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Crab foraging behaviour : prey size and species selection in Carcinus maenas (L.) and Cancer pagurus L.

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Crab Foraging Behaviour: Prey Size and Species Selection in *Carcinus maenas* (L.) and *Cancer pagurus* L.

by

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Summary

This thesis examines the foraging behaviour of *Carcinus maenas* and *Cancer pagurus* when presented with bivalves of contrasting morphology: *Mytilus edulis*, *Ostrea edulis*, *Crassostrea gigas* and *Cerastoderma edule*. Because foraging may be influenced by the relative abundance and morphological characteristics of both predator and prey, these aspects are also considered. Chelal size and strength of these crabs and prey shell shape largely determined handling techniques. When offered a size range of these bivalves individually, crabs attacked all encountered prey but rejected those that remained unbroken after several opening attempts, thus, emphasising the passive nature of their size-selective feeding. When offered paired combinations of mussels, oysters and cockles, larger crabs selected species in the ranked order of their profitability. Species-related preferences exhibited by crabs feeding on prey at or near the optimal size suggest that foraging decisions are partly based on evaluations of overall prey shape and volume, and that shell width constitutes an important feature which crabs recognise and associate with prey value.

Variations in crab strength relative to size accounted for most intra-specific differences in foraging behaviour. Juvenile *C. maenas* are limited in their choice of prey size, and are thus less species-selective. Adult *C. maenas* are not so constrained, and exhibit a higher degree of species-selectivity. *C. pagurus* possesses powerful monomorphic chelae that operate at higher mechanical advantage than the chelae of *C. maenas*, and readily crushed larger mussels relative to their size. Differences in prey size selection between crab species varied with the species of prey offered, suggesting that certain shell features of these bivalves constitute effective barriers to even the powerful chelae of *C. pagurus*. These results are relevant in the context of aquaculture, since predatory impact on commercially reared bivalves might be reduced by combining different prey species that offer predators alternative or preferred sources of food.

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Chapter 1

General Introduction

Predator-prey systems in the marine environment have been extensively studied (e.g. Crayford & Goss-Custard, 1990; Egglestone, 1990a ; Hall *et al.*, 1990; Lee & Kneib, 1994; Paine, 1976), and increasing knowledge regarding these systems has become a major objective in ecological ocean sciences. Predation is known to be an important factor structuring marine populations and communities (Kent & Day, 1983; Raffaelli *et al.*, 1989; Virnstein, 1977). High diversity and species richness in certain assemblages can be related to predation (Leber, 1985; Paine, 1966) and several characteristics including life-history traits are thought to have evolved as a result of predation pressure (Blundon & Kennedy, 1982b; Seed, 1986b; Seed & Brown, 1978; Vermeij, 1980).

As shellfisheries and culture have developed, it has become essential to assess the potential impact of predation on the structure and dynamics of commercially important populations (Beukema, 1991; Castagna & Kraeuter, 1977; McKenzie, 1970). Information on this topic can be used to improve culture strategies of certain species (Bisker & Castagna, 1987; Gibbons & Castagna, 1985; Murdoch *et al.*, 1985), whilst a better understanding of the relationships between populations and their dynamics is needed for a more rational exploitation of marine natural resources.

Crab species have attracted considerable attention because of their importance as major predators of commercially exploited species including mussels (e.g. Dare & Edwards, 1976; Kitching *et al.*, 1959), oysters (e.g. Egglestone, 1990b; Menzel & Hopkins, 1955), clams (Arnold, 1984; Menzel *et al.*, 1976), and scallops (e.g. Lake *et al.*, 1987), and constitute themselves a resource of considerable economic value (Edwards, 1979). Their wide geographical distribution and abundance in coastal areas of the world's oceans (Ingle, 1980; Williams, 1984), as well as their easy manipulation and maintenance in captivity, have contributed to make crabs ideal subjects for laboratory-based investigations.

There have been many studies concerning the feeding ecology of several families of brachyuran crabs e.g. *Portunidae* (Blundon & Kennedy, 1982a, Choy, 1986; Haddon & Wear, 1987; Hill, 1976; Seed, 1990), *Cancridae* (Boulding & Hay, 1984; Juanes & Hartwick, 1990; Lawton, 1989; Yamada *et al.*, 1993), *Xanthidae* (Hughes, 1989; Lin, 1990; Seed, 1980), and *Calappidae* (Hughes & Elner, 1989), and a wide variety of aspects have been extensively documented. These have included detailed descriptions of crab chelal morphology and biomechanics, particularly in relation to the handling techniques used by crabs when feeding on different types of prey (e.g. Brown *et al.*, 1979; Lee & Seed, 1992; Rheinallt & Hughes, 1985). Studies on the impact of crab predation on prey populations (e.g. Menge, 1978; Sanchez-Salazar, 1986; Seed, 1982) and the ecological and evolutionary responses to such interactions are also numerous (e.g. Arnold, 1984; Bertness & Cunningham, 1981; Boulding, 1984; Cornell, 1976). However, much of the work in the last two decades has focused on the foraging strategies and behavioural mechanisms underlying prey selection (Kneib, 1995). Crab foraging behaviour and its predictability by mathematical models has been a recurrent topic in recent research (e.g. Bernstein *et al.*, 1991), and many authors have attempted to relate their findings to Optimal Foraging Theory (OFT; Hughes, 1980; for critical review see Pyke, 1984). According to this theory, crabs are expected to select the most valuable of alternative prey, taking the less valuable only when the opportunity for choice becomes limited (Hughes, 1979; Pyke *et al.*, 1977). The currency used to predict prey value in the classical version of the model is net rate of energy intake or profitability, defined as the yield of flesh per unit of handling time (Charnov, 1976), although alternative currencies, such as energetic efficiency (i.e. the ratio of energy gained to energy lost) have been suggested by other authors (Juanes & Hartwick, 1990). Prey value defined in this way does not involve differences in the metabolic cost associated with different handling activities (Elner & Hughes, 1978). Thus, handling time has a complex variation related to the morphological and ecological characteristics of the prey, and profitability curves must be obtained empirically for each predator-prey combination (Hughes, 1980).

A review of the research on the selective behaviour of a wide variety of brachyuran crabs feeding on hard-shelled prey showed that results of experiments often have been in close, but never total, agreement with the predictions of OFT (Juanes, 1992). In attempting to explain these disparities, four major contending models have appeared in the literature over the last two decades: (1) chelal wear (Juanes, 1992; Juanes & Hartwick, 1990); (2) prey-evaluation (Elner & Hughes, 1978); (3) relative stimulus (Jubb *et al.*, 1983); and (4) mechanical selection (Elner & Hughes, 1978; Lawton & Hughes, 1985; Rheinallt, 1986). Hughes and Seed (1995) provided a detailed discussion of the models in the light of the present and published data, and concluded that they are not mutually exclusive. Moreover, by combining features of the mechanical selection and relative-stimulus models, they propose a key-stimulus model of crab foraging behaviour that accounts for the entire range of observed trends in prey selection by crabs. In addition, the key-stimulus model is not inconsistent with either the chelal wear model or the energy-maximisation premise. The authors suggest that the lack of perfect agreement between results of prey selection experiments and theoretic predictions would be expected if crabs, instead of precisely evaluating prey, respond to a relatively simple set of key stimuli that are strongly, yet imperfectly related with profitability. Supporting this hypothesis are the results of a theoretical work on the rules of thumb for predation hazard assessment. Bouskila and Blumstein (1992) found that there is a 'zone of tolerance' where inaccurate perceptions perform just as well as perfect knowledge of predation hazard. This implies that animals need not have perfect, but only sufficient information, in order to behave optimally.

The mechanisms by which crabs obtain and evaluate information from a particular prey item constitutes an important aspect of crab foraging behaviour studies. In order to comply with OFT, individual decisions on whether to attack a prey item must be based in part on the ability to recognise prey characteristics which correlate with profitability, defined as the potential energy yield per unit of handling time. Mechanisms of prey recognition are relatively well understood amongst visual hunters such as fish (e.g. Croy & Hughes, 1991b; Kislalioglu & Gibson, 1976). Non-visual hunters such as crabs, on the other hand, have been the subject of comparatively few works relating these mechanisms to optimal feeding behaviour (e.g. Kaiser *et al.*, 1993). Both extrinsic factors such as stimuli from other encountered prey (Jubb, *et al.*; 1983), patchiness in prey distribution (Lawton & Hughes, 1985), intra- and inter-specific competition (Kaiser *et al.*, 1990), and risk of predation (Hughes & Seed, 1981); and intrinsic factors such as hunger (Wallace, 1973), experience (Cunningham, 1983), chelal strength and morphology (Lee & Seed, 1992), as well as prey shape, architectural design, and fracture resistance (Boulding & LaBarbera, 1986) can influence decisions at various moments during the foraging bout. It is important, therefore, to identify the nature of prey characteristics related to profitability in order to fully understand how optimal selection is achieved.

Whilst most research has been dedicated to the study of the feeding behaviour of adult crabs, very little information has been published regarding juveniles. Not only is

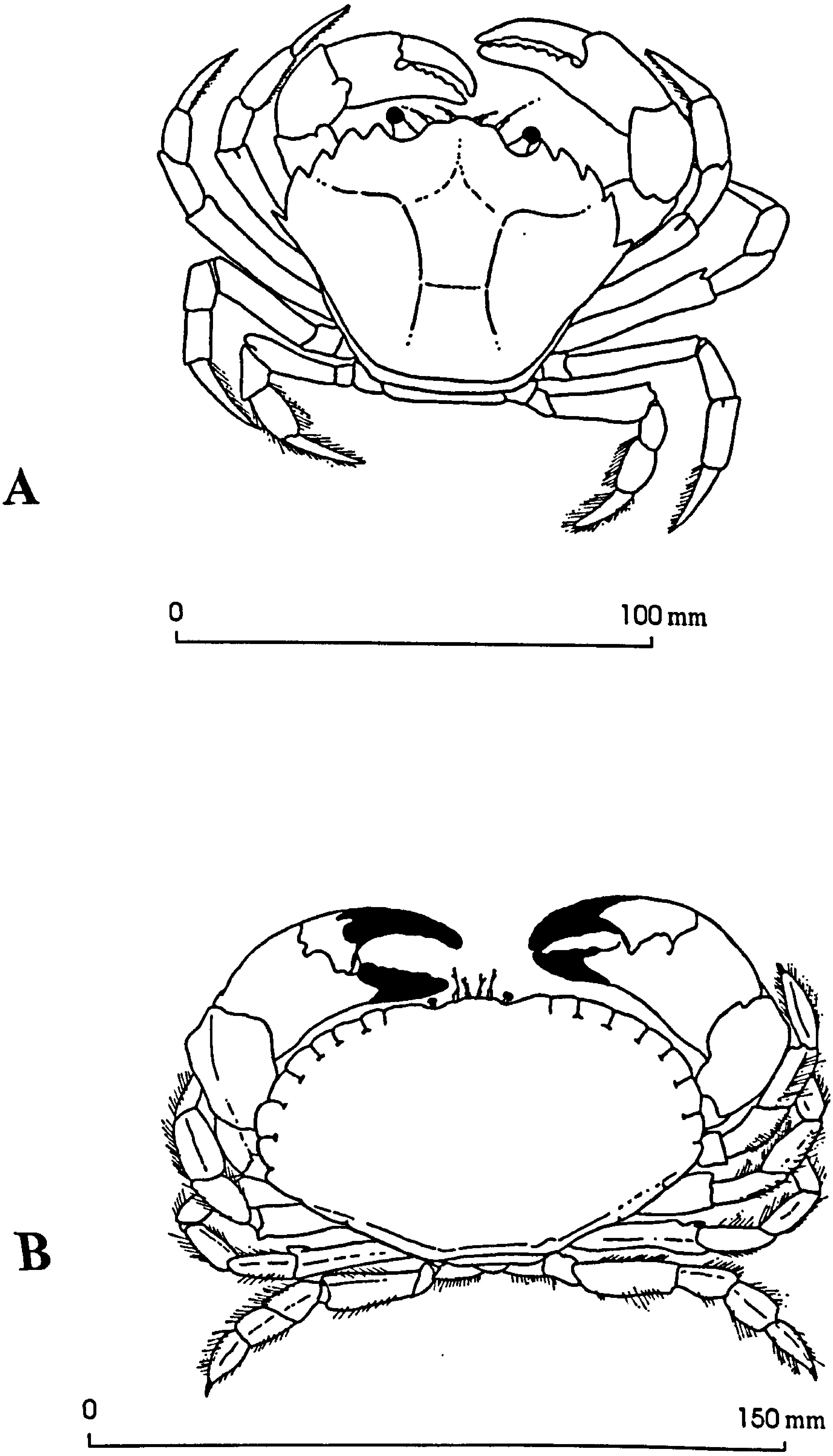


Figure 1.1. The common shore crab, *Carcinus maenas* (Linnaeus) (A) and the European edible crab, *Cancer pagurus* Linnaeus (B).

