against their shell length for three crab size groups

● Crabs 40 mm CW, $y = 10^{0.076\ SL + 1.05}$, $r = 0.98$

▲ Crabs 50 mm CW, $y = 10^{0.078\ SL + 0.87}$, $r = 0.98$

○ Crabs 60 mm CW, $y = 10^{0.087\ SL + 0.53}$, $r = 0.99$


BREAKING TIME ( sec. )
200
100
8
12
16
20
Shell Length ( mm )

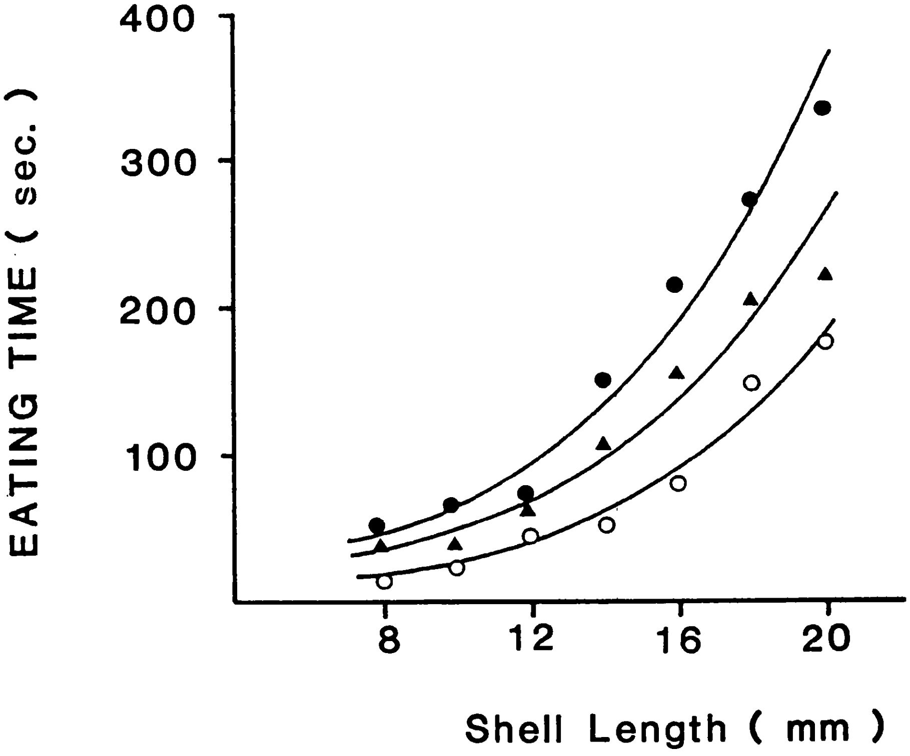

EATING TIME ( sec. )
400
300
200
100
8
12
16
20
Shell Length ( mm )

Figure V.2.7 Dry weight of three bivalve species plotted against their shell length. Curves are fitted according to the regression equations of the bivalves as follows:

△ *Macoma balthica* $y = 10^{0.094\ SL + 0.027}$, $r = 0.98$

□ *Cerastoderma edule* $y = 10^{0.11\ SL - 0.252}$ , $r = 0.98$

● *Scrobicularia plana* $y = 10^{0.079\ SL - 0.058}$, $r = 0.98$

(each point on the figure represents five specimens)

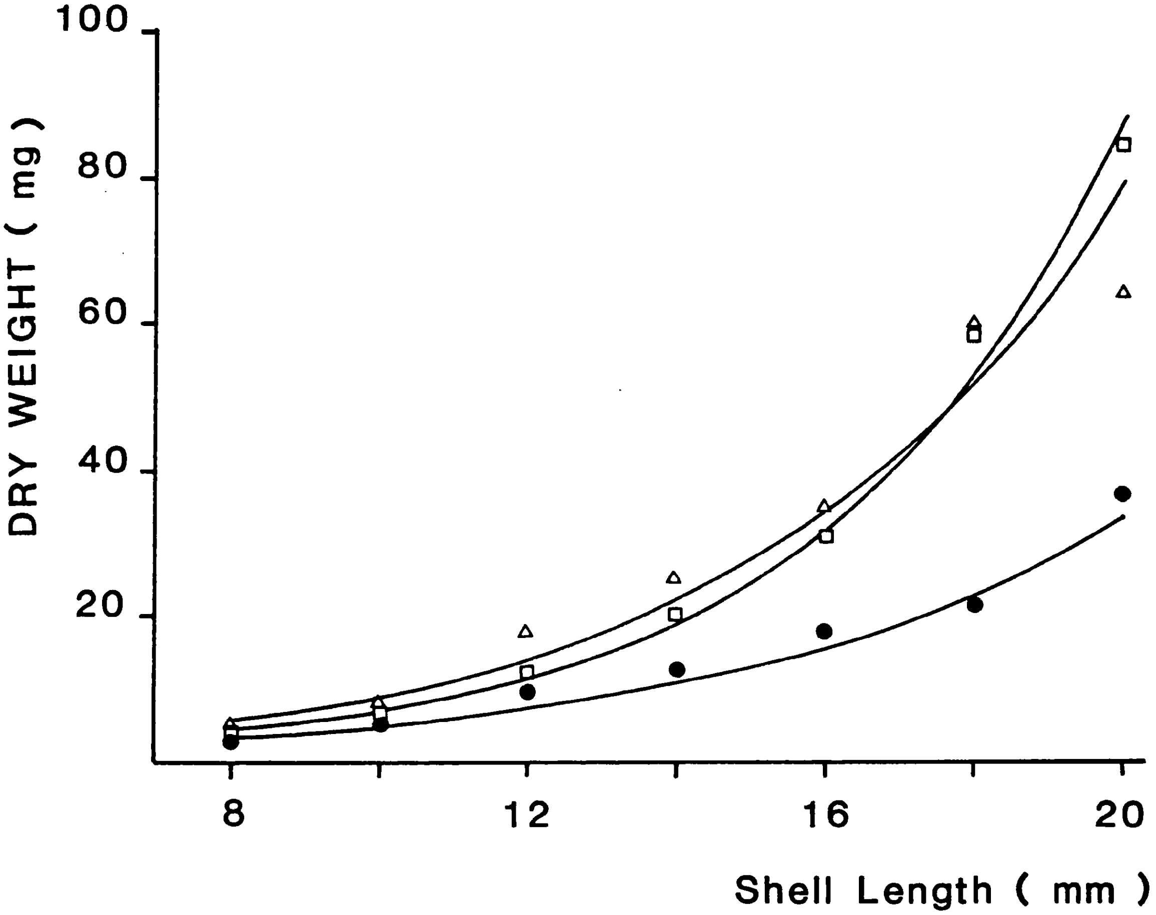
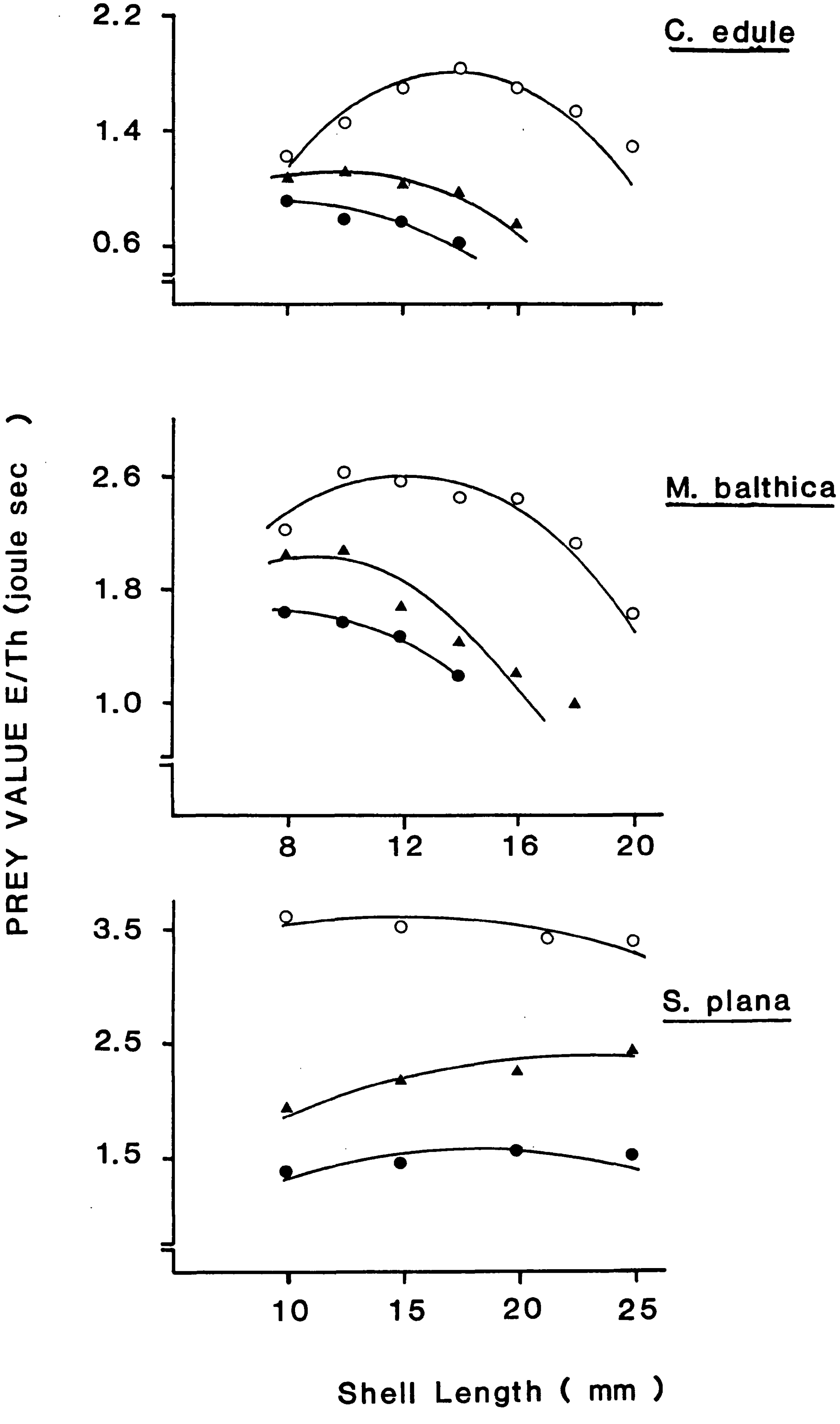

100
80
60
40
20
DRY WEIGHT ( mg )
8
12
16
20
Shell Length ( mm )

Figure V.2.8 Prey value, energy/handling time (Joule $sec^{-1}$) of *C. edule*, *M. balthica* and *S. plana* plotted against their shell length (mm) for three size groups of crab

● 40 mm CW

▲ 50 mm CW

○ 60 mm CW



2.2
1.4
0.6
C. edule
2.6
1.8
1.0
M. balthica
8
12
16
20
3.5
2.5
1.5
S. plana
10
15
20
25
PREY VALUE E/Th (joule sec$^{-1}$)
Shell Length ( mm )

Figure V.2.9 Daily feeding rates of three size classes of crab fed on different size groups of buried *C. edule*

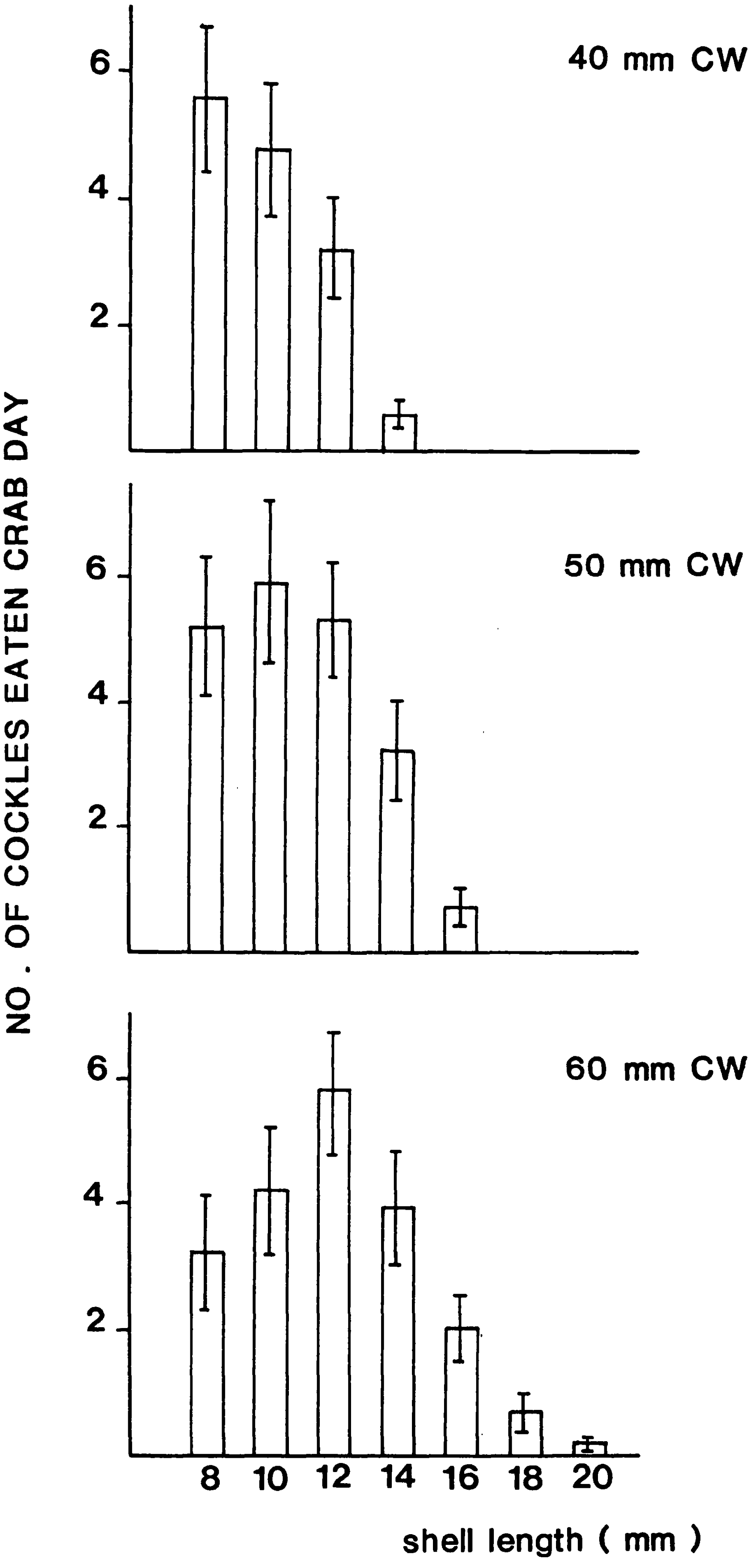

40 mm CW
50 mm CW
60 mm CW
NO. OF COCKLES EATEN CRAB$^{-1}$ DAY$^{-1}$
6
4
2
6
4
2
6
4
2
8
10
12
14
16
18
20
shell length ( mm )

Figure V.2.10 Daily feeding rates of three size classes of crab fed on different size groups of *M. balthica*

A aquarium devoid of sand

B aquarium with sand

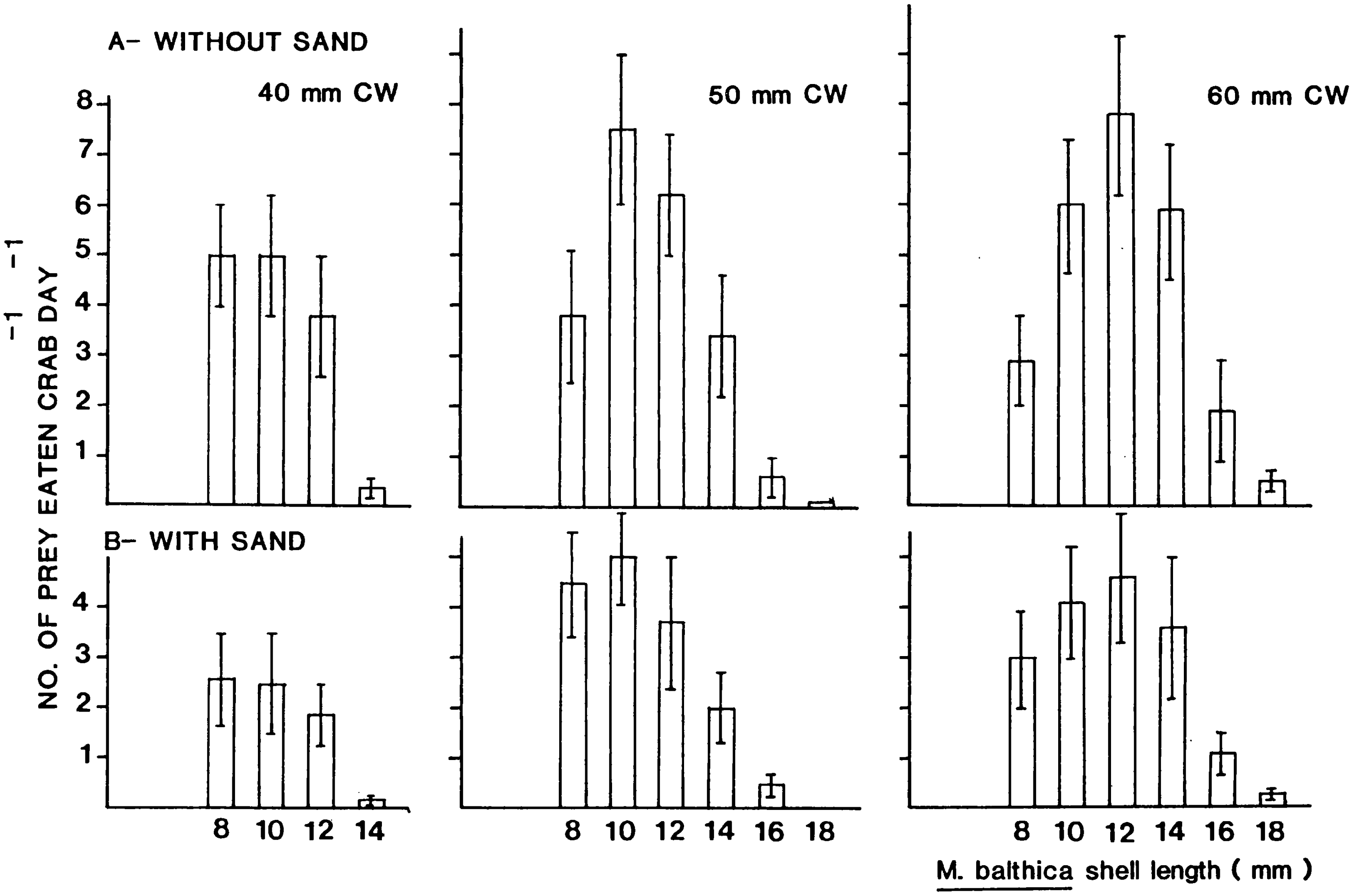

A– WITHOUT SAND
40 mm CW
50 mm CW
60 mm CW
B– WITH SAND
NO. OF PREY EATEN CRAB$^{-1}$ DAY$^{-1}$
8
7
6
5
4
3
2
1
4
3
2
1
8 10 12 14
8 10 12 14 16 18
8 10 12 14 16 18
M. balthica shell length ( mm )

Figure V.2.11 Daily feeding rates of two size classes of crab (40 and 60 mm CW) fed on four different size groups of S. plana

A aquarium without sand

B aquarium with sand

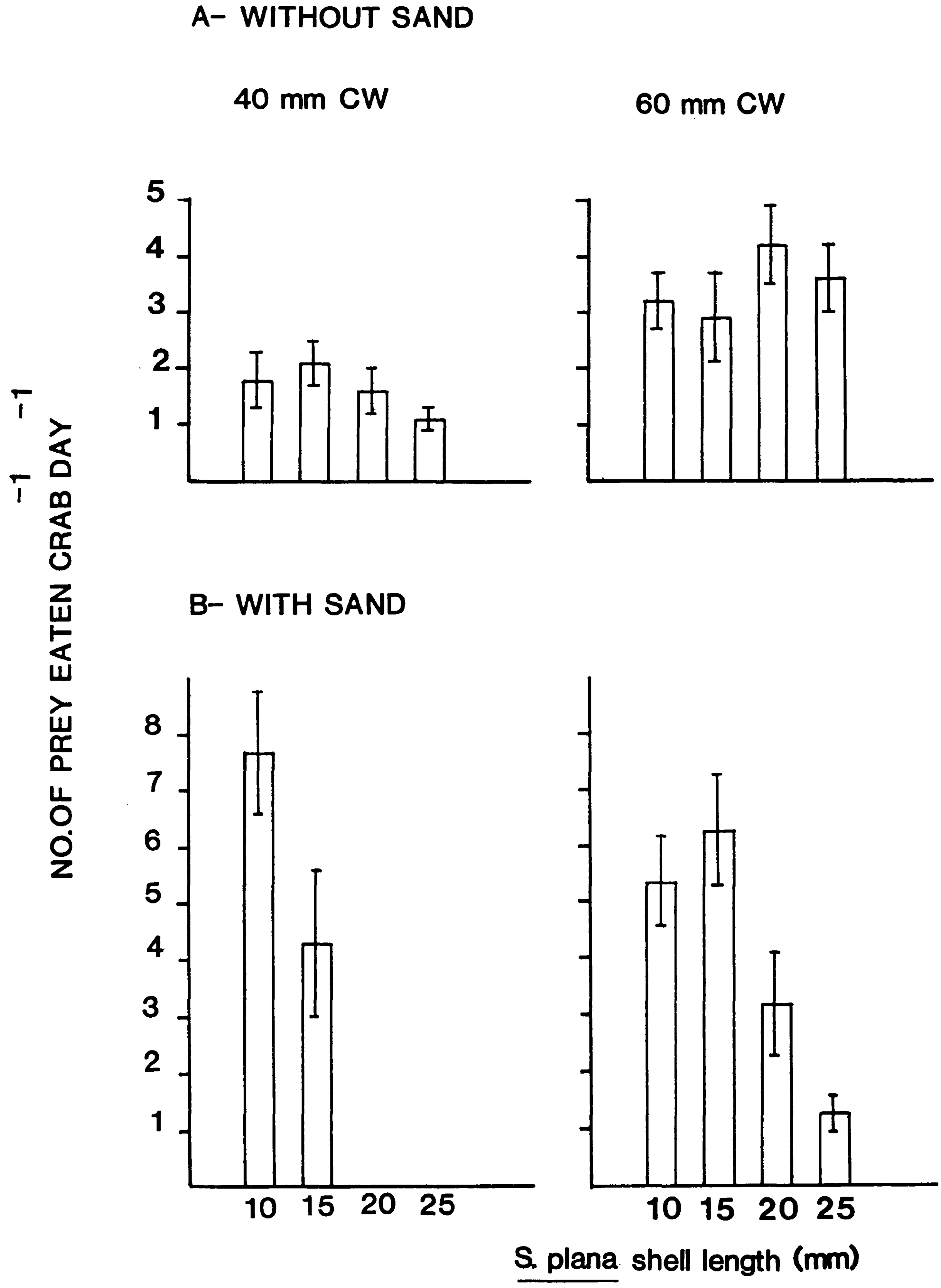

A- WITHOUT SAND
40 mm CW
60 mm CW
5
4
3
2
1
NO.OF PREY EATEN CRAB$^{-1}$ DAY$^{-1}$
B- WITH SAND
8
7
6
5
4
3
2
1
10 15 20 25
10 15 20 25
S. plana shell length (mm)

Figure V.2.12 Daily feeding rates (mean ± SD) for three size classes of crab (40, 50, 60 mm CW) fed on mixed prey of *C. edule* and *M. balthica* (10 mm SL) presented in aquarium

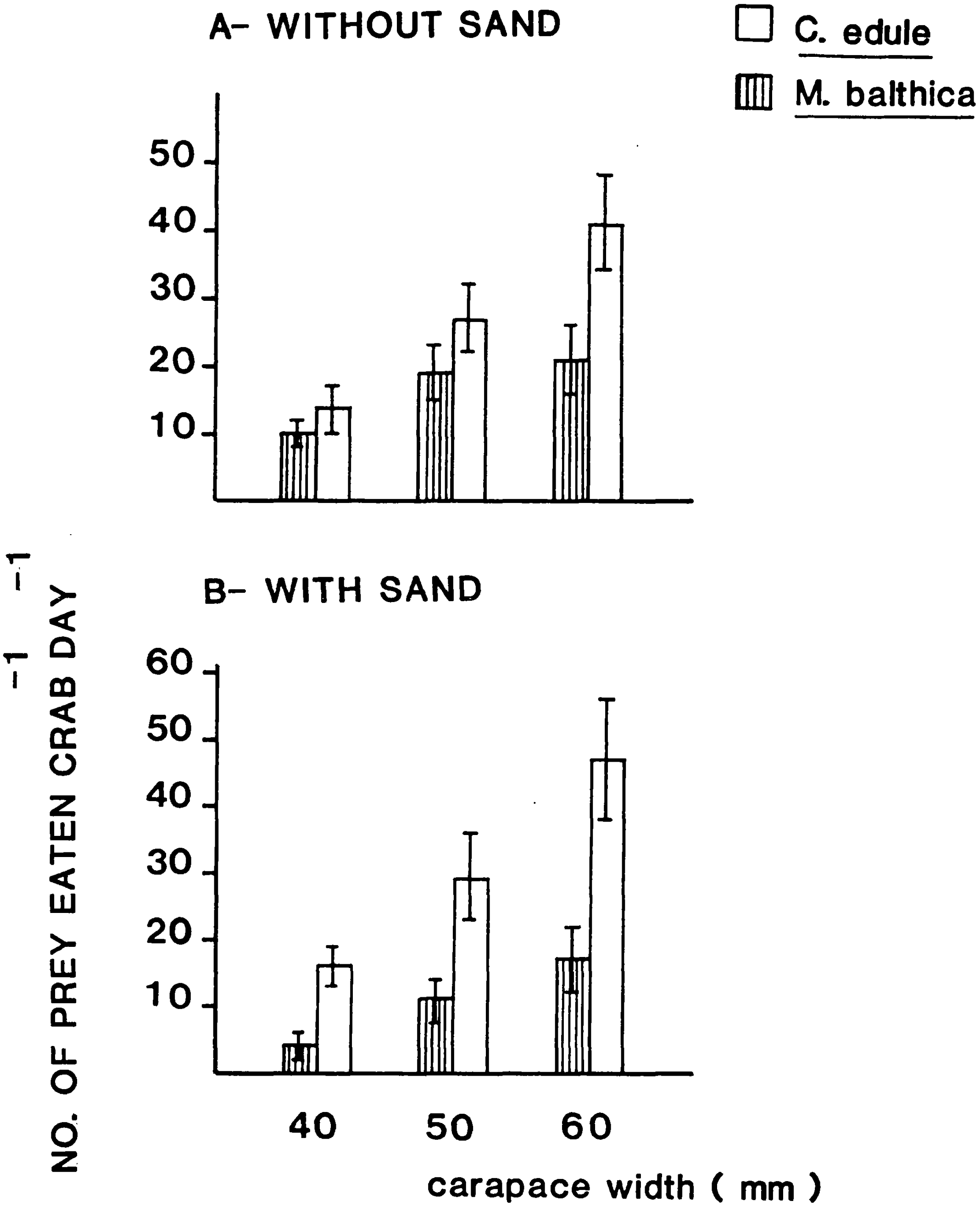
A without sand

B with sand

Figure V.2.13 Daily feeding rates (mean ± SD) for crabs (50 mm CW) fed on mixed prey of *C. edule* and *M. balthica* (12 mm SL) presented in aquarium with and without sand