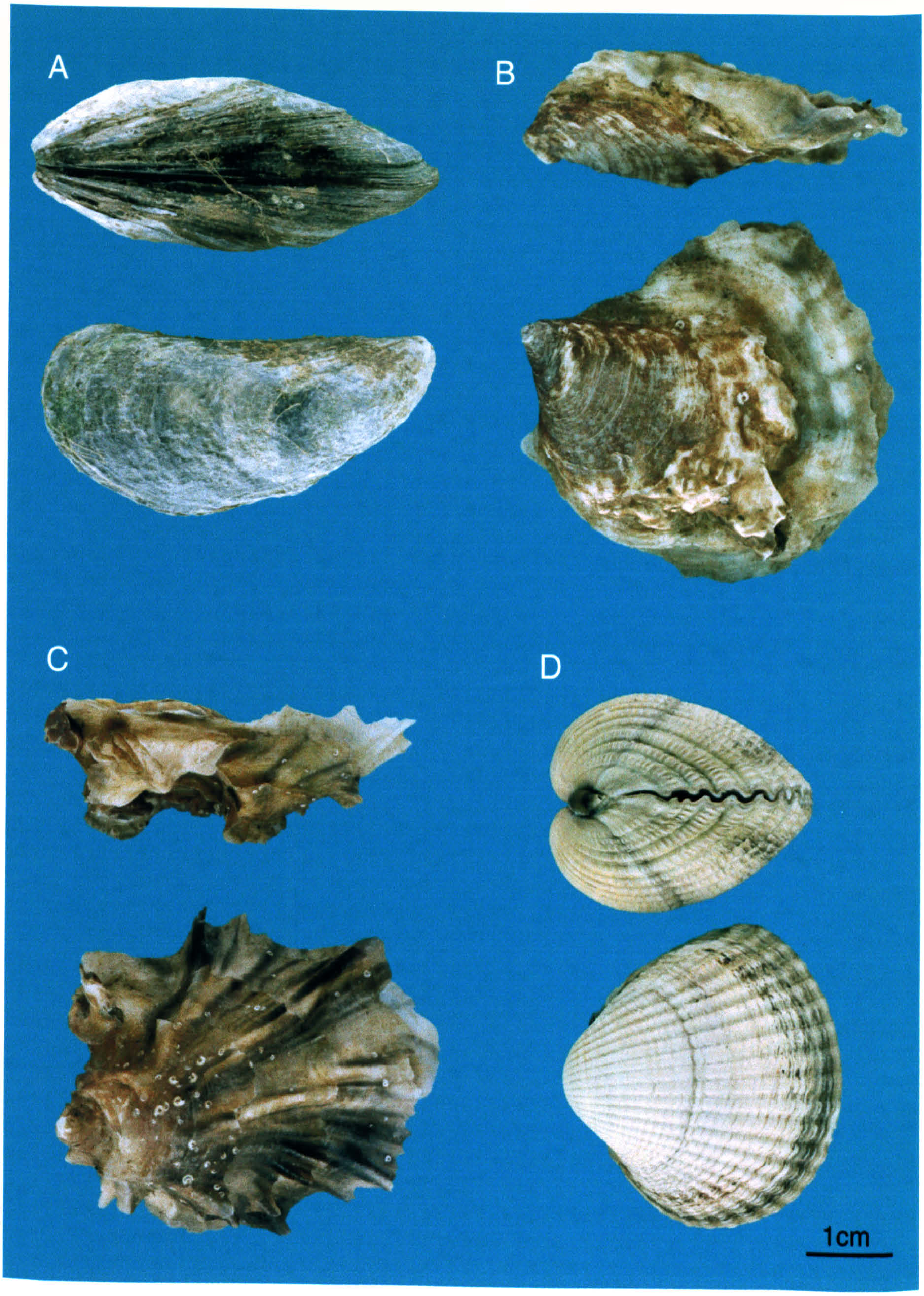


Plate 1. *Mytilus edulis* Linnaeus (A); *Ostrea edulis* Linnaeus (B); *Crassostrea gigas* (Thunberg) (C) *Cerastoderma edule* (Linnaeus) (D) from the Isle of Anglesey.

their spatial distribution on the shore different from that of adults (Edwards, 1958; Eriksson & Edlund, 1977; Naylor, 1958; 1962), but also their feeding habits and food preferences contrast with those of their larger conspecifics (Paul, 1981; Rangely & Thomas, 1987; Ropes, 1968). Crab size is an important aspect to consider when studying prey selection, since chelal strength and dexterity varies as crabs increase in carapace width (Hartnoll, 1974; Brown *et al.*, 1979). Smaller crabs may not have the physical strength to open larger or thicker shelled prey, and may, therefore, exhibit a higher degree of size selection than larger crabs choosing from a wider range of prey sizes (Whetstone & Eversole, 1981). Moreover, metabolic rate also varies with crab size. Food intake of large crabs is higher than that of small crabs, but weight-specific ingestion rates are higher for small than for large individuals (Wallace, 1973). This reflects the fact that younger crabs grow at a faster rate than older ones, and hence need larger amounts of food to satisfy their energetic requirements (Klein Breteler, 1975b).

The variability in the feeding patterns throughout a wide size range of crabs can be of particular relevance in terms of inferring the impact of crab predation on prey populations. The size-frequency distribution and abundance of crabs varies seasonally, thus affecting the average food intake over a period of time if this variability is considered (Walne & Dean, 1972). On the shore, juvenile crabs are relatively more abundant than adults (Crothers, 1970), and the relative abundance of certain age groups, in turn, varies throughout the intertidal and subtidal regions of the shore (Dare & Edwards, 1981; Hunter & Naylor, 1993). Thus, differences in both temporal and spatial distributions within a crab population will influence accessibility to prey, resulting in modifications of the patterns of prey mortality when crabs of different size are considered.

In order to provide valuable information for a better understanding of the basis of selective feeding amongst brachyuran crabs, the present research will examine the foraging behaviour of the shore crab, *Carcinus maenas* (Linnaeus) and the European edible crab, *Cancer pagurus* Linnaeus (Figure 1.1) when feeding on several bivalves of contrasting shell morphology. These are the blue mussel, *Mytilus edulis* Linnaeus, the edible cockle *Cerastoderma edule* (Linnaeus), the flat oyster, *Ostrea edulis* Linnaeus and the Pacific oyster, *Crassostrea gigas* (Thunberg) (Plate 1, A-D), four bivalve species of high commercial value. Since few studies have focused on the feeding habits of juvenile crabs, the present work will direct special attention to the foraging behaviour of juvenile *C. maenas*, and the information obtained will be compared with previous and present results regarding the feeding behaviour of adult shore crabs. In addition, the present research will contribute to the knowledge of the morphological, behavioural and ecological features of *C. maenas* and *C. pagurus* that should facilitate a comparison of their respective roles in benthic community organisation and dynamics.

Both *C. maenas* and *C. pagurus* are abundantly distributed around the Isle of Anglesey in North Wales (Campbell, 1976; Ingle, 1980). They are known to forage extensively on the mussel, *M. edulis* (Dare *et al.*, 1983), and the oyster, *C. gigas* (Richardson *et al.*, 1993). Studies have demonstrated the effect of shore crab predation on the distribution patterns of the cockle, *C. edule* in Traeth Melynog, Menai Strait (Sanchez-Salazar *et al.*, 1987b). Although cancrids have generally been more associated with predation on gastropods, various species of the genus *Cancer* have been reported to forage on commercially important bivalves (Boulding & Hay, 1984; Elner & Jamieson, 1979; Elner & Lavoie, 1983). In addition, the edible crab, *C. pagurus* in the British Isles itself constitutes an important exploitable natural resource (Edwards, 1979).

The present work comprises a general description of the main ecological features of selected crab and prey populations around the Isle of Anglesey in North Wales, and their variations both throughout the year and from one location to another (Chapter 2). Because chelal morphology and biomechanics can influence prey selection, the present work also includes an account of the morphology, occlusive geometry, and biomechanics of crab chelae over a wide size range of *C. maenas* and amongst juvenile *C. pagurus* (Chapter 3). This information is subsequently related to detailed observations of the different handling techniques used by crabs to open their prey, taking into account differences in shell strength, morphology and design as various bivalve prey increase in size (Chapter 4). Experiments to determine the size ranges of each individual prey species that are mostly preferred by different size categories of *C. maenas* and juvenile *C. pagurus* form the basis of Chapter 5. Thereafter, an examination of the foraging behaviour in terms of prey size and species selection was undertaken by offering these crabs mussels, oysters and cockles in various combinations where the availability of prey types was manipulated (Chapter 5). Further evaluation of the basis for such selective behaviour was accomplished by examining differences in prey profitability, shell shape and flesh odour, and between inedible models of prey with no energetic quality (Chapter 6). This made the identification of the most significant prey characteristics possible, and their relative importance at distinct decisive moments during the foraging bout could be established. Finally, several experiments on the learning capability of adult *C. maenas*, and its effect on crab selective feeding were also undertaken (Chapter 6).

It is uncertain to what extent laboratory observations are representative of the field situation. In natural conditions, crabs can find alternative sources of food; they are subject to inter- and intra-specific competition, pressures from their own predators, and of abiotic environmental conditions that constrain the breadth of their foraging activities (Lawton & Zimmer-Faust, 1992; Leber, 1985; Revelas, 1982; Sponaugle & Lawton, 1990). Bearing in mind the limits to which laboratory results can be used to assess the effect of predation on local prey populations, the present research constitutes an initial approximation to establish the potential impact of interactions between *C. maenas* and *C. pagurus* and commercially important bivalves. Furthermore, this information can be useful for species management in polyculture, a form of aquaculture that is presently gaining interest as it can result in increased and more diverse stock productions of both fresh-water and marine resources (Ardizzone *et al.*, 1988).

Chapter 2

Ecological Features of Crab and Prey Populations

2.1. Introduction

The common shore crab, *Carcinus maenas*, is native to the Atlantic, Baltic and North Sea coasts of Europe (Cohen *et al.*, 1995; Ingle, 1980), with a distribution range extending northwards to southern Iceland and south to Morocco (Broekhuysen, 1936). Multiple independent invasions due to human activities, however, have resulted in growing populations of introduced shore crabs in eastern and western North America (Williams, 1984), South Africa and Australia (Grosholz & Ruiz, 1996). *C. maenas* is one of the commonest and most adaptable crabs around the British Isles, inhabiting a wide variety of estuarine and open shores, from near high-water mark down to at least 200 m below low-water mark of spring tides (Crothers, 1968). Population density varies with the nature of the shore and with the availability of cover, with maximum abundance being attained in the most sheltered situations (Crothers, 1970). Crab density also varies seasonally (Dare & Edwards, 1981), from year to year (Beukema, 1991), and with spring-neap tidal cycles (Naylor, 1962). Adult shore crabs migrate to the intertidal zone to feed with each flooding tide in all but the coldest winter months when they generally remain in a relatively inactive state in deeper waters (Klein Breteler, 1976). Few studies have examined the ecology of juvenile shore crabs even though they are more abundant on the shore than adults (Crothers, 1970), and thus have been suggested to play a key role in structuring the benthic community of some intertidal areas (Gee *et al.*, 1985; Jensen & Jensen, 1985).