NS no sand

WS with sand


A- WITHOUT SAND
C. edule
M. balthica
50
40
30
20
10
B- WITH SAND
60
50
40
30
20
10
NO. OF PREY EATEN CRAB$^{-1}$ DAY$^{-1}$
40
50
60
carapace width ( mm )

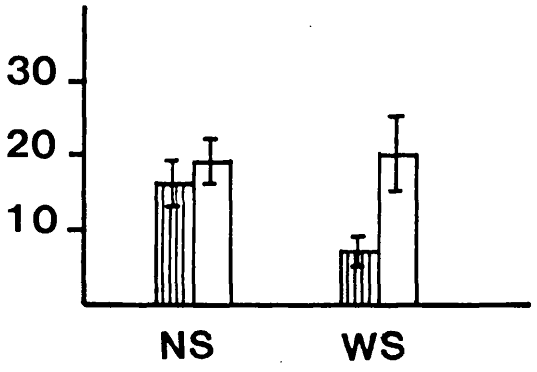

30
20
10
NS
WS

Figure V.2.14 Daily feeding rates (mean ± SD) for 50 mm CW crabs fed on mixed 14 mm SL bivalves (*C. edule*, *M. balthica* and *S. plana*) presented in aquarium without sand (NS) and with sand (WS) in four different combinations

A *C. edule* and *S. plana*

B *C. edule* and *M. balthica*

C *M. balthica* and *S. plana*

D. All three bivalves together

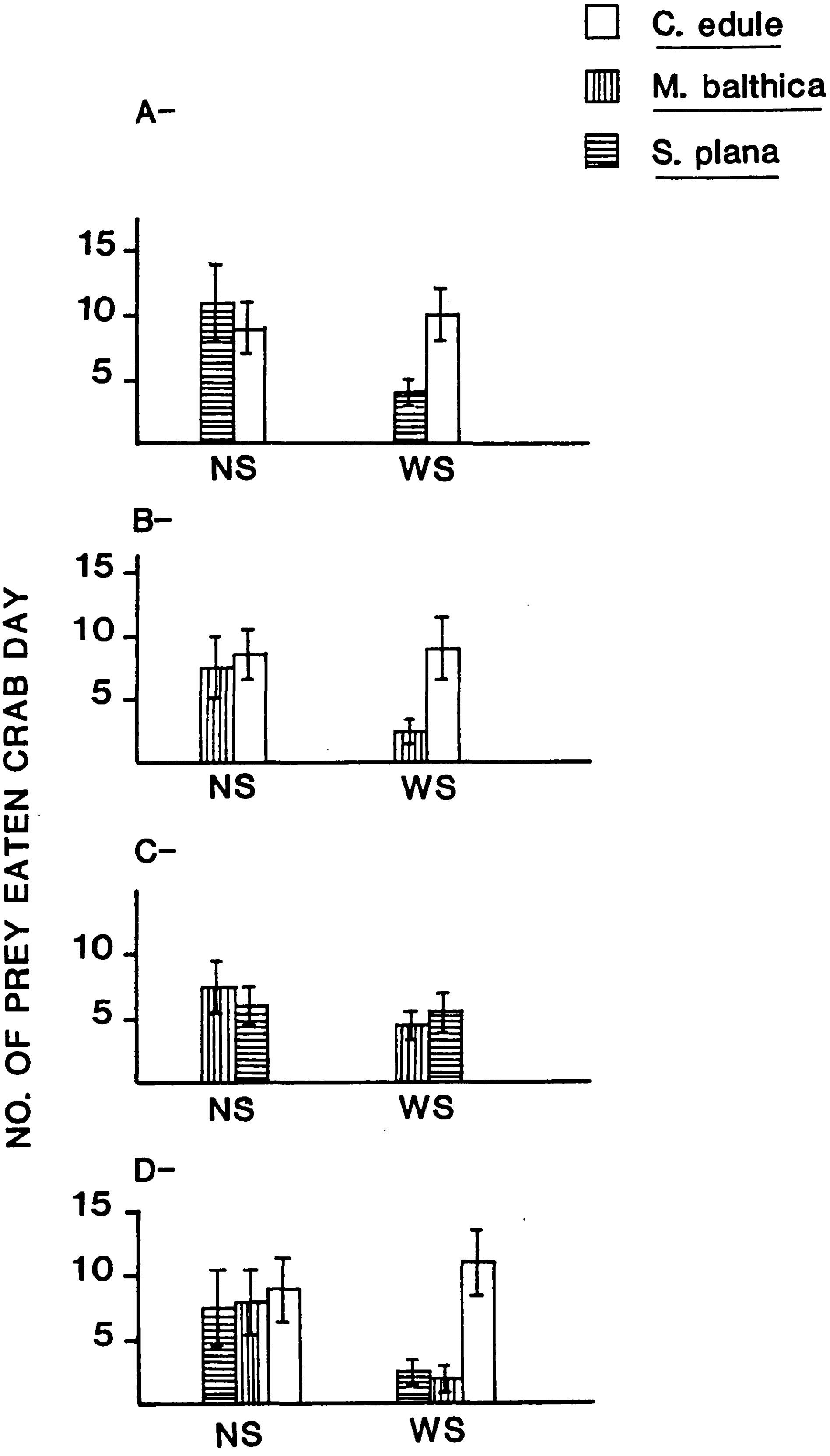

C. edule
M. balthica
S. plana
A–
B–
C–
D–
NO. OF PREY EATEN CRAB⁻¹ DAY⁻¹
15
10
5
NS
WS

Figure V.2.15 Daily feeding rates (mean ± SD) for three size classes of crab (40, 50, 60 mm CW) fed on *C. edule* (10 mm SL) presented in aquarium with and without sand

Figure V.2.16 Daily feeding rates (mean ± SD) for three size classes of crab (40, 50, 60 mm CW) fed on *M. balthica* (10 mm SL) presented in aquarium with and without sand

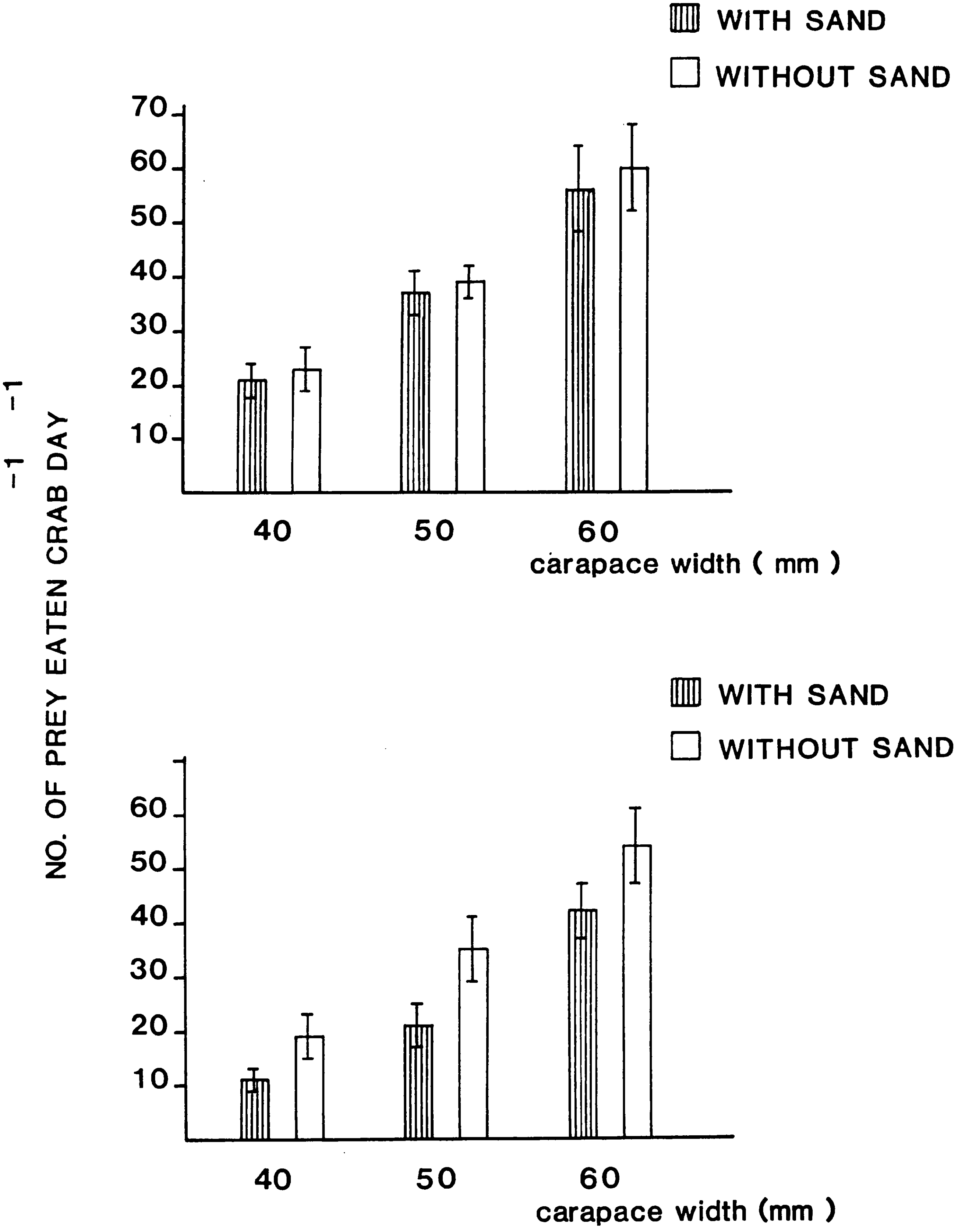

▥ WITH SAND
☐ WITHOUT SAND
70
60
50
40
30
20
10
40
50
60
carapace width ( mm )
NO. OF PREY EATEN CRAB -1 DAY -1
▥ WITH SAND
☐ WITHOUT SAND
60
50
40
30
20
10
40
50
60
carapace width (mm )

Figure V.2.17 Daily feeding rates (mean ± SD) of 50 mm CW crab fed on *C. edule* (12, 14, 16 mm SL) presented in aquarium with and without sand

Figure V.2.18 Daily feeding rates (mean ± SD) for 50 mm CW crab fed on *M. balthica* (12, 14, 16 mm SL) presented in aquarium with and without sand

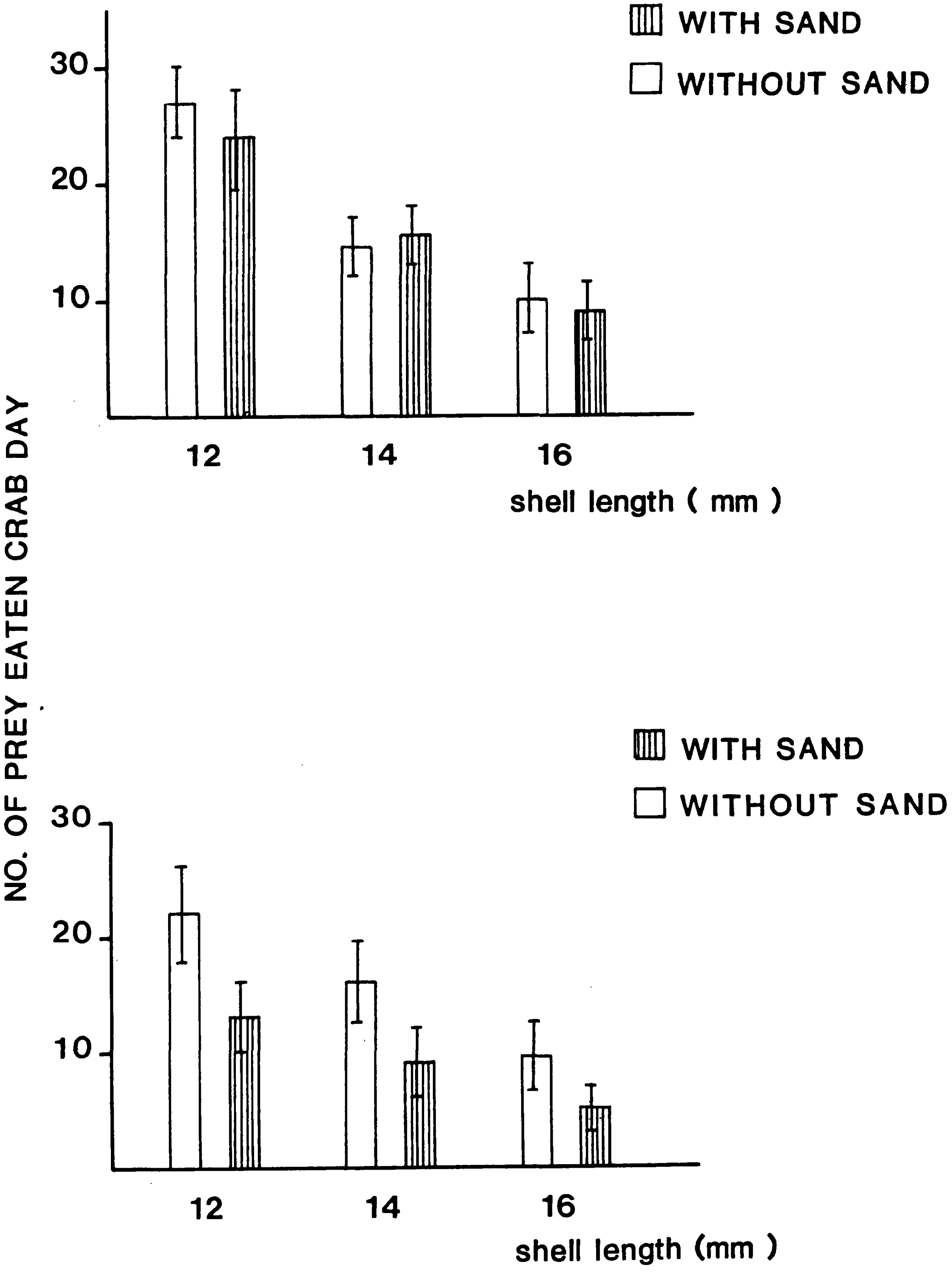

▥ WITH SAND
☐ WITHOUT SAND
30
20
10
12
14
16
shell length ( mm )
NO. OF PREY EATEN CRAB$^{-1}$ DAY$^{-1}$
▥ WITH SAND
☐ WITHOUT SAND
30
20
10
12
14
16
shell length (mm )

Figure V.2.19 Daily feeding rates (mean ± SD) for three size classes of crab (40, 50, 60 mm CW) fed on different size groups (10, 15, 20 mm SL) of *S. plana* presented separately in aquarium with and without sand

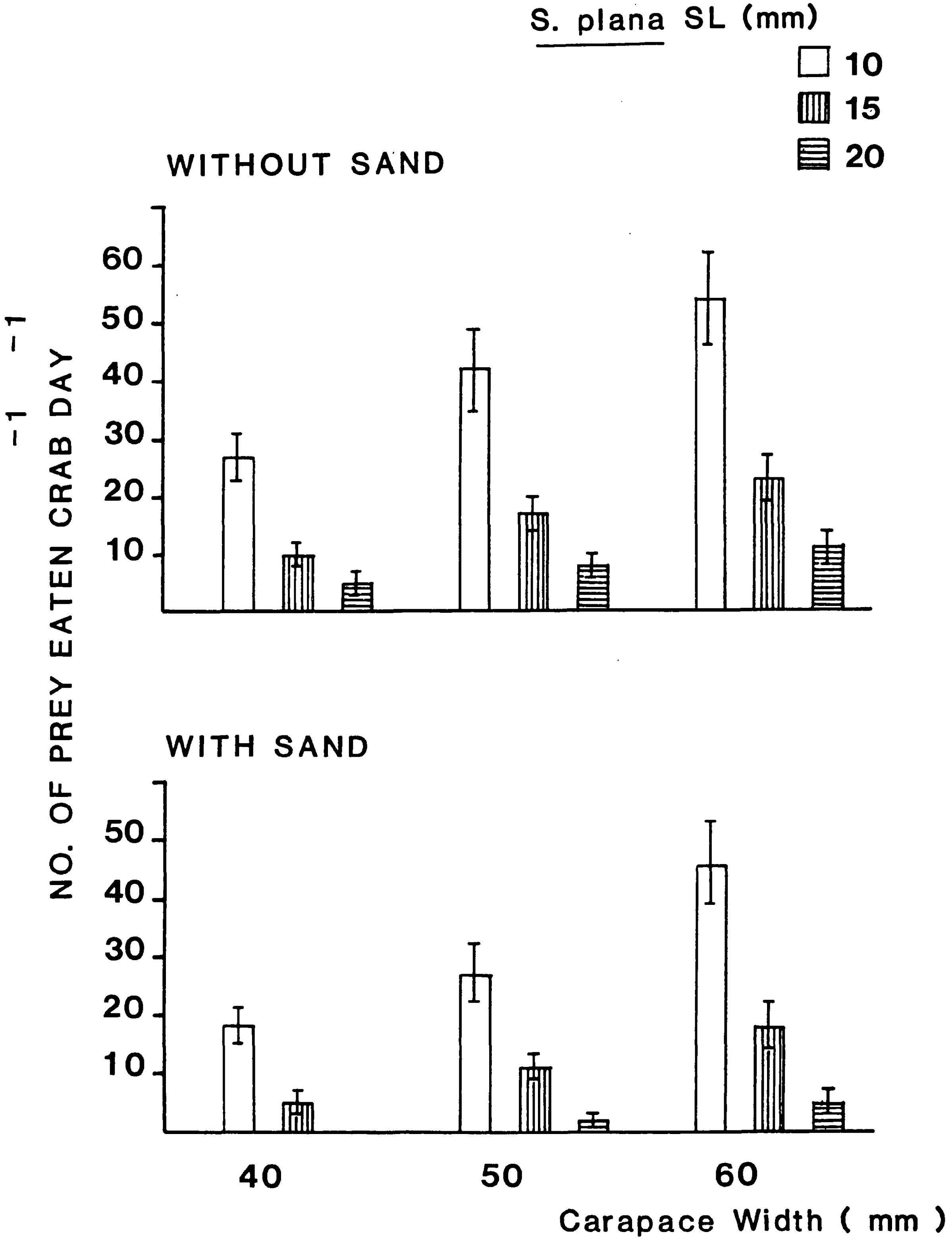

S. plana SL (mm)
10
15
20
WITHOUT SAND
WITH SAND
NO. OF PREY EATEN CRAB -1 DAY -1
60
50
40
30
20
10
40
50
60
Carapace Width ( mm )

Figure V.2.20 Numbers of cockles (12 mm SL) required to satiate crabs (50 mm CW) starved for different lengths of time. Data are means with SD. Corresponding figures of dry weight are shown on the opposite scale

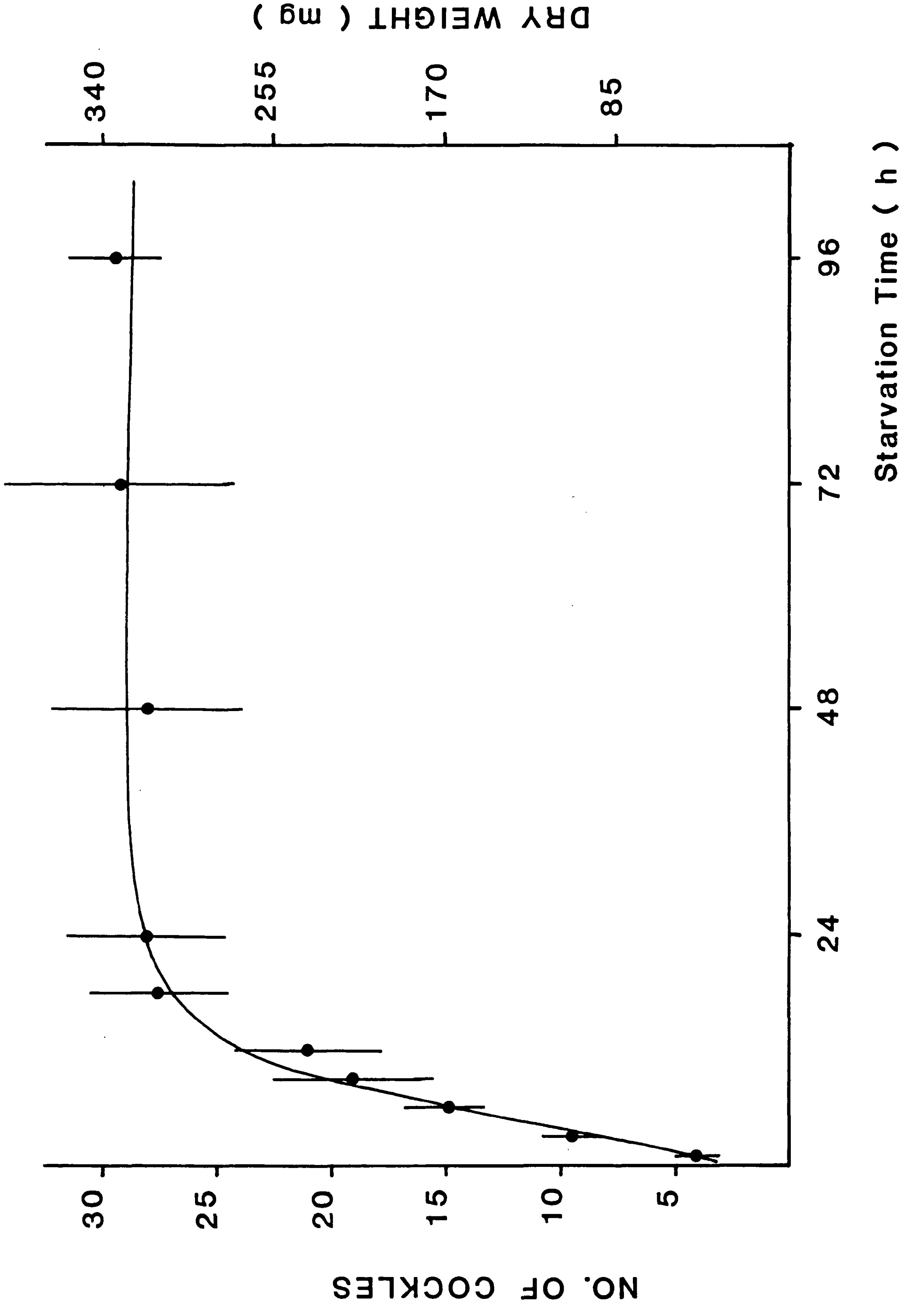
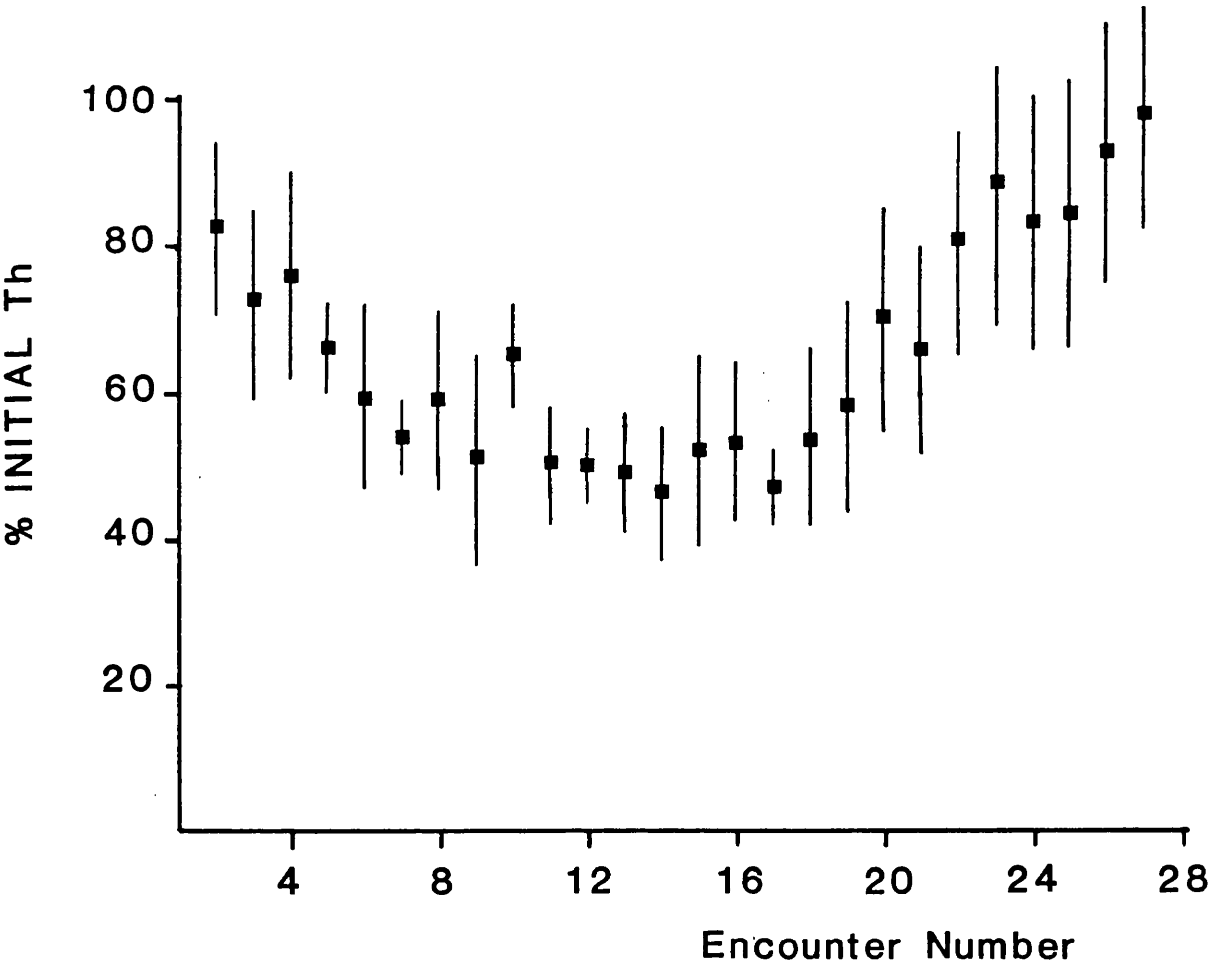

DRY WEIGHT ( mg )
340
255
170
85
NO. OF COCKLES
30
25
20
15
10
5
24
48
72
96
Starvation Time ( h )

Figure V.2.21 Mean handling time with standard deviations for successive cockles eaten, expressed as percentage of the handling time for the first prey encountered

Figure V.2.22 Number of *C. edule* (12 mm SL) eaten by 50 mm CW crab in each 10 minute interval till satiation