The European edible crab, *Cancer pagurus*, is distributed throughout the Mediterranean, Atlantic, English Channel, and North Sea (Ingle, 1980), and is abundant around the British Isles, where it sustains an important fishery (Edwards, 1979). It inhabits the lower regions of the shore and subtidally down to approximately 100 m (Campbell, 1976). Postlarval edible crabs can be observed close inshore during the summer (Lawton, 1983), and juveniles are often found between tide marks (Hall *et al.*, 1993; Howard, 1982). However, when sexual maturity is attained (males: 110 mm; females: 130 mm CW), *C. pagurus* leaves these nursery habitats and moves to the sublittoral fringe, where large individuals are frequently found buried in the soft sediment beneath rocks and boulders (Edwards, 1979). Although there is less information on the rhythmic behaviour of cancrid than of portunid crabs (Hill, 1976; Naylor, 1958), diving observations on some cancrids

Figure 2.1. Location of study sites on the Isle of Anglesey, North Wales: **A**) Treborth : circles I, II, III are 30 m^2 quadrats where crabs were collected by searching under rocks and boulders; **B**)Gallows Point; **C**) Traeth Melynog; **D**) Aberffraw; ⊗ CEFAS oyster beds at Brynsiencyn: the line IV-V indicates the location of the transects of baited traps at each site. Black dotted and continuous lines are mean low water and high water marks, respectively. Maps A (1:10,000 scale) and B (1:25,000 scale) were obtained from Admiralty Chart # 1464 (1997). Maps C and D (1:50,000 scale) were obtained from Ordnance Survey, Landranger # 114 /Anglesey (1994).

have revealed that they are nocturnally active and usually passive during the day, and that most of this nocturnal activity appears to be related to foraging activities (Brown, 1982).

This chapter will describe seasonal changes in the abundance and size-frequency distributions of *C. maenas* and *C. pagurus* at four different sites around the Isle of Anglesey, North Wales. Although most of the information contained in this chapter relates to adult *C. maenas*, variations in the relative abundance of the smaller sizes of *C. maenas* and juvenile *C. pagurus* will be included. Studies on foraging behaviour demand knowledge of the size distribution and abundance not only of the predator but also of the prey populations. This chapter will also describe seasonal variations in the relative abundance and size-frequency distributions of natural and commercially reared populations of the mussel, *Mytilus edulis*, and the cockle, *Cerastoderma edule*. Both bivalve species are known to be part of the natural diet of these and other brachyuran crabs (Choy, 1986; Paul, 1981; Sanchez-Salazar, 1986; Wear & Haddon, 1987) and can be found co-occurring with *C. maenas* and *C. pagurus* populations at some of the sites examined in this study.

2.2. Materials and Methods

2.2.1. Study area.

The animals used in this study were collected at four sites around Anglesey (Figure 2.1): Treborth, Traeth Melynog, and Gallows Point, on the Menai Strait; and Aberffraw on the south-west coast of the island.

The sampling area at Treborth (A) is located at the south-east bank of the Menai Strait, extending approximately 600 m west from the piers of the Menai Bridge. The somewhat steep stretch of shore line has an exposed distance of 50 m from mean high to mean low-water of spring tides (MHWS-MLWS). *Carcinus maenas* is abundant beneath rocks and boulders or amongst kelps in the lower part of the shore, but can be found throughout the intertidal region. Large, adult *Cancer pagurus* (> 115 mm CW; Edwards, 1979) are mostly distributed subtidally, although juvenile edible crabs are frequently found buried in the sediment under rocks and stones at low water mark. Prey species known to be part of the diet of both *C. maenas* and *C. pagurus*, such as gastropods (e.g. *Littorina* spp., *Nucella lapillus*) and barnacles (e.g. *Elminius modestus, Semibalanus balanoides*), are found in considerable densities, but mussels and cockles are generally absent at this sampling site.

Traeth Melynog (B) is a sheltered sandy beach located at the southern end of the Menai Strait. It is an extensive area of approximately 330 ha, with a gentle slope and a large tidal range that results in an exposed sandflat of 1 km ^{2} at low water of spring tide. The river Braint flows seaward from the northern corner, forming a series of shallow channels at the low part of the beach, and at low-water mark the sand bank falls steeply into a deep channel. The substratum consists of fine sand with small amounts of mud. Cockles occur in a broad intertidal band, ranging from about 100 m from mean high water of spring tide to the lowest levels of the intertidal. The size distribution of cockles varies across the intertidal gradient, the high shore supporting mainly small cockles, whilst the mid and low shore are dominated by larger individuals (Sanchez-Salazar *et al.*, 1987b).

The third collection site in the Menai Strait (C) is adjacent to a commercial mussel bed approximately 1 km south of Gallows Point. It is a moderately sheltered shore with an exposed area of 7500 m ^{2} from mean high to mean low water mark of spring tides. The sediment consists of angular shingle in the uppermost intertidal, and very fine sand and mud in the mid and low intertidal. Sediments are inhabited by polychaete worms, such as *Lanice conchilega* and *Arenicola marina*, whilst the rocks are abundantly covered with the barnacle *Elminius modestus*. Below the *Ascophyllum nodosum* band, extensive fucoid patches are densely covered with the polychaete worm *Spirorbis spirorbis*. The mussel population is characterised by clumps of a few larger individuals (> 50 mm SL), distributed from the mid to the low intertidal and subtidally. Where rocks give way to the muddy mussel bed, *Littorina littorea* and *L. obtusata* are sufficiently common to encourage semi-commercial harvesting (Jones, 1983).

Aberffraw (D) is a wave-exposed bay, with the northern- and southern-most extremities dominated by rock outcrops, and a sandy beach extending seaward from the dunes at the centre of the bay. The sampling area is a small inlet of 4.5 ha, situated on the west bank of the mouth of the River Ffraw. Here the mussel beds are found in tight carpet-like clumps on the rocky areas that cover the high intertidal region of the shore (2500 m ^{2}). Mussels are completely absent from the mid to the low intertidal, which is characterised by soft sand substratum, extending in a gentle slope towards the sea. The mussel population is dominated by small individuals (5-25 mm SL), with only a few mussels > 40 mm occurring on the sides of rocks at the boundary with the mid shore.

2.2.2. Sampling of crab populations.

Monthly samples of both *C. maenas* and *C. pagurus* were collected at Treborth in the Menai Strait, from June, 1995 to May 1996. Samples were taken from three 30 m ^{2} rectangular quadrats, that were always placed approximately 200 m from each other at low-water mark during spring tides (I, II, III in Figure 2.1, A). Sampling was carried out by searching for crabs under the rocks and boulders present within each quadrat over a 20 minute period. Crabs were collected by hand, maximum carapace width (CW) measured to the nearest 0.1 mm using vernier callipers, and sex and species recorded before releasing the crabs in the sampling area. The density of each species was estimated by dividing the number of crabs found in each 20 minute search by 30 (i.e. the number of square m in each quadrat). Values of the three quadrats were then averaged to obtain the mean relative abundance of crabs per month. Carapace width measurements were used to compare size-frequency distributions of the crab population in each monthly sample. Mean monthly water temperatures were obtained from daily records taken by the UCES unit at the School of Ocean Sciences, University of Wales-Bangor.

Seasonal samplings of the crab population were carried out in May (spring), August (summer), and November (autumn) 1996, and February (winter) and June (late spring) 1997. Samples were collected using three baited traps (mesh size: 6.5 mm) at Treborth, Gallows Point and Aberffraw, and six baited traps at Traeth Melynog. Traps were placed along a transect at high-, mid- and low-water mark at low spring tide. Following one complete tidal cycle (12 h), the traps were emptied and all crabs were taken to the laboratory and deep frozen for further examination. Crabs were then sexed and their CW measured to the nearest 0.1 mm. Comparisons of crab abundance between sites and seasonal samples were based on the total number of crabs present in all traps along each transect (crabs • tran. $^{-1}$). Carapace width measurements were used to compare size-frequency distributions of the total number of crabs in each transect (= seasonal sample). The number of crabs with damaged or entirely missing chelae was also determined.

Because only large crabs were found in the traps, the relative abundance of the smaller individuals at Traeth Melynog was determined separately in June 1997. Bait was tied up in a fine mesh and buried in the sand at high, mid and low shore, with 3 replicates per shore level. The following day, samples were collected by digging up an area of 625 cm ^{2} to a depth of 10 cm surrounding the bait, and wet sieving the sand through a 1.5 mm nylon mesh. In addition, 2 further quadrats of similar area were sampled for crabs in each shore level to compare between baited and unbaited samples. All the crabs present were returned to the laboratory, counted and measured across the carapace to the nearest 0.01 mm with a micrometric graticule and microscope. The density of juvenile crabs was expressed as the number of crabs • m $^{-2}$. Carapace width measurements were used to construct comparable size-frequency distributions of the total number of crabs found in each shore level. A two-way ANOVA was carried out to test whether the number of crabs • m $^{-2}$ and mean CW differed significantly from baited/unbaited quadrats and between shore levels.

2.2.3. Sampling of prey populations.

All prey populations were sampled on a seasonal basis at the same time the crab samples were collected. The natural population of *Mytilus edulis* at Aberffraw was studied by collecting all mussels in 6-10 random quadrats of 10 x 10 cm at high shore. Quadrats of such size were used to enable the adequate collection of the samples. However, to facilitate the counting of the mussels, when samples were returned to the laboratory, a standardised procedure was followed in which each sample was divided into ten random sub-samples. The shell length (SL: maximum dimension of the shell; Figure 4.1) of all mussels in one sub-sample (of each quadrat) was measured to the nearest 0.1 mm with vernier callipers. Six to ten 25 x 25 cm random quadrats at high, mid and low shore, were used to sample the mussel beds at Gallows Point. All mussels in each sample were counted and their SL measured to the nearest 0.1 mm. Shell length measurements were used to construct size-frequency distributions, whilst mussel density estimates from the two sampling sites were obtained from the numbers of mussels per m ^{2}.

The *Cerastoderma edule* population at Traeth Melynog was sampled along a transect line running from mean high water of spring tide to mean low water of spring tide.

Table 2.1. (A) Mean number (no.•m $^{-2}$) and carapace width (mm CW) of *Carcinus maenas* and *Cancer pagurus* per season at low water mark at Treborth by standard search time, and (B) the total number and mean CW of *C. maenas* in baited traps set at high, mid and low shore at Treborth, as well as the mean number and CW of crabs per transect. The mean number of crabs of the four sampling seasons (year) is also given. Values are means ± se.