% INITIAL Th
100
80
60
40
20
4
8
12
16
20
24
28
Encounter Number

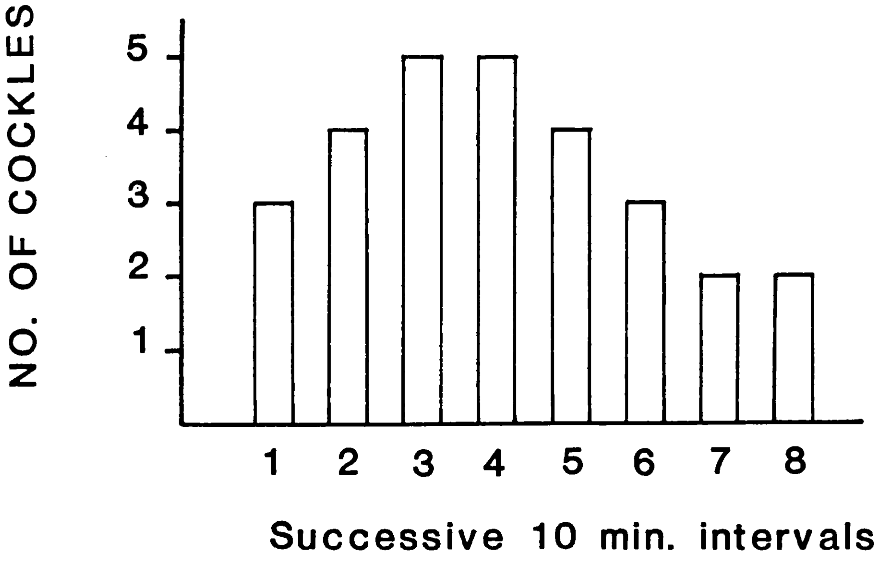

NO. OF COCKLES
5
4
3
2
1
1
2
3
4
5
6
7
8
Successive 10 min. intervals

Figure V.2.23 Relation between prey value and size selection for three size classes of crab

● 40 mm CW

▲ 50 mm CW

○ 60 mm CW

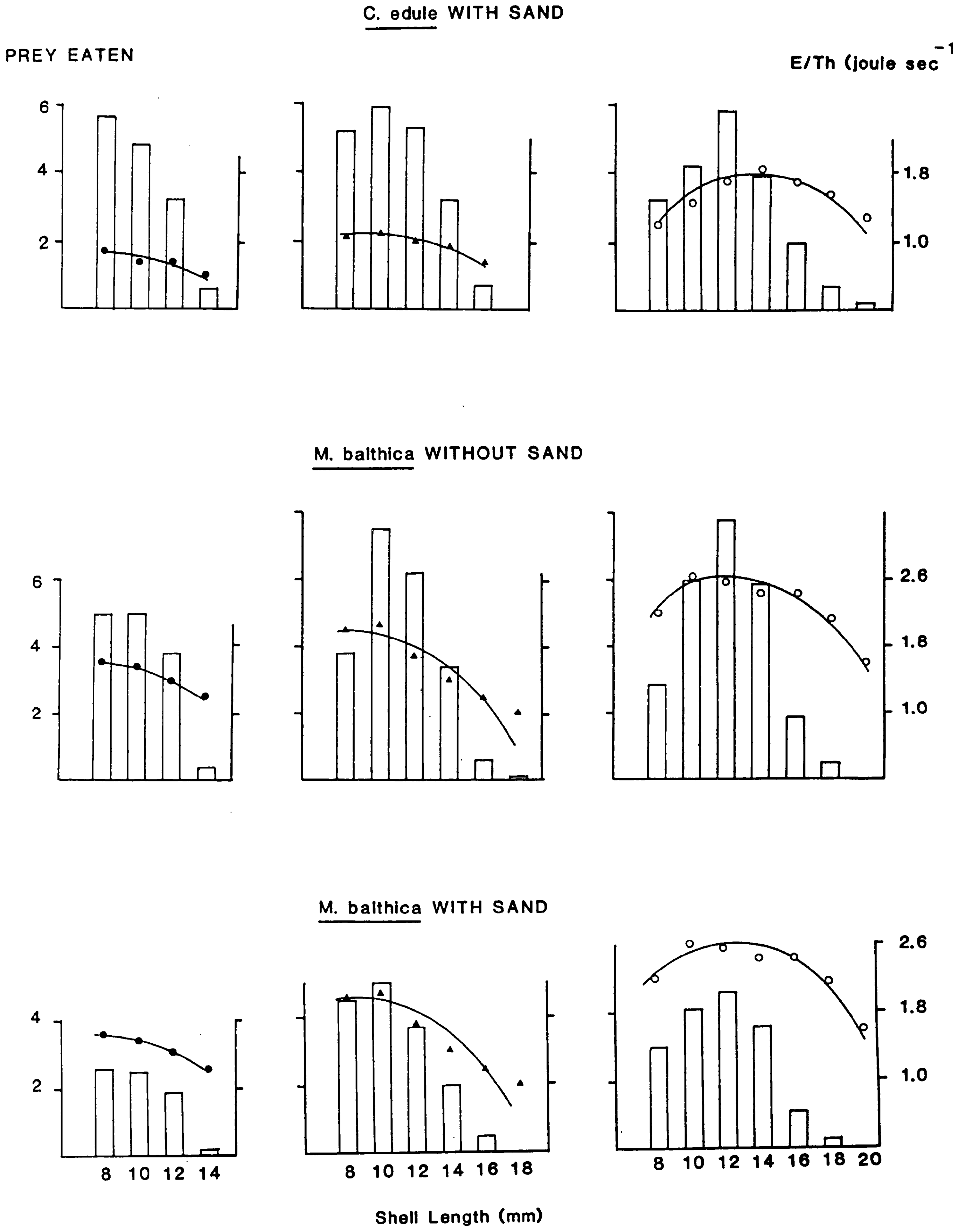

C. edule WITH SAND
PREY EATEN
E/Th (joule sec$^{-1}$
6
4
2
1.8
1.0
M. balthica WITHOUT SAND
6
4
2
2.6
1.8
1.0
M. balthica WITH SAND
4
2
2.6
1.8
1.0
8 10 12 14
8 10 12 14 16 18
8 10 12 14 16 18 20
Shell Length (mm)

Table V.2.1 Result of the bivalve burrowing depth
Figures shown are means ± SD

| Shell length | Bivalve | | |
|---|---|---|---|
| (mm) | C. edule | S. plana | M. balthica |
| 8 | 2 ± 0.7 | 18 ± 2 | 20 ± 2 |
| 10 | 3.4 ± 1.1 | 23 ± 2 | 28 ± 4 |
| 12 | 3.6 ± 1 | 26 ± 3 | 31 ± 3 |
| 14 | 4.2 ± 2 | 32 ± 5 | 37 ± 5 |
| 16 | 5.1 ± 3 | 39 ± 6 | 43 ± 7 |
| 18 | 6.2 ± 2 | 51 ± 5 | 52 ± 5 |
| 20 | 6.9 ± 3 | 57 ± 4 | 56 ± 6 |
| 25 | 7.8 ± 2 | 72 ± 5 | - |
| 30 | 8.3 ± 3 | 87 ± 6 | - |

Table V.2.2 Spot values of energy content in the flesh (dry weight) of three bivalve species, *C. edule*, *M. balthica* and *S. plana*

| Bivalve | Energy content | |
|---|---|---|
| | 500 mg (kJ) | 1 mg (joules) |
| *C. edule* | 10.4 | 20.8 |
| *S. plana* | 11.71 | 23.42 |
| *M. balthica* | 11.97 | 23.94 |

Table V.2.3 Dry weight (W) in mg and energy content (E) in joules for different size groups of the three bivalve species

| Bivalve shell length | C. edule | | M. balthica | | S. plana | |
|---|---|---|---|---|---|---|
| (mm) | W | E | W | E | W | E |
| 8 | 4.3 | 89 | 6.0 | 144 | 3.7 | 87 |
| 10 | 7.0 | 146 | 9.3 | 223 | 5.4 | 126 |
| 12 | 11.6 | 241 | 14.3 | 342 | 7.8 | 183 |
| 14 | 19.4 | 404 | 22.0 | 527 | 11.2 | 262 |
| 16 | 32.2 | 670 | 34.0 | 814 | 16.1 | 377 |
| 18 | 53.5 | 1113 | 52.4 | 1254 | 23.1 | 541 |
| 20 | 88.7 | 1845 | 80.7 | 1932 | 33.3 | 780 |

Table V.2.4 Percentage of each size group of prey in the diet of three size classes of crab fed daily on different size groups of M. balthica

| M. balthica SL (mm) | Carapace width of crab | | | | | |
|---|---|---|---|---|---|---|
| | 40 mm CW | | 50 mm CW | | 60 mm CW | |
| | NS | S | NS | S | NS | S |
| 8 | 35 | 36 | 17.5 | 28.6 | 11.5 | 18 |
| 10 | 35 | 35 | 35 | 31.8 | 24 | 24.5 |
| 12 | 27 | 26 | 29 | 23.5 | 31.5 | 27.5 |
| 14 | 3 | 3 | 15.5 | 12.7 | 23.5 | 21.5 |
| 16 | | | 2.5 | 3 | 7.5 | 6.5 |
| 18 | | | 0.5 | 0 | 2 | 2 |

S Sand present

NS No sand present

Table V.2.5 Number of cockles (14 mm SL) eaten by 50 mm CW crab monitored at different intervals on three types of containers: A = PVC; B = Glass trough with rough bottom; C = glass trough

| Surface type | Time interval (minutes) | No of cockles eaten | Mean ± SD |
|---|---|---|---|
| A | 30 | 59 | 7.37 ± 3.1 |
| | 60 | 16 | 2.0 ± 1.0 |
| | 90 | 4 | 0.5 ± 1.0 |
| | 120 | 1 | 0.12 ± 0.3 |
| | Total | 80 | 10 ± 2.6 |
| B | 30 | 46 | 5.75 ± 1.8 |
| | 60 | 21 | 2.6 ± 2.0 |
| | 90 | 5 | 0.62 ± 0.9 |
| | 120 | 4 | 0.5 ± 0.8 |
| | Total | 76 | 9.5 ± 2.4 |
| C | 30 | 41 | 5.1 ± 3.4 |
| | 60 | 15 | 1.87 ± 1.0 |
| | 90 | 9 | 1.1 ± 1.1 |
| | 120 | 5 | 0.62 ± 0.7 |
| | Total | 70 | 8.7 ± 3.4 |

Table V.2.6 Clearance rate of soft tissue and shell fragments from the crab fore-gut

Water temperature 16°C
+ presence, - absence

| Time after feeding (hours) | Soft tissue | Shell fragments | State of stomach |
|---|---|---|---|
| 1 | + | + | Full |
| 3 | + | + | Nearly full |
| 6 | + | + | 75% full |
| 12 | + | + | 50% full |
| 18 | - | + | Nearly empty |
| 24 | - | + | Empty apart from a few shell fragments |
| 36 | - | - | Empty |
| 48 | - | - | Empty |
| 72 | - | - | Empty |

Table V.2.7 Time elapsed between feeding and defaecation

F Faeces (sometimes incorporating shell fragments)
SF Shell fragments present in the faeces

| Time after feeding (hours) | Crab 1 F | Crab 1 SF | Crab 2 F | Crab 2 SF | Crab 3 F | Crab 3 SF | Notes |
|---|---|---|---|---|---|---|---|
| 1 | - | - | - | - | - | - | No faeces or shell fragments |
| 3 | - | - | - | - | - | - | " |
| 6 | - | - | - | - | - | - | " |
| 12 | + | - | + | - | + | + | Few fragments in the faeces |
| 24 | ++ | ++ | ++ | ++ | ++ | ++ | Many fragments |
| 36 | ++ | + | ++ | + | ++ | - | Few fragments |
| 48 | + | + | + | - | + | - | Fewer fragments |
| 72 | + | - | + | - | + | - | Faeces without shell fragments |
| 96 | + | - | + | - | + | - | |

# SECTION VI

# FIELD EXPERIMENTS ON PREDATOR EXCLUSION

## VI.1 INTRODUCTION

It is now generally recognised that predation is an essential component of the biological interations which determine species abudance in natural communities. Connell (1972) reviwed studies on its evaluation in field conditions on rocky shores. A review of predation studies using cages in mud flat communitites was given by Peterson (1979).

In many studies designed to evaluate predation by crabs and other aquatic predators on infaunal communities in soft sediments, cages were mainly used to exclude the predators (Reise, 1977a and b; Virnstein, 1978; Holland _et al_, 1980). Other workers designed experiments either to exclude or include predators in the cages (Virnstein, 1977; Botton, 1984). However, in British waters, caging studies have been conducted on epifaunal molluscs only, either by including crabs in the cages (Ebling _et al_, 1964) or excluding them (Davies _et al_, 1980; Cunningham, 1983).

Excluding predators from soft sediments generally leads to an increase not only in the abundance of fauna, but also of species richness (Peterson, 1979).

Although there are many problems involved in conducting caging experiments in the field, it is generally agreed that they are a valuable tool in the study of ecological relationships, particularly the role of predation (Virnstein, 1978).

Studies conducted on the cockle population in the Burry Inlet by MAFF, clearly showed the role of the avian predator, the oyster-catcher, (_Haematopus ostralegus_) on _C. edule_. It was responsible for the sharp decline in the density of second winter cockles ( $\approx$ 23 mm SL) during the cold months (Davidson, 1967). Furthermore, field experiments designed to exclude oyster-catchers by fencing some areas showed that the loss of second winter cockles in the fenced areas was greatly decreased (Hancock and Urquhart, 1965).

In the present study, stomach contents analysis of adult crabs indicates that cockles are an important food item in their diet (see Section IV), while laboratory experiments showed that crabs feed mainly on small size cockles ($< 20$ mm SL). Adult crabs usually visit the intertidal area of the Inlet (where the cockle beds and other bivalves are present) under cover of water throughout the year except in the cold months (Section III). Stomach contents analysis of the flounder Platichthys flesus (L.) in the Inlet showed that these flat fish also constitute a source of predation for small cockles during the summer months (Hancock and Urquhart, 1965).

The principal purpose of this section is to examine the effect of predator exclusion on the abundance of small cockles in the cockle beds during the time when potential predators, such as crabs and fish, are present.