	A				B							
	Crabs per standard search time				Crabs in baited traps (*C. maenas*)							
	C. maenas		*C. pagurus*		High shore		Mid shore		Low shore		Total	
	no.•m $^{-2}$	CW	no.•m $^{-2}$	CW	no.•trap	CW	no.•trap	CW	no.•trap	CW	no.	CW
Summer	0.60 ± 0.03	34.9 ± 3.9	0.21 ± 0.02	48.0 ± 2.0	31	76.1 ± 2.6	6	52.6 ± 1.5	3	60.4 ± 1.3	13.3 ± 7.3	63.0 ± 5.6
Autumn	0.54 ± 0.02	26.3 ± 1.0	0.13 ± 0.04	36.0 ± 2.8	11	51.4 ± 2.4	2	70.3 ± 4.8	0	-	4.3 ± 2.8	60.9 ± 6.7
Winter	0.17 ± 0.04	23.2 ± 2.1	0.13 ± 0.08	44.8 ± 8.1	0	-	6	69.5 ± 1.5	37	66.2 ± 1.3	14.3 ± 9.4	67.9 ± 1.2
Spring	0.47 ± 0.07	40.9 ± 3.7	0.30 ± 0.06	46.3 ± 5.2	1	43.9	27	57.2 ± 2.1	0	-	9.3 ± 7.2	50.6 ± 4.7
Year	0.44 ± 0.05		0.19 ± 0.03								10.3 ± 1.9	

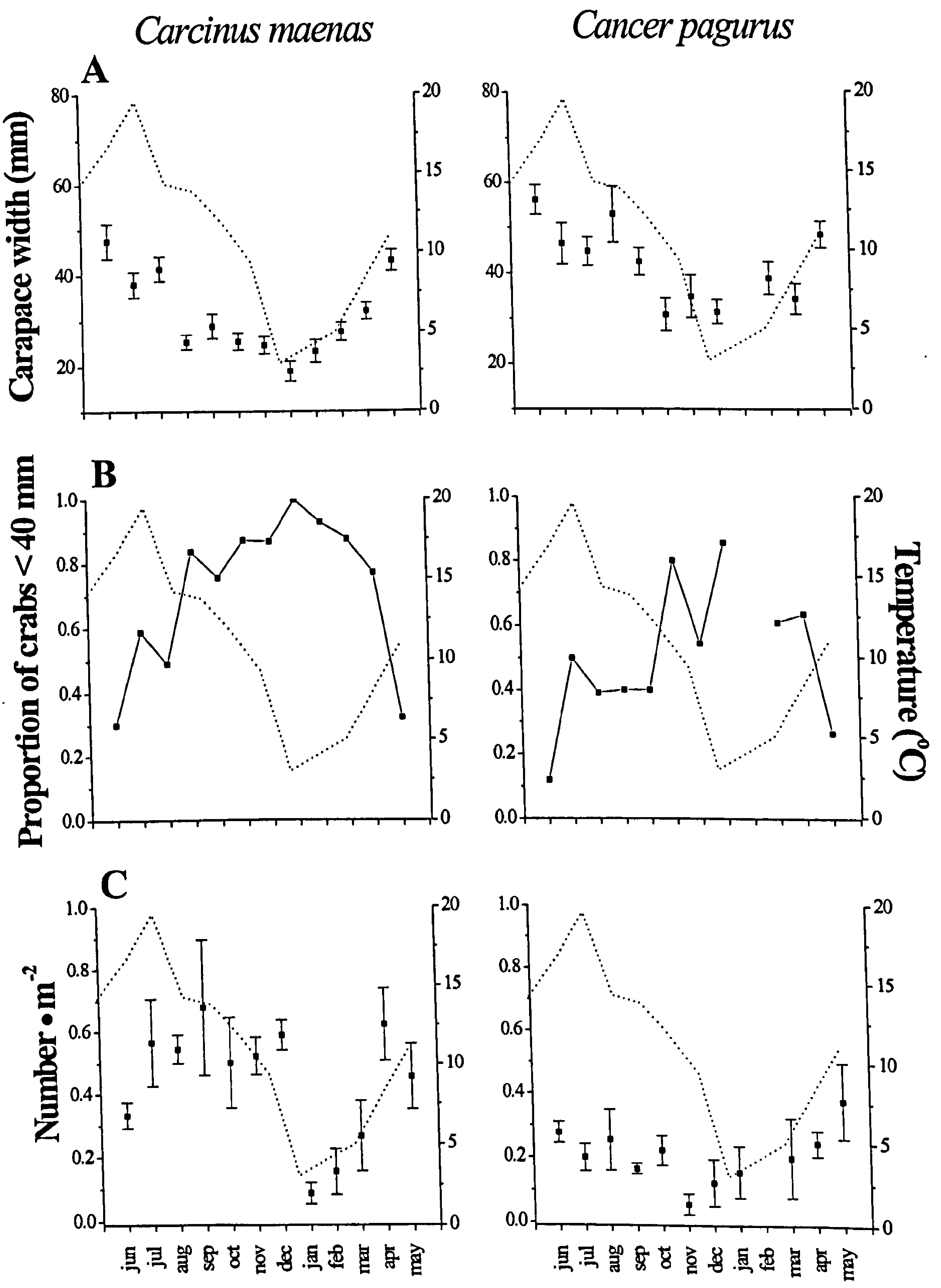


Figure 2.2. Annual fluctuations in (A) mean carapace width (± se), (B) the proportion of crabs < 40 mm CW, and (C) the mean number of crabs m^{-2} (± se) for *Carcinus maenas* and *Cancer pagurus* found at Treborth at low water mark of spring tides. The dotted line represents monthly mean water temperature in the Menai Strait. Insufficient data on *C. pagurus* in February.

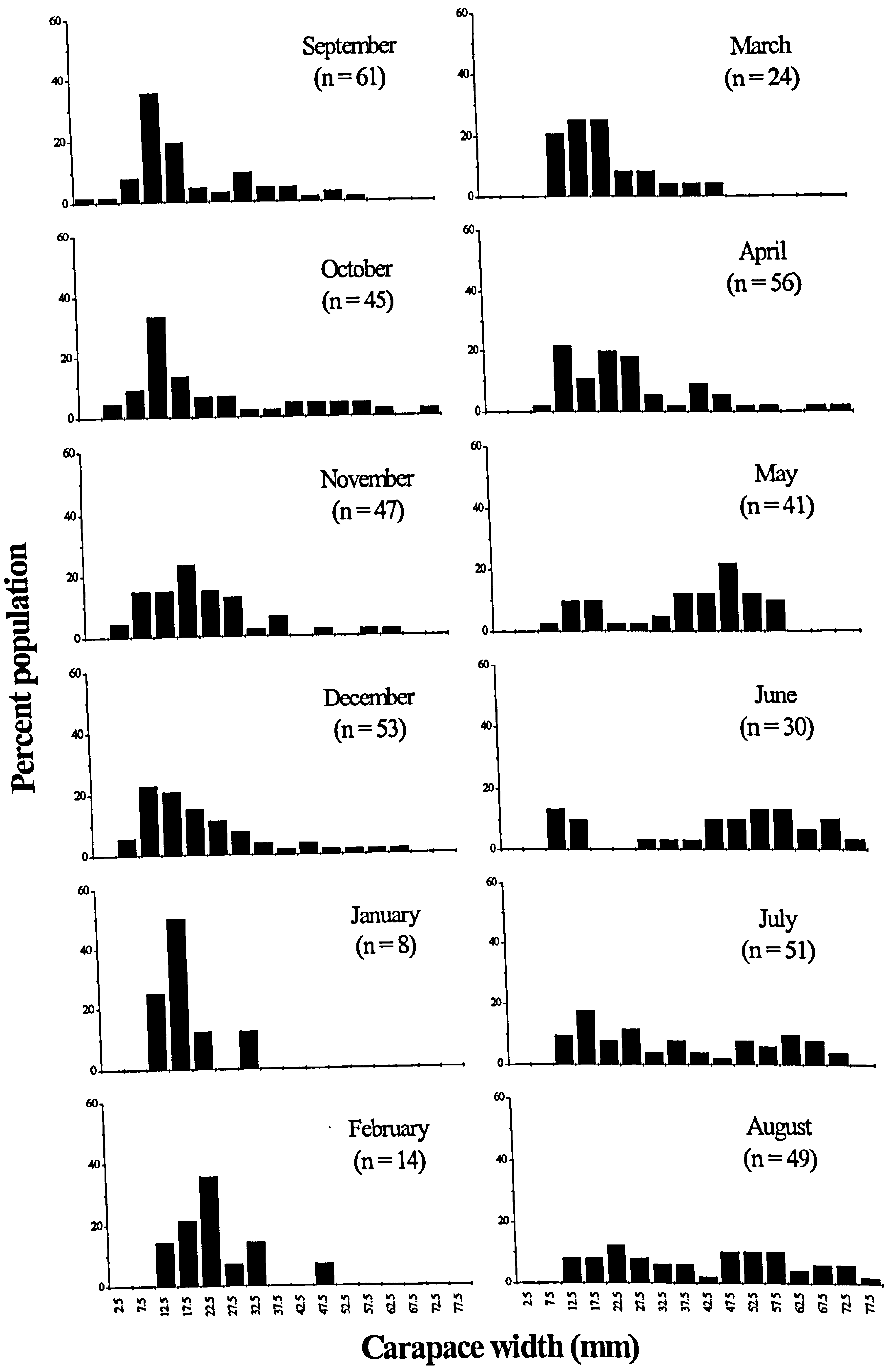


Figure 2.3. Monthly size-frequency distribution of *Carcinus maenas* found per standard search time at Treborth at low water mark of spring tides. Values represent the proportion of crabs in each size category of the total number of crabs found in all three quadrats (Appendix A1).

Estimates of the density of cockles were made at intervals along the transect from 15 random 25 x 25 cm quadrats. The uppermost 5 cm of sand in each quadrat was sieved (mesh size: 6.5 mm) and all cockles removed. The shell length (Figure 4.1) of each cockle was measured to the nearest 0.1 mm with vernier callipers and population size-frequency distributions constructed.

2.3. Results

2.3.1. Crab populations.

Treborth

In the low shore at Treborth, *Carcinus maenas* was significantly more abundant than *Cancer pagurus* (mean year density: 0.44 ± 0.05 and 0.19 ± 0.03 crabs • m^{-2}, respectively; $t = 4.10$; $p < 0.001$; Table 2.1; Appendix A1). The density of *C. maenas* was lowest from January (0.09 ± 0.03) to March (0.27 ± 0.11), when mean water temperature ranged from 3-5 °C (Figure 2.2). Densities increased towards the warmer months attaining the highest values in July (0.57 ± 0.05) to September (0.68 ± 0.22) when the mean water temperatures were 16-20 °C. *C. pagurus* showed less marked fluctuations in density with temperature than *C. maenas*; density was lowest between November (0.06 ± 0.03) and February (0.02 ± 0.01), and highest during May (0.38 ± 0.12; Figure 2.2). Mean carapace width (CW) of both crab species increased during the warmer months and decreased in the colder months of the year (Figure 2.2). Similarly, the proportion of both *C. maenas* and *C. pagurus* < 40 mm CW was highest in winter, and lowest in spring (Figure 2.2), indicating a seasonal variation in the size composition of crabs that remain in the low intertidal when the tide recedes.

The monthly size distribution of *C. maenas* reveals this seasonal variation in more detail (Figure 2.3). Small shore crabs (10-30 mm CW) were present in the intertidal throughout the year, but were relatively more abundant from September to April. *C. maenas* < 10 mm CW were only present in samples from September to December (Figure 2.3). Large shore crabs (40-80 mm CW), by contrast, were more abundant in the intertidal zone from May to August, and became increasingly scarce from September to April, with very few crabs > 40 mm CW occurring from January to March (Figure 2.3). The female to

Table 2.2. Variations in the female : male ratio from samples of *Carcinus maenas* per standard search time at Treborth (resident) and using baited traps at Treborth (migratory), Traeth Melynog, Gallows point, and Aberffraw. Annual mean female : male ratios for each site are also given. Values were calculated from the total number of crabs found per monthly (Appendix A1) or seasonal sample (Appendix A2).

Site	May	August	November	February	June	Year
Treborth (resident)	1.29 : 1	0.72 : 1	0.46 : 1	0.33 : 1	0.79 : 1	0.67 : 1
Treborth (migratory)	-	0.25 : 1	0.63 : 1	0.11 : 1	0.22 : 1	0.30 : 1
Traeth Melynog	2.33 : 1	1.16 : 1	0.98 : 1	all fem	0.42 : 1	1.23 : 1
Gallows Point	0.76 : 1	0.68 : 1	0.77 : 1	0.28 : 1	1.11 : 1	0.72 : 1
Aberffraw	0.46 : 1	1.11 : 1	1.50 : 1	0.34 : 1	1.21 : 1	0.92 : 1

Table 2.3. Mean number (no.•m $^{-2}$) and carapace width (mm CW) of juvenile *Carcinus maenas* found per shore level at Traeth Melynog in June 1997 using baited quadrats. The percentage of crabs in each of three size categories (2.5-3.5, 3.5-4.5, and 4.5-5.5 mm CW) are also shown. Values are means ± se; n is the number of quadrats used in each case.

				Percentage of crabs		
Shore level	no.•m^{-2}	CW	n	2.5-3.5 mm	3.5-4.5 mm	4.5-5.5 mm
High shore	102 ± 26.2	4.1 ± 0.43	5	51.6	32.3	9.7
Mid shore	106 ± 20.0	3.8 ± 0.19	5	42.4	39.4	12.1
Low shore	80 ± 14.3	4.3 ± 0.26	5	24	40	24

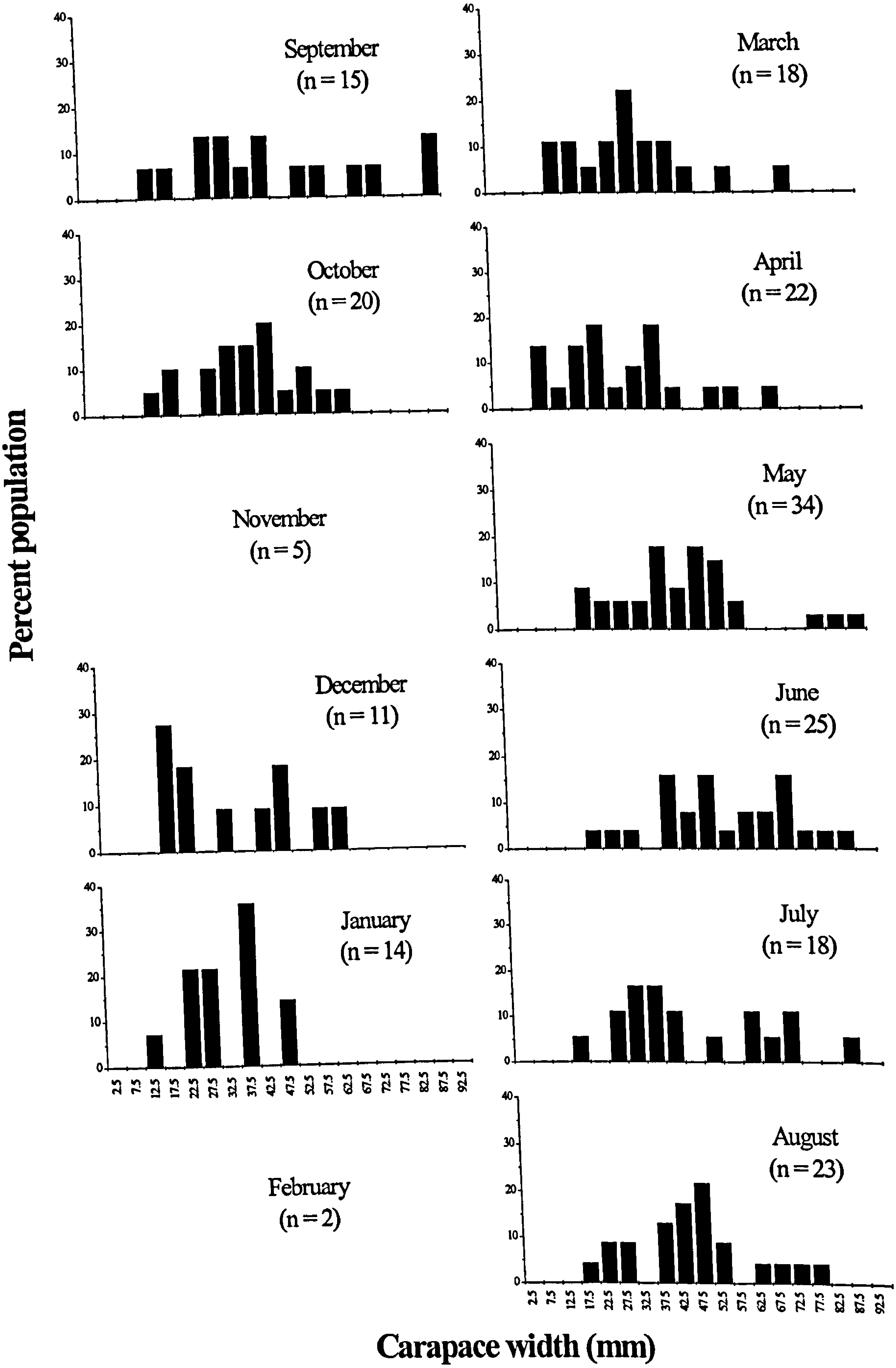


Figure 2.4. Monthly size-frequency distribution of *Cancer pagurus* found per standard search time at Treborth at low water mark of spring tides. Values represent the proportion of crabs in each size category of the total number of crabs found in all three quadrats (Appendix A1). Insufficient data in November and February.

male ratio had a mean value of 0.67:1, with the maximum and minimum values in May (1.29:1) and February (0.33:1), respectively (Table 2.2). The highest number of berried females and mating pairs was observed in the field during April and May.

The monthly size distribution of juvenile *C. pagurus* also showed a seasonal variation. Small edible crabs (10-30 mm CW) were more abundant from December to April, whereas larger crabs (30-60 mm CW) were more abundant from May to October (Figure 2.4). Edible crabs > 70 mm CW were only present in samples from May to September, whilst crabs < 10 mm CW were never found in the intertidal throughout the sampling year.

Seasonal sampling using baited traps at the same site gave contrasting results compared to those obtained by searching for crabs under rocks and boulders (Table 2.1). *C. pagurus* was never caught in baited traps at any shore level or at any of the four sampling sites. The absolute number of *C. maenas* caught in traps at high shore was comparable to the seasonal pattern of shore crab relative abundance per standard search time. However, traps set out at mid shore caught more *C. maenas* in the late spring sample (June) than in any other month, whilst traps in the low shore caught more crabs in the winter sample (February), and none during autumn (November) or spring. This resulted in the mean number of crabs per transect being highest in summer (August) and winter, and lowest in autumn and spring. Another difference between the two sampling methods is that the mean CW of crabs caught in baited traps at all shore levels did not present such a marked seasonal variation and was significantly larger ($t = -6.90$; $p < 0.001$) than that of crabs found by searching under rocks and boulders throughout the year (Table 2.1). In addition, the mean female to male ratio (0.30:1), and both the maximum (0.63:1) and minimum (0.11:1) values obtained using baited traps, were lower than those obtained by searching for crabs at low-water mark (Table 2.2). The minimum values using both sampling methods were recorded in winter (February). However, the maximum value for samples using baited traps was recorded in autumn (November), whereas the maximum value for crabs found per standard search time was recorded in spring (May).

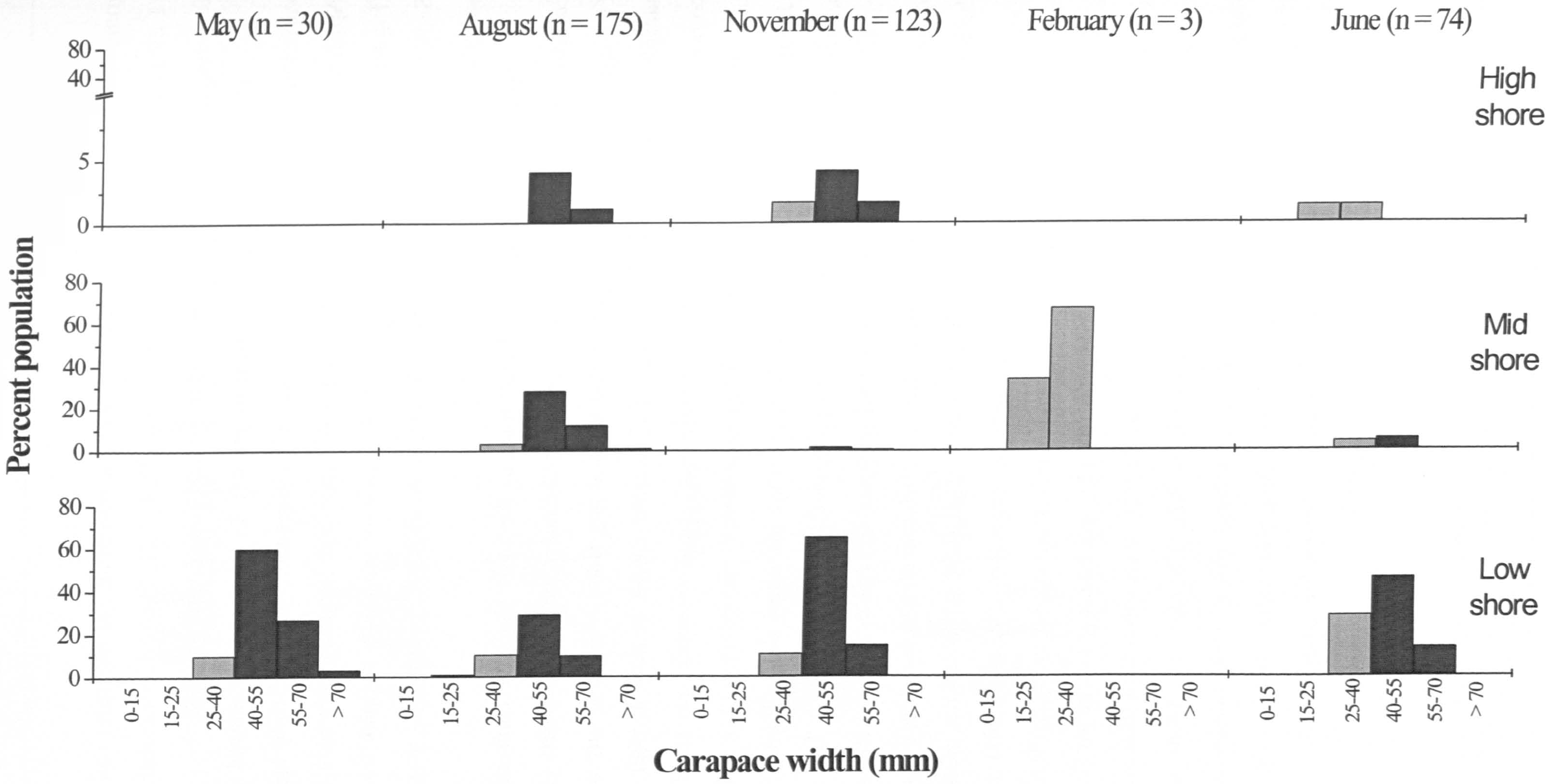


Figure 2.5. Seasonal variations in the size-frequency distribution of *Carcinus maenas* captured with baited traps set at high, mid and low shore at Traeth Melynog. Values represent the percentage of crabs in each size category of the total number of crabs captured per transect (= seasonal sample; Appendix A2); dark shaded columns: crabs > 40 mm CW, light shaded columns: crabs < 40 mm CW.