## VI.2 MATERIALS AND METHODS

Predator exclusion experiments were conducted in two different areas of the Burry Inlet. The first area (Area 1) was near the centre of the commercial cockle beds at Llanrhidian Sands and the second (Area 2) was near Salthouse Point (see map, Fig. VI.1)

A preliminary survey was conducted in both the areas prior to the caging experiments in order to choose the most appropriate site to set up the cages. The experiment at Area 1 will be described first.

### Area 1

At Llanrhidian Sands, two replicate sites (A and B) were used for the experiments, separated from each other by approximately 100 metres. These replicate sites had been used several years previously for a different scientific study. It was convenient to use these two sites as they were well-chosen as typical examples of the environment and cockle population. Each site was well-marked by large posts enclosing a square with sides of nearly 6 metres. Four different treatments were used at each site as shown in Table VI.1.

Cages measuring 200 x 200 x 30 cm in height were constructed of galvinised weld mesh over aluminium posts (Fig. VI.2). The 70 cm legs and 15 cm of the bottom edge of the sides (types 1 and 2) were driven into the sediment with a hammer to keep the cages in place and to prevent predators from digging under them. Similar posts were used to mark the corners of type 4 treatment which provided the control. Cages here were set up on 24 April 1983. This was before settlement of cockles had started. The site and the cages in their position are shown in the photograph (Plate VI.1). The population of cockles at both sites (A and B) was sampled near the cages first on 24 April 1983 (the date the cages were established) and later, on 24 August 1983, following the main summer spatfall period. For various reasons the caged populations were not subsampled during the course of the experiment. The cages were not designed for repeated opening and reclosing. Furthermore, the experiment was designed to study only long-term effects. The experiment at site A was terminated on 24 October 1983 and that at site B on 25 November 1983. Sampling was carried out by taking five 0.1 $m^2$ quadrats to a depth of 5 cm for each treatment.

### Area 2

This was a brief experiment conducted at Salthouse Point taking advantage of an abundance of small cockles there. Five similar cages were set up, spaced out from each other by approximately 15-20 metres. Each cage measured 100 x 100 x 30 cm in height with 70 cm legs. They were all covered with one type of mesh (2.4 cm). All five cages were set up in the area on 15 August 1983. This experiment was terminated for two cages on 26 October 1983 and for the other three cages on 22 November 1983. The object of ending on different dates was to determine the influence of predator exclusion over a short term (2 and 3 months). Sampling was made at the beginning of the experiment and at the end. When the experiment was terminated, four quadrats of 0.1 $m^2$ were taken outside and inside the cages to a depth of 5 cm. Control samples (outside the cages) were taken 2 metres away from the cage in each direction. Sampling inside the cages was away from the edge sides by about 10-15 cm.

The contents of each sample were washed on site through a 2.0 mm sieve and kept in separate polythene bags. In the laboratory, the bivalves were counted and their shell length measured to the nearest 1 mm using Vernier calipers.

During the time of the experiment, visits were undertaken at least monthly to check the state of the cages and to remove any seaweeds or other materials fouling the 'Weldmesh' netting.

Terminal differences in the density of cockles outside and inside the cages at Salthouse Point were analysed using Student's t test. For the data of the Llanrhidian Sands experiments, the F test was applied first and then significant results were analysed further using the Newman-Keules multiple range test (Zar, 1974).

## VI.3 RESULTS

Area 1

The size frequency histograms in Figure VI.3 indicate that settlement of cockles spat occurred after the cages had been set up at Llanrhidian Sands. On 26 April 1983 the peak for cockles smaller than 20 mm SL was 15 and 16 mm (site A and B respectively), while it was 12 mm on 24 August 1983. The cohort of small cockles (1982 spatfall) seen in April had grown to merge with the larger cockles by August. There is a clear increase in the density of cockles at both sites between April and August. Numbers of cockles per $m^2$ increased at site A from 1108 to 2278 and from 2018 to 3140 at site B.

When the experiment was terminated at site A on 24 October 1983, after the cages had been in place for six months, the total density of cockles in the cage with fine mesh was significantly greater ($P < 0.05$) than the other three treatments (Fig. VI.4). The mean ± SD of cockles in type 1 cage was 2442 ± 330 per $m^2$, 1852 ± 220 in type 2, 1378 ± 300 in type 3 and 1168 ± 390 in the control. More cockles were found in type 2 than type 3 and the control ($P < 0.05$), but no significant difference was recorded between the density of the control and type 3 ($P > 0.05$).

When the experiment was terminated at site B on 25 November 1983 a similar result to that of site A was found, but with slightly higher densities. In type 1 cage the density of cockles (± SD) was 3278 ± 208 per $m^2$, while it was 2534 ± 126 in type 2, 1814 ± 117 in type 3 and 1866 ± 112 outside the cages in the control area.

Area 2

During the time of the experiment at Salthouse Point a general increase in the modal size from 11 mm in August to 13 mm in October and November is shown in Figure VI.5.

Figure VI.6 shows that cockles are more abundant inside than outside the cages. On 26 October 1983 the mean and standard deviation was 2054 ± 591 cockles per $m^2$ inside and only 1416 ± 322 outside the cages ($P < 0.01$). The corresponding figures for November, after the cages had been in place for more than three months, were 2062 ± 408 cockles per $m^2$ in the cages and only 1276 ± 348 in the uncaged area ($P < 0.01$).

The mortality of vulnerable small cockles (up to 20 mm SL) in the different types of treatment at the end of the experiment is shown in Table VI.2. It is clear that the loss was greater in the control (treatment 4) and the cages with a gap (treatment 3). It reached a maximum of 78% after the cages had been in place for seven months at site B. A minimum loss (1%) was recorded in the fine mesh cage at Salthouse Point after three months of the experiment. However, this last result might be slightly spurious, it is possible that further settlement of spat occurred that autumn (above the base line value).

## VI.4 DISCUSSION

Physical changes to the habitat caused by the cage, such as sedimentary modifications can be a factor affecting the ultimate fauna density in this type of experiment (Virnstein, 1978). Indeed, Hulberg and Oliver (1980) in their study on the abundance of polychaetes, concluded that the high density recorded inside their cages was due to the deposition of sediment which attracted the mobile polychaetes to invade the cage. In the case of the C. edule such locomotory activity is presumably not possible.

No analysis of the sediment was made during the present study, but observations indicated only very limited accumulation inside the cages at Salthouse Point (2-3 cm), and no visible changes inside the large cages at Llanrhidian Sands. The large size of cages used in the experiment ($4m^2$ at Llanrhidian Sands) may have reduced the problem of sedimentation. Holland et at (1980) and Botton (1984) reported a negative correlation between cage size and sedimentation.

The accumulation of drifted seaweed on the cages is another matter which can be expected to increase the physical effects of the cages. In the present study, the problem was noticed mainly in the late summer-autumn. Davies et al (1980) constructed weed barriers to capture drifted weed and minimise the problem but that could affect the predators' movement. Reise (1977b) avoided fouling problems by adding several periwinkles Littorina littorea to each cage which removed all diatoms and other settling algae by grazing preferably on the mesh.

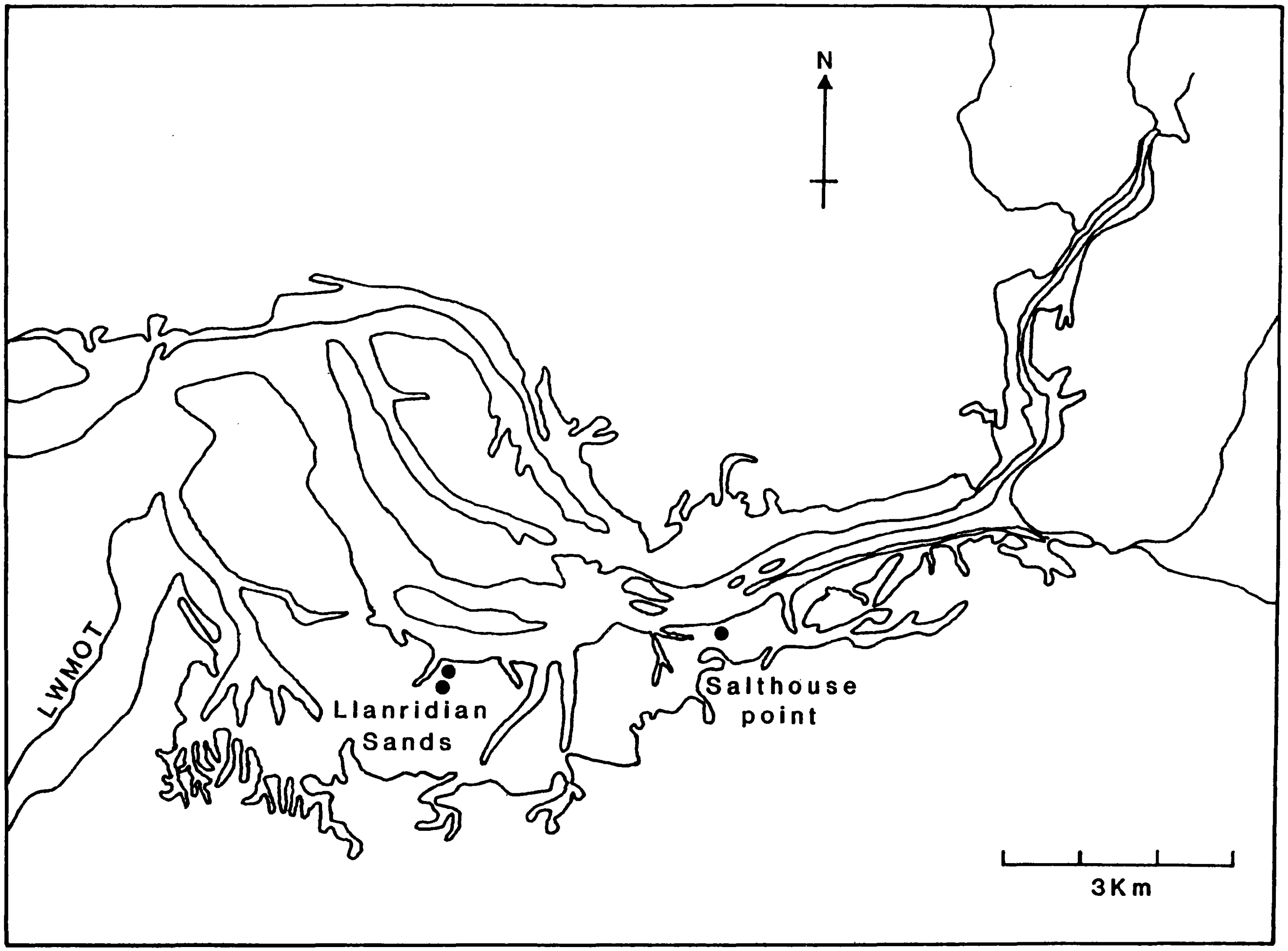
As the results of this study show, a large increase of cockles was recorded inside the cages at all sites. The cages with fine mesh (designed to exclude all potential predators) showed higher abundance of cockles than the other three treatments and reached twice the density of the control. However, the cages with coarse mesh (designed to permit the crabs only) protected more cockles than the control situation and in the cage with reduced sides. It is possible that crabs may be deterred by netting whose mesh is large enough for them to enter and this then leads to underestimating their foraging impact. More study is needed on the bahaviour of predators (crabs and fish) when they encounter a cage.

The lack of significant difference shown between the control and the unsided cages (designed to exclude birds) indicates that they had little effect on the density of cockles in that area on this occasion.

In his study on the growth of C. edule in the field, Orton (1926) reported that C. maenas is a great enemy of small cockles. The feeding experiments in the present study and the results of their natural diet suggested that shore crabs are a serious predator on brood cockles. However, the damage caused to small cockles by fish still needs to be clarified.

There are different ways of interpreting the loss of cockles in the different treatments (Table VI.2). It is clear that the fine mesh cage, as expected, excluded all the different predators and so helped to increase the survivorship of the cockles. If the coarse mesh cage (treatment 2) worked as designed, it shows that crabs contribute to the mortality of cockles but to a small degree and a larger contribution is probably due to fish. However, if the crabs were deterred by the coarse mesh, as they may have been, their contribution to the young cockle mortality was underestimated.