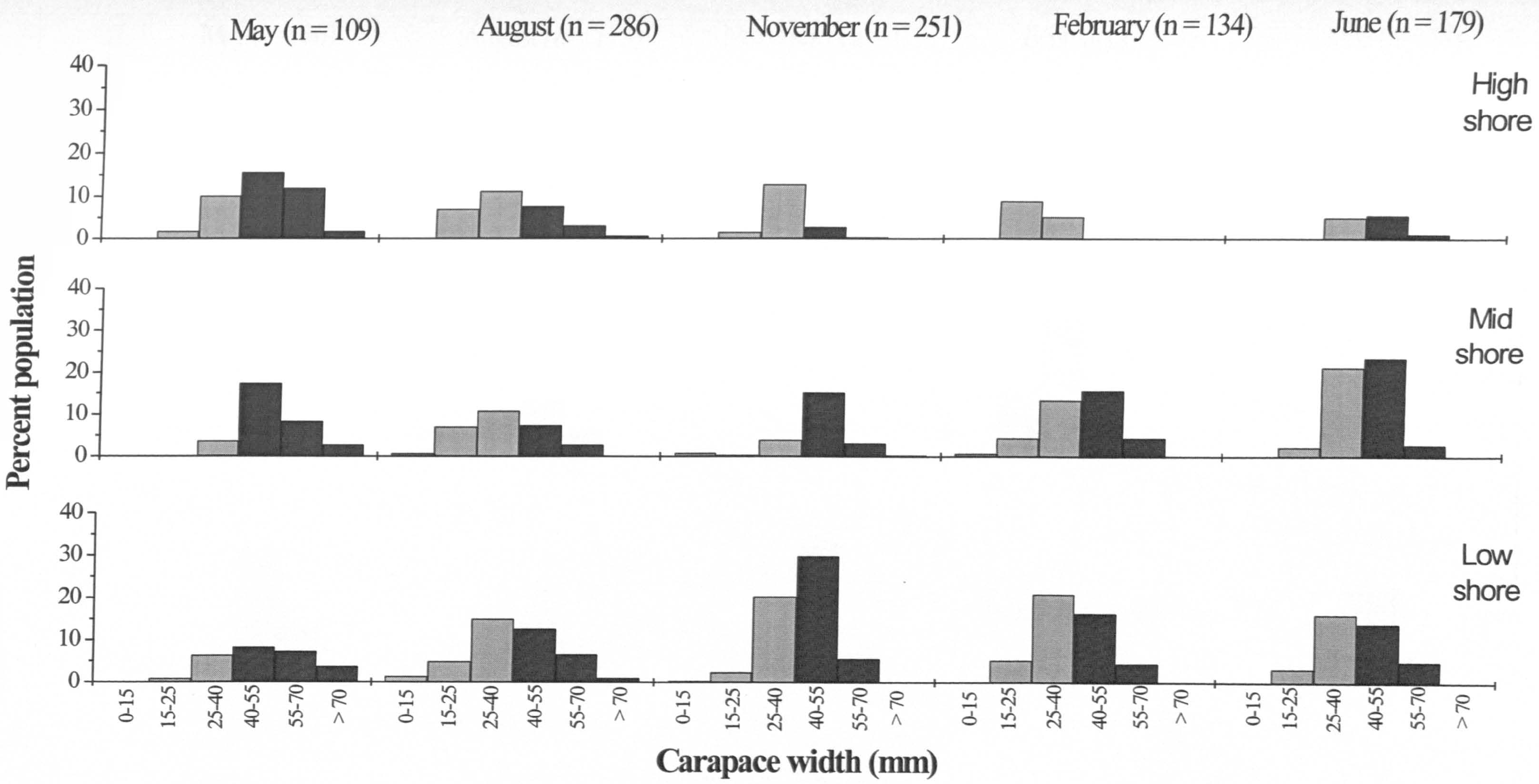


Figure 2.6. Seasonal variations in the size-frequency distribution of *Carcinus maenas* captured in baited traps set at high, mid and low shore at Gallows Point. Values represent the percentage of crabs in each size category of the total number of crabs captured per transect (= seasonal sample; Appendix A2); dark shaded columns: crabs > 40 mm CW, light shaded columns: crabs < 40 mm CW.

Traeth Melynog

The seasonal sampling of *C. maenas* at Traeth Melynog using baited traps (Appendix A2) showed that the highest percentage of crabs of all size categories was generally found in traps at low shore. The percentage of crabs < 40 mm CW was very low throughout the year (Figure 2.5) and, although samples were strongly dominated by crabs 40-55 mm CW, crabs 55-70 mm CW were also abundant (Figure 2.8). Whilst the proportion of crabs > 40 mm CW found at mid shore and high shore increased in August and November, all crabs caught in traps set at mid shore in February, and high shore in June, were 15-40 mm CW. The mean female to male ratio was 1.23:1, with a maximum value (2.33:1) in May, and a minimum value (0.42:1) in June (Table 2.2).

Crabs < 15 mm CW were never caught using baited traps at Traeth Melynog. However, the sampling method specifically designed to capture juvenile crabs used in June 1997 showed that crabs < 15 mm CW are abundant at all shore levels (Table 2.3). Crabs captured with this sampling method were 2.5-8.6 mm CW (only one crab 15.3 mm CW was found at high shore). Neither the number of crabs per m^2 nor the mean CW differed significantly between samples using baited and unbaited quadrats (no.•m^{-2}: $F = 0.95, p = 0.35$; CW: $F = 0.33, p = 0.56$), between shore levels (no.•m^{-2}: $F = 0.25, p = 0.78$; CW: $F = 0.88, p = 0.42$), or due to the interaction between the two factors (baited/unbaited x shore level; no.•m^{-2}: $F = 1.05, p = 0.39$; CW: $F = 1.18, p = 0.31$). More than 85 % of crabs at all three shore levels were 2.5-5.5 mm CW (Table 2.3). However, most of the crabs at high shore were 2.5-3.5 mm CW (51.6 %), whilst at mid shore the percentage of crabs of 2.5-3.5 (42.4 %) and 3.5-4.5 (39.4 %) were broadly similar. At low shore, most crabs were 3.5-4.5 mm (40 %; Table 2.3), indicating a slight increase in CW at lower tidal elevations.

Gallows Point

C. maenas samples from the commercial mussel bed near Gallows Point (Appendix A2) showed that the percentage of crabs in each size category did not vary markedly in their distribution across the intertidal gradient throughout the year. In August, November and February, crabs < 40 mm CW were found in a slightly higher proportion in the low-shore than in the mid- and high-shore traps (Figure 2.6). In June, most crabs < 40 mm CW were found at mid shore, whereas in May most crabs of these size categories

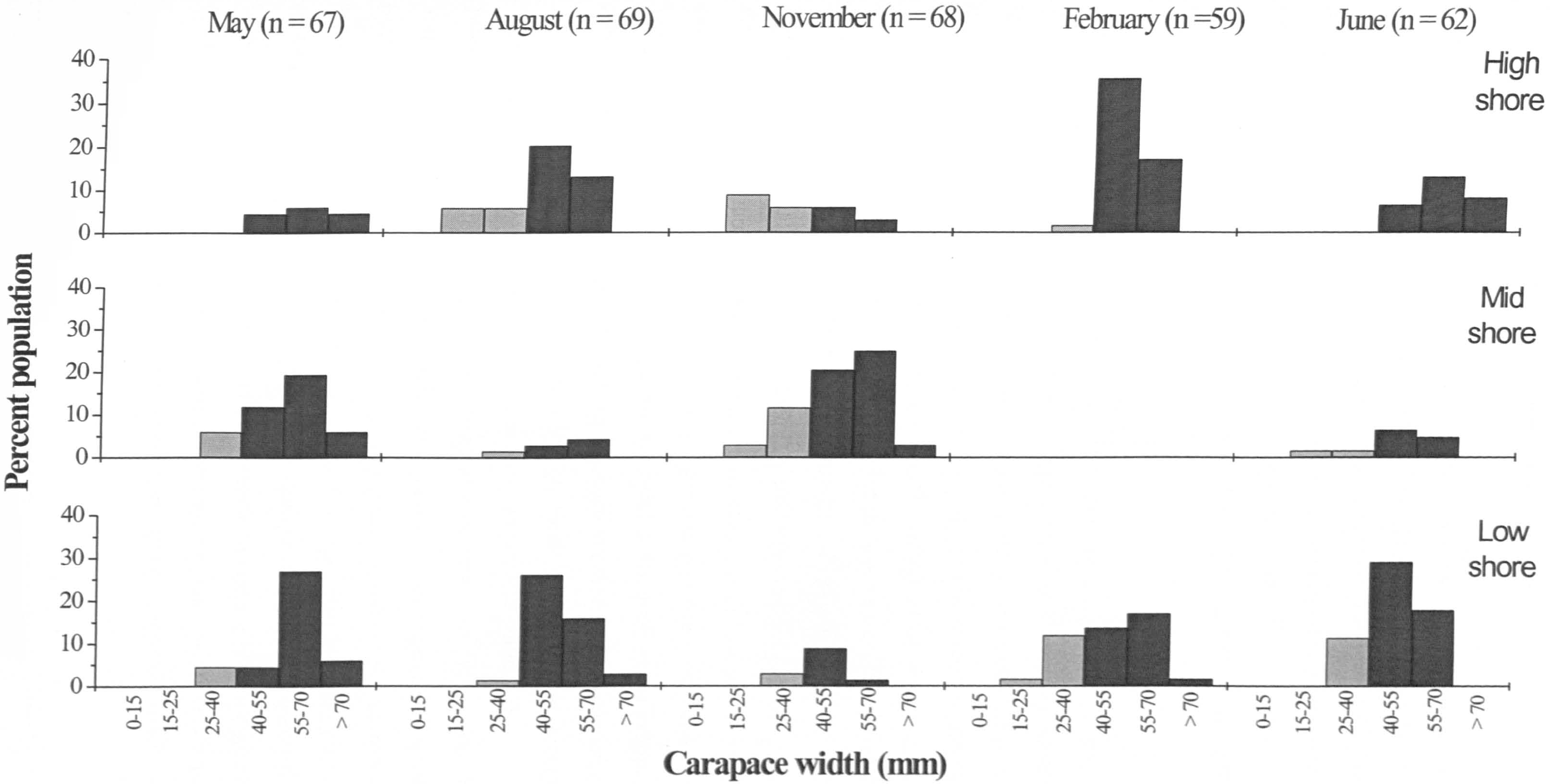


Figure 2.7. Seasonal variation in the size-frequency distribution of *Carcinus maenas* captrued with baited traps set at high, mid and low shore at Aberffraw. Values represent the percentage of crabs in each size category of the total number of crabs captured per transect (= seasonal sample; Appendix A2); dark shaded columns: crabs > 40 mm CW, light shaded columns: crabs < 40 mm CW.

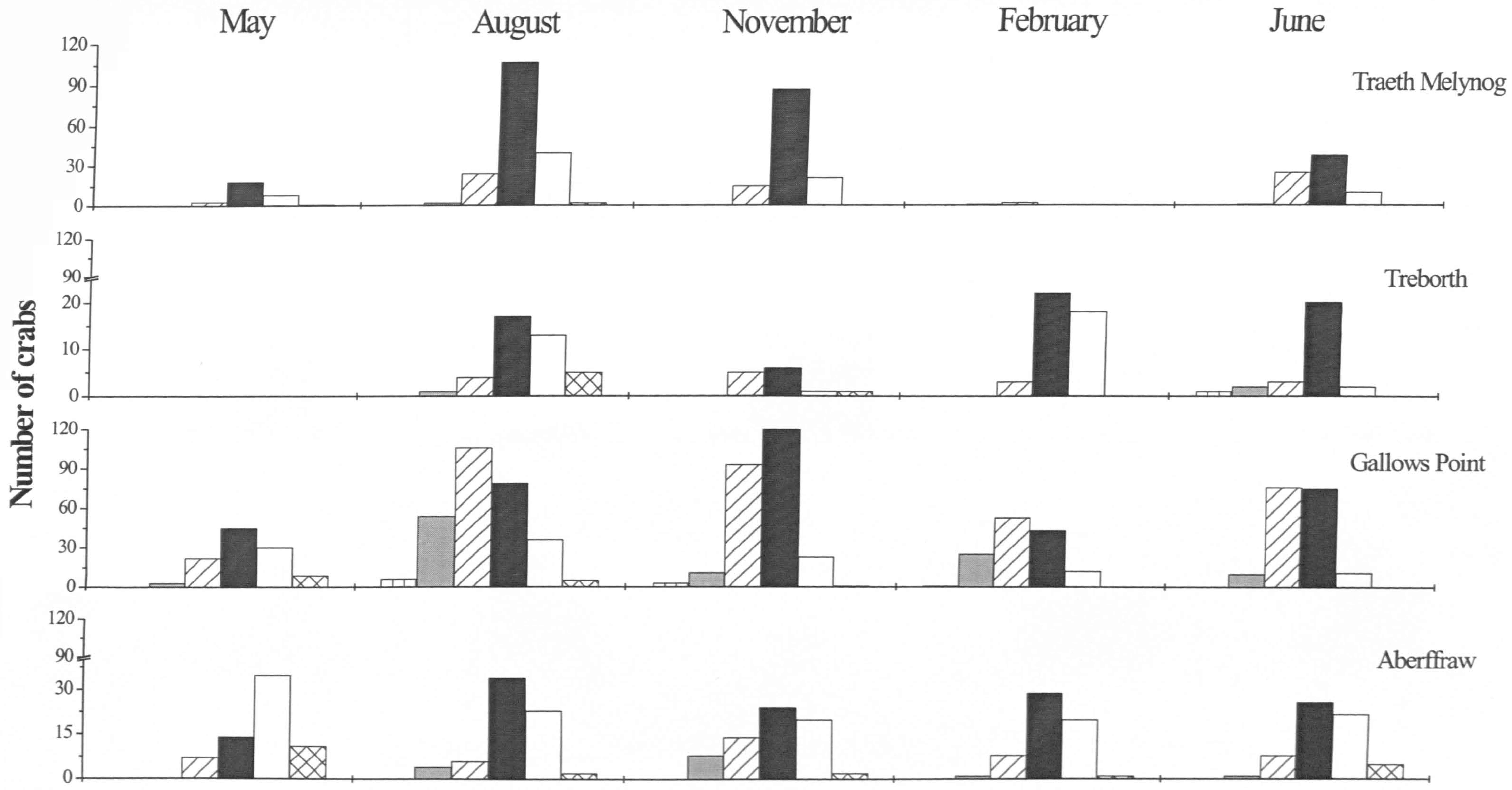


Figure 2.8. Seasonal variations in the number of *Carcinus maenas* in each of six size categories found in baited traps set along transects at Traeth Melynog, Treborth, Gallows Point, and Aberffraw;
▥ 0-15 mm CW ▩ 15-25 mm CW ▨ 25-40 mm CW ■ 40-55 mm CW □ 55-70 mmCW ⊠ 70-80 mm CW.

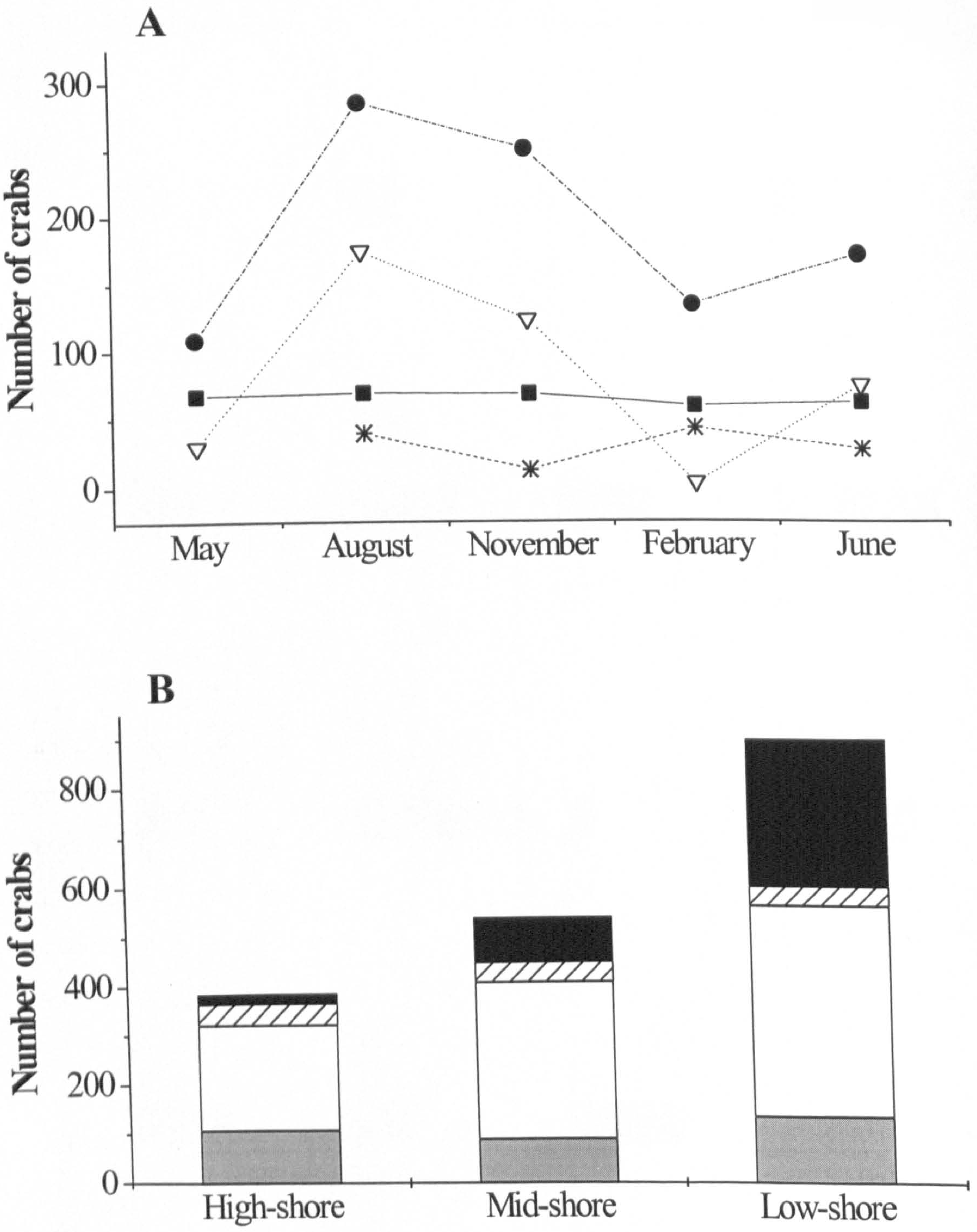


Figure 2.9. Comparisons between captures of *Carcinus maenas* at Aberffraw, Gallows Point, Treborth and Traeth Melynog using baited traps. (**A**) seasonal variations in the total number of crabs from all three shore levels; (**B**) total number of crabs from all seasonal samples found at high, mid and low shore.

—■— Aberffraw	···●··· Gallows Point	···✱··· Treborth	···▽··· Traeth Melynog
▒	□	▨	■

were found in the high-shore trap. Crabs > 40 mm CW were generally found in a higher proportion in the low and mid shore than in the high-shore trap, except for the sample in May, when these larger crabs were found in similar proportions throughout the transect (Figure 2.6). Very few crabs > 40 mm CW were found in the high-shore trap in November, and no crabs of this size category were found in the high-shore trap in February. Although some crabs < 15 mm CW were found at low and mid shore during the warmer months, the crab population at Gallows Point was dominated by individuals 25-55 mm CW throughout the year (Figure 2.8). The mean female to male ratio was 0.72:1, with similar values in May (0.76:1), August (0.68:1), and November (0.77:1), but with a much lower value in February (0.11:1; Table 2.2).

Aberffraw

C. maenas samples from baited traps set at Aberffraw (Appendix A2) showed that the percentage of crabs < 40 mm CW increased in the mid- and high-shore traps in August and November (Figure 2.7). In February, however, most crabs < 40 mm CW were found at the low shore, whilst very few were found at the high shore, and no crabs of any size category were caught in the mid-shore trap. In June and May, crabs < 40 mm CW were only found at mid- and low-shore levels. Crabs > 40 mm CW were generally found in the highest proportion in the low-shore traps throughout the year, except for samples in November and February, where a higher proportion of crabs > 40 mm CW was found in the traps set at mid and high shore, respectively (Figure 2.7). Overall, for the transect at Aberffraw, the number of crabs > 40 mm CW was always larger than that of crabs < 40 mm CW, and crabs < 15 mm CW were never caught in traps at this site (Figure 2.8). The mean female to male ratio was 0.92:1, with a maximum value (1.50:1) in November, and a minimum value (0.34:1) in February. The female to male ratio in May, however, was considerably low (0.46:1; Table 2.2).

Comparisons between sites

A comparison of the total number of *C. maenas* (from the three shore levels) captured each month at the four different sites shows that crabs were most abundant at Gallows Point (Figure 2.9). The number of crabs per transect in Traeth Melynog and

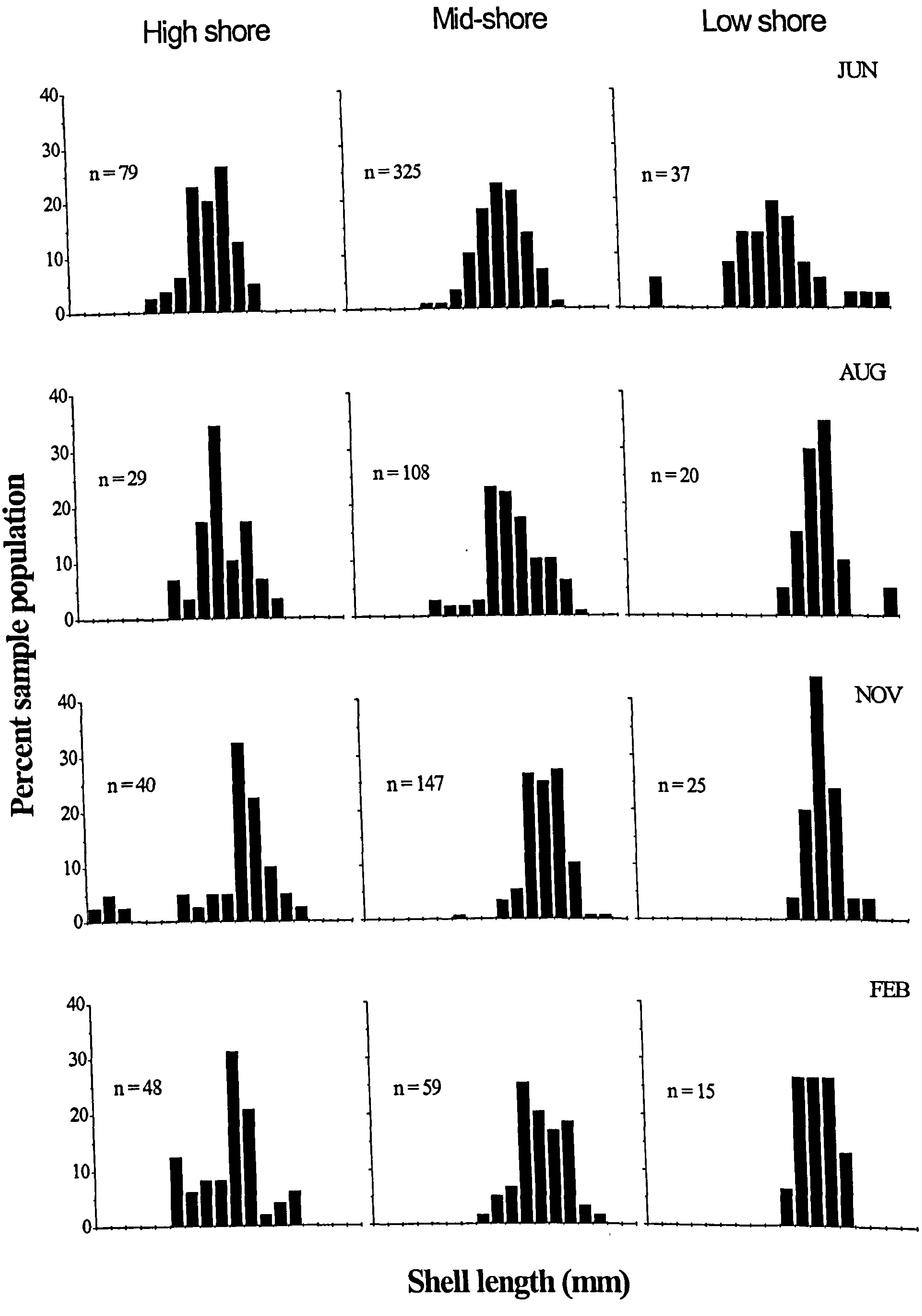


Figure 2.10. Seasonal variations in the size-frequency distribution of *Cerastoderma edule* collected at high, mid and low shore at Traeth Melynog. Values represent the proportion of cockles in each size class of the total number of cockles collected per shore level on each sampling date.