Figure VI.1 The sites of the cages at Llanrhidian Sands and Salthouse Point


N
LWMOT
Llanridian
Sands
Salthouse
point
3Km

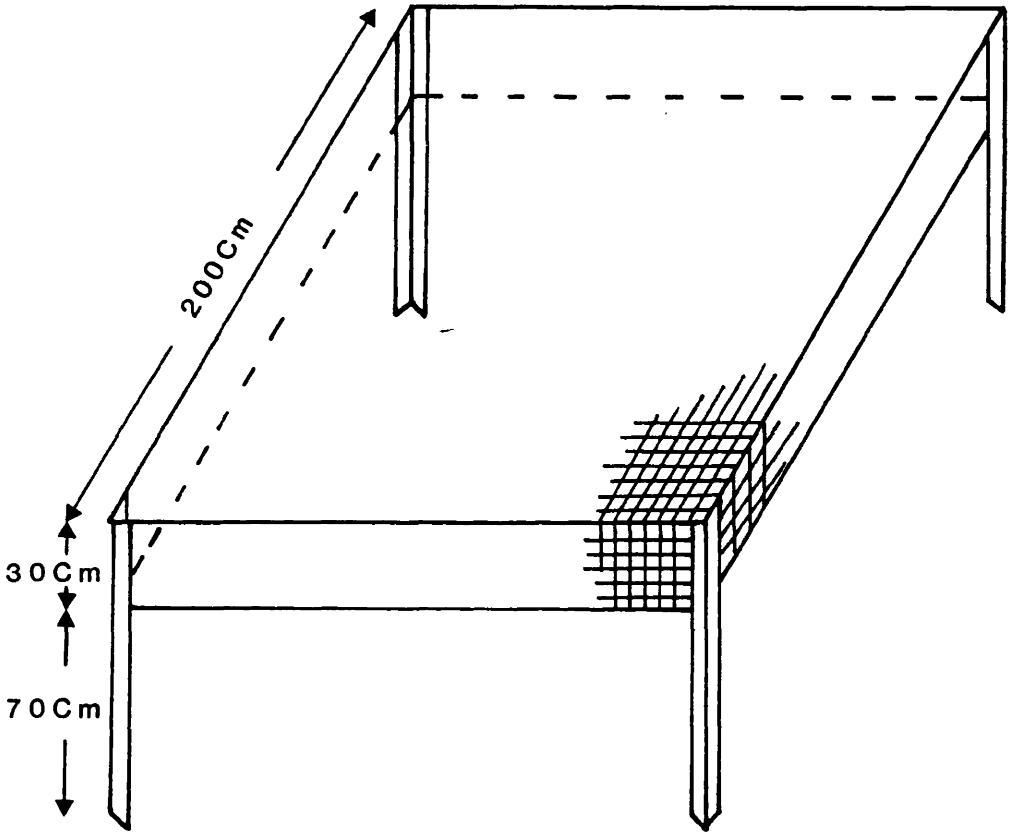


Figure IV.2 Shape of the cage used to exclude predators.
Dimensions in the figure for cages at Llanrhidian Sands

Figure VI.3 Size-frequency histograms for cockles sampled at Llanrhidian Sands (sites A and B) on different sampling dates and when the experiment was terminated. The four different treatments are:

a Control

b. Cage with coarse mesh and reduced side walls

c Cage with coarse mesh

d Cage with fine mesh

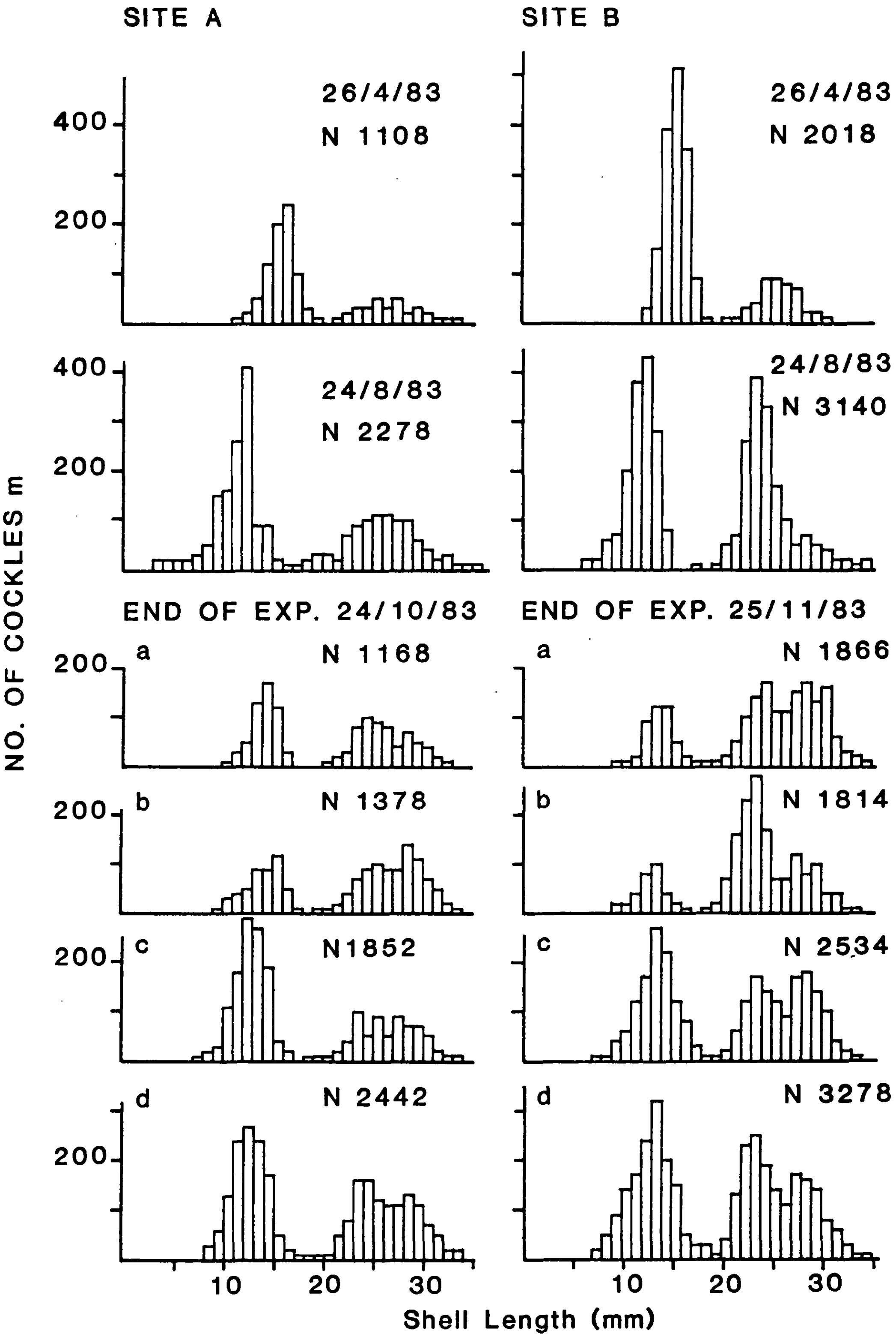

SITE A
SITE B
26/4/83
N 1108
26/4/83
N 2018
24/8/83
N 2278
24/8/83
N 3140
END OF EXP. 24/10/83
END OF EXP. 25/11/83
a
N 1168
a
N 1866
b
N 1378
b
N 1814
c
N1852
c
N 2534
d
N 2442
d
N 3278
400
200
NO. OF COCKLES m⁻²
10
20
30
Shell Length (mm)

Figure VI.4 Means ± SD for total density of cockles per $m^2$ at Llanrhidian Sands (sites A and B). Values are shown for the different treatments when the experiment was terminated

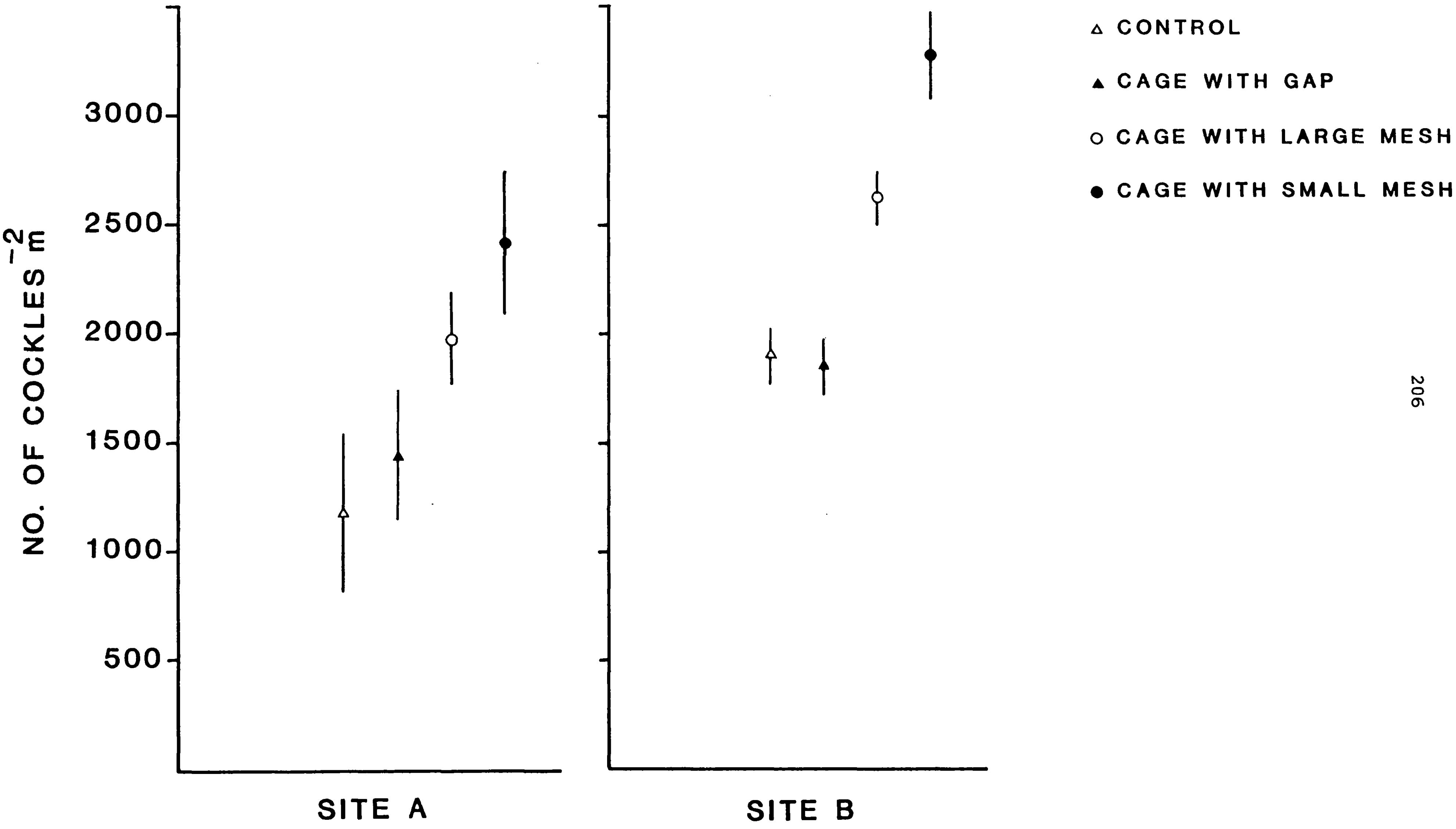

NO. OF COCKLES $m^{-2}$
3000
2500
2000
1500
1000
500
SITE A
SITE B
△ CONTROL
▲ CAGE WITH GAP
○ CAGE WITH LARGE MESH
● CAGE WITH SMALL MESH

Figure VI.5 Size-frequency of cockles on different sampling dates in the caged and uncaged area at Salthouse Point

C caged UC uncaged

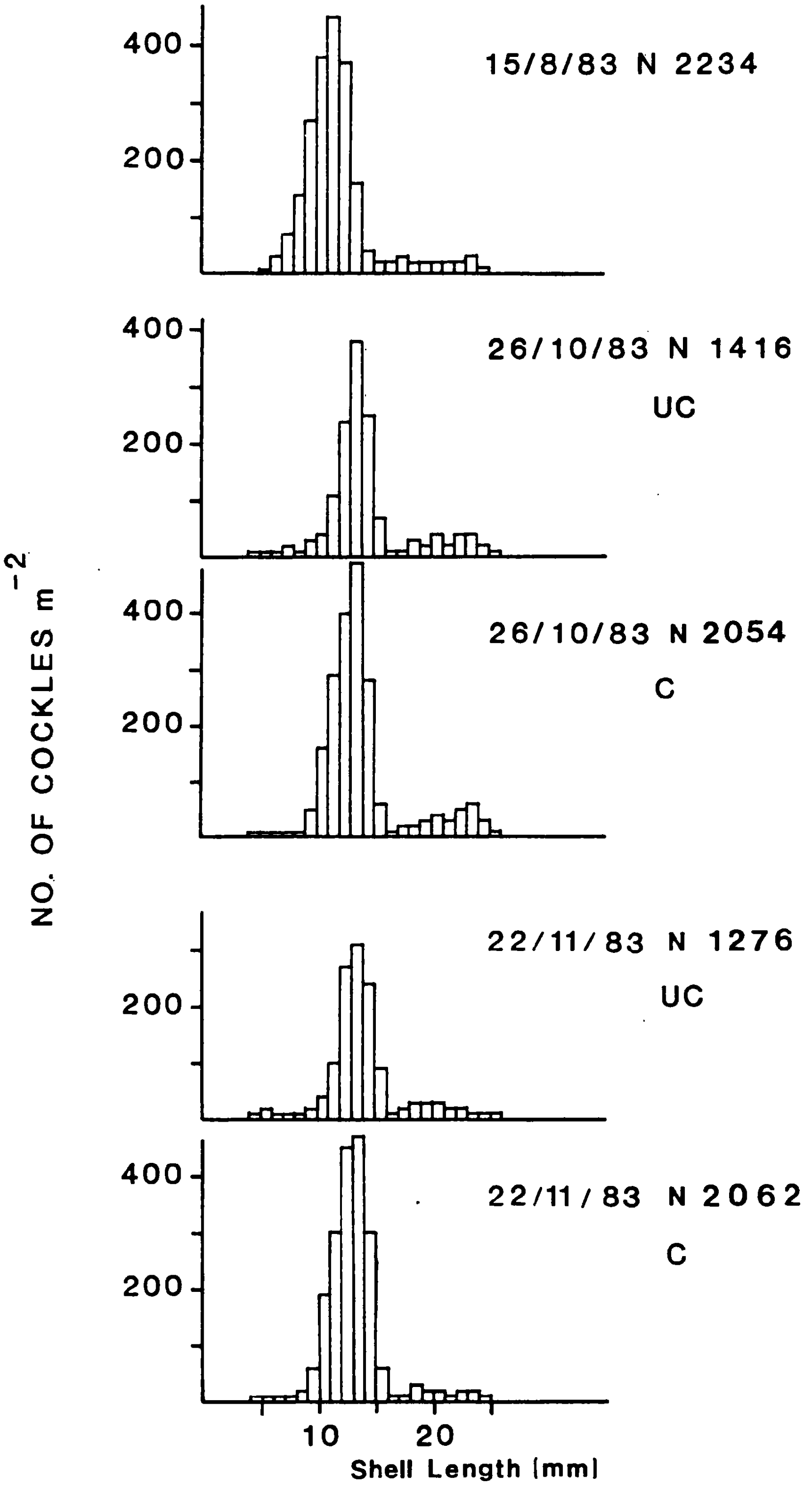

400
200
15/8/83 N 2234
400
200
26/10/83 N 1416
UC
400
200
26/10/83 N 2054
C
200
22/11/83 N 1276
UC
400
200
22/11/83 N 2062
C
NO. OF COCKLES m$^{-2}$
10
20
Shell Length (mm)

Figure VI.6 Means ± SD for total density of cockles per $m^2$ at Salthouse Point. Values are shown for sampling at the beginning of the experiment and then from caged and uncaged areas when the experiment was terminated

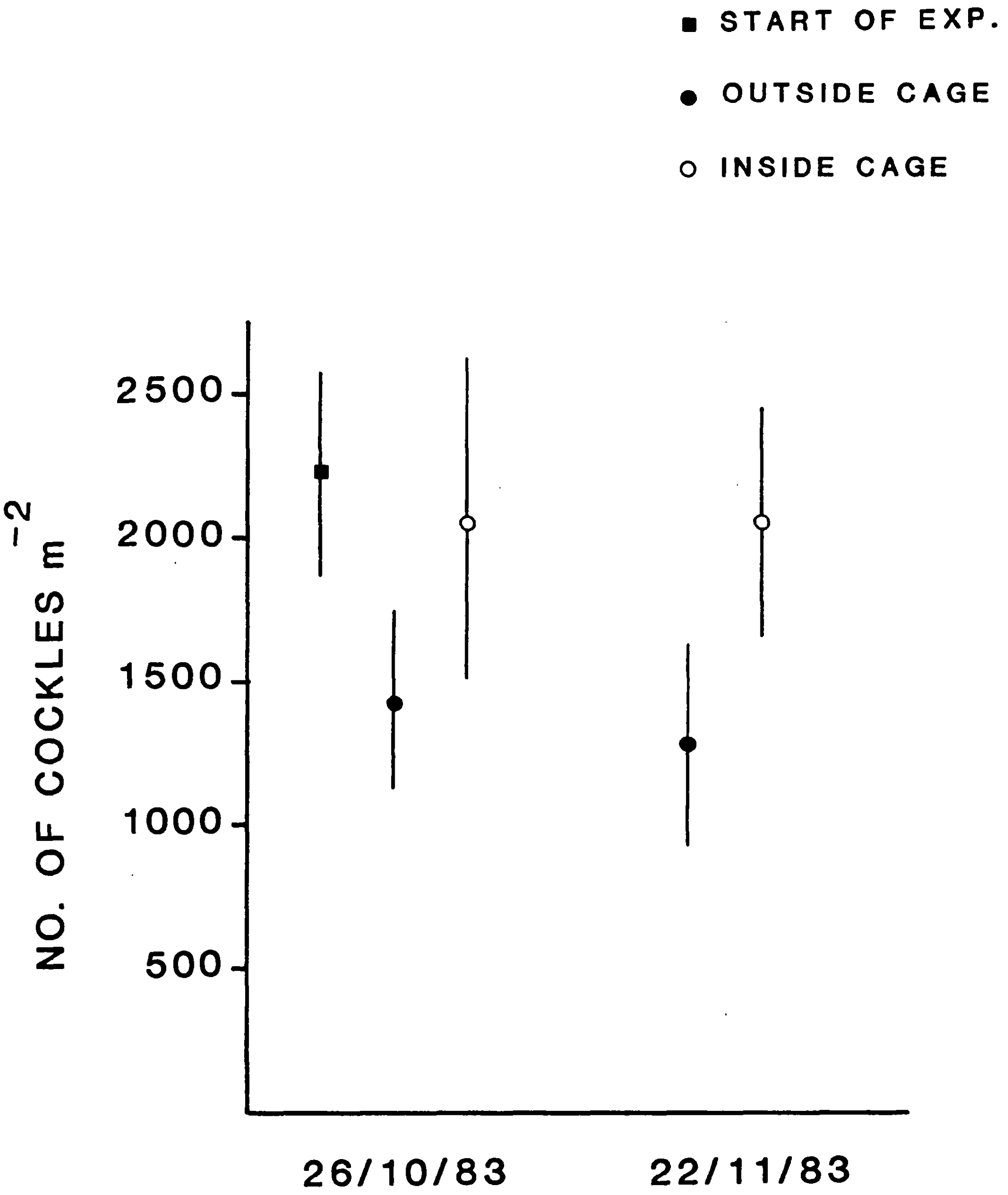

■ START OF EXP.
● OUTSIDE CAGE
○ INSIDE CAGE
NO. OF COCKLES m⁻²
2500
2000
1500
1000
500
26/10/83
22/11/83

Table VI.1 Cage experiments at two replicate sites at Llanrhidian Sands

| Type of treatment | Purpose |
|---|---|
| 1. Cage with 2.4 cm mesh | To exclude all migratory crabs and other predators. |
| 2. Cage with 5 cm mesh | To permit entry of most crabs but to exclude fish and birds. |
| 3. Cage with 5 cm mesh and reduced side walls | To permit entry to predators such as crabs and flat fish but to exclude most wading birds. |
| 4. Uncaged area (control) | To allow access for all potential predators including birds. |

Table VI.2 Mortality (%) of cockles (up to 20 mm SL) in the different treatments at the end of the caging experiment. For details of the four treatments see Table VI.1

| Area | Date and treatment | No of cockles per $m^2$ | Loss | % | No of cockles lost per $m^2$ per day |
|---|---|---|---|---|---|
| Llanrhidian Sands | 24.08.83 | 1417 (base line) | | | |
| Site A | 24.10.83 | | | | |
| | 1 | 1250 | 167 | 12 | 2.8 |
| | 2 | 1174 | 243 | 17 | 4.1 |
| | 3 | 482 | 935 | 66 | 15.6 |
| | 4 | 548 | 869 | 61 | 14.5 |
| Site B | 24.08.83 | 1580 (base line) | | | |
| | 22.11.83 | | | | |
| | 1 | 1512 | 68 | 4 | 0.8 |
| | 2 | 1152 | 428 | 27 | 4.7 |
| | 3 | 354 | 1226 | 78 | 13.6 |
| | 4 | 410 | 1170 | 74 | 13.0 |
| Salthouse Point | 15.08.83 | 2014 (base line) | | | |
| | 26.10.83 | | | | |
| | caged | 1882 | 132 | 6.5 | 1.9 |
| | control | 1282 | 732 | 36 | 10.5 |
| | 24.11.83 | | | | |
| | caged | 1996 | 18 | 1 | 0.2 |
| | control | 1215 | 799 | 40 | 8.0 |

Plate VI.1 Site B at Llanrhidian Sands where the different cages are in position. The main channel is visible in the background.

# SECTION VII

# GENERAL DISCUSSION AND CONCLUSION

It is immediately clear that the assumptions made at the outset of this study were largely justified. The Burry Inlet has been demonstrated to support a considerable population of Carcinus maenas which are active predators of the bivalve populations for the greater part of the year.

The number of specimens an individual crab could find and open of the different bivalve species was investigated and vulnerability of the various age groups considered. An approximate assessment of the overall impact of this predation on the bivalves in general and individual species in particular can now be made.

Various provisos need to be borne in mind. For instance, it is apparent that the Burry Inlet is far from uniform and most bivalve species are patchy in their distribution which could influence the distribution of the crabs. The bivalve distribution patterns are probably governed by sediment type, salinity and tidal level (Poopetch, 1980), but it was not the object of this present study to investigate them. Detailed studies of Cerastoderma distribution (Hancock and Urquhart, 1965) and Mya (Flores, 1983) exist.

Similarly, it is not easy to estimate the total numbers or normal density of the migratory crabs in the Inlet (see Section III.3). However, the results of the different techniques used to estimate the approximate numbers indicated that many crabs invade the intertidal sand flat during the time of high tide throughout the year except the cold months. The most accurate method of estimating crab density on the bivalve beds is believed to be direct observation by diving, but due to the uneven habitat and the patchy distribution of the prey, as mentioned earlier, it would need many divers at different sites in the Inlet to gather adequate information on the overall pattern of crab density. It was not possible to carry out such a comprehensive survey during the course of this study. Moreover, the diving studies were confined to day-light hours and trapping results suggest larger numbers of crabs occur at night. Using the best information available, rough calculation of their density (made in Section III.3) suggested an overall average of 0.2 crabs $m^{-2}$ (1 crab per 5 $m^2$) and as many as 0.35 $m^{-2}$ on a cockle bed.

It is clear from previous studies that Carcinus are opportunistic and actively predate whatever prey is most easily available. In the Burry Inlet, they are not restricted to buried bivalves although stomach contents analysis shows that they represent the most important food item in their diet (see Section IV). The seasonal variation in their food demonstrated that availability of alternative prey could result in the shore crab switching between prey types as the abundance of those prey changed. This could relieve predation pressure on the less abundant species.

In the Burry Inlet, crabs feeding intertidally appear to be faced with more food than they need. It was clear that factors other than the food supply were controlling the predator population in the area. So the predators are not food-limited; it is clear that the area contains enough cockles and other bivalves (quite apart from other food sources) to feed far more crabs. However, it is obvious that a very large increase in the number of crabs would be a serious threat to the cockle industry. The factors which limit the shore crabs in the Burry Inlet are not known, but several probable influences are apparent. The study revealed that young crabs occupy nursery areas near HWNT, but there are only a few suitable areas of this sort (Section III.1). It seems likely that the spread of Spartina grass may have destroyed former nursery areas of the crabs. There are stony areas near HWNT where the grass now dominates.

In the laboratory, shore crabs used different techniques to open bivalves and these varied according to the type and the size of the mollusc and correlated to their shell strength (Section V.1).

For any given crab size there was an optimal prey size at which the ratio of prey energy content to handling time was at a maximum. In the laboratory, there was a positive selection by the crabs towards the most profitable size group of the prey. In the case of C. edule and M. balthica this was apparent even when they were buried in sand (in an aquarium). It was observed that crabs included more small specimens in their diet when M. balthica were allowed to burrow in sand. However, crabs would feed randomly on S. plana when offered in plain aquarium; in that case the crabs were capable of breaking easily the whole size range of prey available. On the other hand, when they were allowed to burrow in sediment, the accessibility to crabs was reduced and it seems that the prey value decreased due to the inclusion of digging time in the prey handling time. That is believed to be associated mainly with large bivalves that burrow deeply in sediment. Presumably, it was more beneficial for crabs to feed on the smaller prey that occur near the sand surface as shown clearly in the case of buried S. plana.

The strategy of burrowing behaviour adopted by the bivalves obviously reduced the predation pressure and forced the crabs to forage on the shallow burrowing specimens. Defence mechanisms among bivalves species varied. Individuals of species that live near the sand surface (such as C. edule) attain a size which resists the ability of crabs to open them, while other species with fragile shells (such as S. plana and M. arenaria) reduce predation by burrowing deeply in the sediment. However, M. balthica which occurs not lower than 6 cm below the surface has a strong shell in contrast to the others. When Carcinus are presented with a mixed prey of the same size group of C. edule, M. balthica and S. plana where all are buried in sand, the crabs fed heavily on the shallow burrower, C. edule.

Although S. plana are deep burrowers, it is likely they lose many of their young members in the field by predation until they reach a size able to go deep enough in the sediment away from the accessibility of crabs and other predators such as wading birds and fish. The same is true of M. arenaria (Flores, 1983). Overall, full-grown specimens of all species of bivalve (except M. balthica) are thus immune to crab predation.

The exclosure (or cage) experiment (Section VI) lent circumstantial support to the belief that crabs were at least partly responsbile for the damage to young cockles in the field. More study is needed to show the role of fish as another potential predator.

Unlike the oyster-catcher who prefers second winter cockles (Hancock and Urquhart, 1965), the present study showed that shore crabs feed on first and second summer cockles.

It is difficult to quantify the overall predation pressure of C. maenas on the bivalves in the field. However, it is possible to calculate a likely theoretical maximum value based on the results of laboratory and field observations. It is possible to estimate the number of crabs feeding on a cockle bed such as Llanrhidian ($\approx 3$ km$^2$ as estimated by Davidson, 1967) assuming that crabs are evenly distributed at an average of 0.2 crabs m$^{-2}$ (see Section III.3). The value is around 600,000 crabs. An average size crab (ca. 50 mm CW) consumed daily around 20 cockles (ranged between 8-16 mm SL). Nearly 12 million cockles would be consumed daily. During a period from August to November (ca. 100 days) that number of crabs would be capable of consuming a total number of young cockles around 1,200 million. This would represent 30% of recent mean annual stock (stock estimates suggest that the average number of brood cockles present at Llanrhidian Sands each August is in the order of 4,000 million) (Hancock and Urquhart, 1965). The figure of 1,200 million is based on the assumption that crab density in the feeding area is only 0.2 per m$^2$ and that exclusively cockles are consumed. Higher and lower values are arrived at if other assumptions are made. For instance, a density of 0.35 crabs per $m^2$ was observed by divers on a Cerastoderma bed where there were few Macoma. Using this value the figure of 1,200 million is increased to 2,100 million. On the other hand, if cockles form only 50% of the diet the value would be reduced to 1,050 million. This value is in line with observed depletion of young cockles during that period of the year as reported by Hancock and Urquhart (1965) to be around 1,000 million. The striking agreement between these two figures appears to suggest that the shore crab represents an important predator of young cockles in the area.

(This sort of calculation cannot be made for Macoma and Scrobicularia because there is insufficient information about their population dynamics.)

In their study of the natural mortality of cockle stock, Hancock and Urquhart (1965) were under the impression that only a few adult crabs were present in the area and that these contributed only to a small degree to the summer mortality of cockles. The present study seems to indicate that the predation pressure of crabs on brood cockles is at present more serious than they suggested.

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