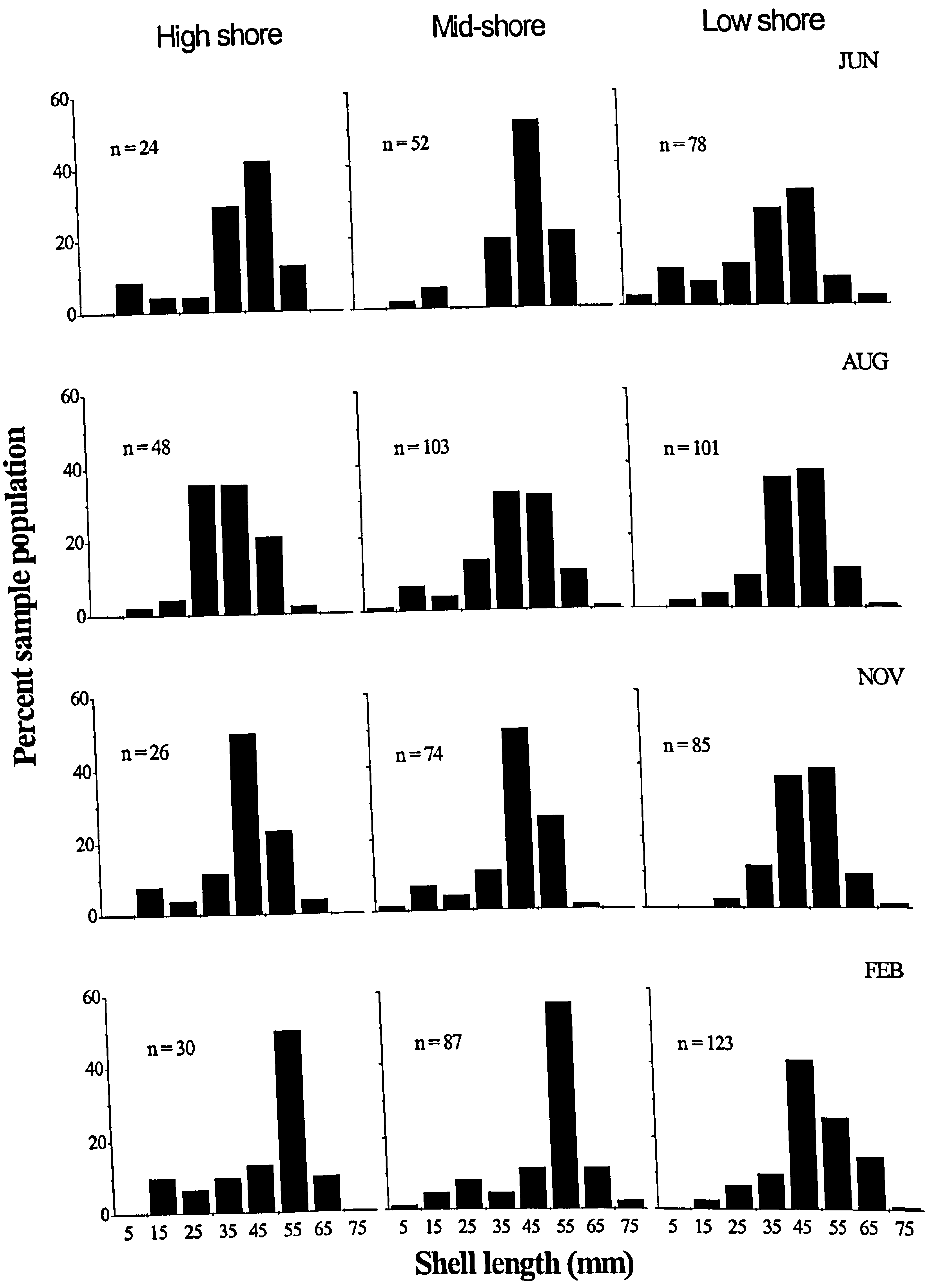


Figure 2.11. Seasonal variations in the size-frequency distribution of *Mytilus edulis* collected at high, mid and low shore at Gallows Point. Values represent the proportion of mussels in each size class of the total number of mussels collected per shore level on each sampling date.

Table 2.4. Mean number (no.•m^{-2}) of *Mytilus edulis* found at Aberffraw (only at high shore) and Gallows Point, and of *Cerastoderma edule* found at Traeth Melynog per shore levels in each month. The mean number of prey at the four seasons (year) is also given. Values are means ± se; n is the number of random quadrats used in each case.

	Aberffraw *Mytilus edulis*		Gallows Point *Mytilus edulis*						Traeth Melynog *Cerastoderma edule*					
	High		High		Mid		Low		High		Mid		Low	
	no.•m^{-2}	n	no.•m^{-2}	n	no.•m^{-2}	n	no.•m^{-2}	n	no.•m^{-2}	n	no.•m^{-2}	n	no.•m^{-2}	n
June	38167 ± 4536	6	192 ± 57	2	416 ± 102	2	624 ± 34	2	316 ± 81	4	650 ± 137	8	144 ± 42	4
August	46667 ± 4730	6	384 ± 136	2	824 ± 322	2	808 ± 141	2	155 ± 31	3	173 ± 18	10	160 ± 34	2
November	37700 ± 3153	10	104 ± 49	4	395 ± 123	3	453 ± 240	3	160 ± 15	4	392 ± 214	6	80 ± 16	5
February	41500 ± 1021	6	240 ± 124	2	696 ± 232	2	984 ± 300	2	154 ± 27	5	189 ± 160	5	48 ± 16	5
Year	41800 ± 1790		230 ± 51		583 ± 92		717 ± 99		196 ± 35		351 ± 97		108 ± 23	

Gallows point increased in August and November and decreased considerably in February. By contrast, the number of crabs per transect at Treborth and Aberffraw did not vary markedly throughout the year. In addition, the number of crabs < 40 mm CW at all sites increased in August and November (Figure 2.8), but generally decreased in February, June and May. The largest number < 40 mm CW was found at Gallows Point in all seasonal samples (Figure 2.8).

Whereas the total number of crabs (from all seasonal samples) found at Treborth and Aberffraw were evenly distributed across the high, mid, and low shore, the number of crabs found at Traeth Melynog and Gallows Point increased markedly at lower tidal levels (Figure 2.9). The percentage of crabs with damaged or entirely missing chelae was lowest at Gallows Point (9.7 %), compared with Aberffraw (25.5 %), Treborth (22.6 %), and Traeth Melynog (26.2 %).

2.3.2. Prey populations.

Cerastoderma edule

The size distribution of *Cerastoderma edule* (Figure 2.10) shows that cockles found at mid and low shore have a larger shell length than those at high shore. Cockles < 18 mm SL were most abundant at high shore throughout the year. Results of cockle density show that the highest densities of cockles were generally found at mid shore, whilst the lowest was consistently found at low shore (Table 2.4). Cockles were overall more abundant in June than in any other month, except for samples taken at low shore in August and June, which had a similar density of cockles.

Mytilus edulis

Samples of *Mytilus edulis* at Gallows Point showed the population to be dominated by mussels 40-60 mm SL at all shore levels, and that the size distribution of mussels did not vary markedly with season (Figure 2.11). Mussels < 20 mm SL were scarce in samples from all months, although they could be found in a slightly higher proportion at mid and high shore than at low shore. Mussel density was highest at low shore, and decreased with increasing shore level for all samples throughout the year, and was highest in August and February at all three shore levels (Table 2.4). Samples of *M. edulis* taken at the high shore

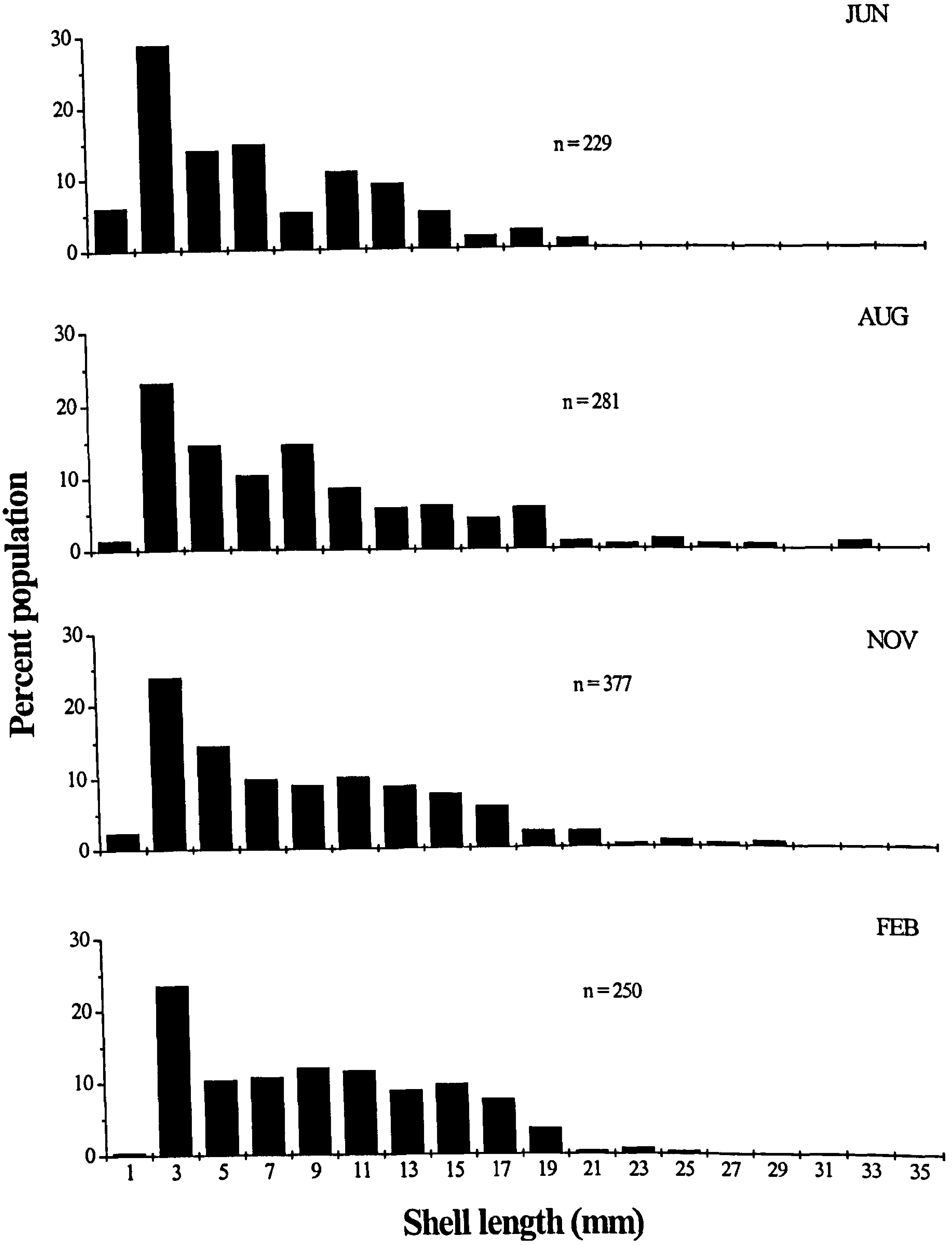


Figure 2.12. Seasonal variations in the size-frequency distribution of *Mytilus edulis* collected at high shore at Aberffraw. Values represent the proportion of crabs in each size class of the total number of mussels collected on each sampling date.

at Aberffraw showed little variation in the size distribution and mussel density throughout the year (Table 2.4, Figure 2.12). Mussels between 2-4 mm SL were always found in the highest proportion. Whilst mussels > 16 mm SL overall were scarce, those > 26 mm SL were only present in samples taken in August and November.

2.4. Discussion

2.4.1. Crab populations.

The numbers of *Carcinus maenas* found across the intertidal region can vary markedly with factors such as season, locality, food supply, and the neap-spring tide cycle (Beukema, 1991; Crothers, 1970; Naylor, 1958). These variations have been partly associated with the migratory habit of species such as *C. maenas* (Dare & Edwards, 1981), and make the determination of crab population density complex and frequently imprecise. The present study showed that the estimated number of shore crabs at Treborth was strongly influenced by the sampling method used during collection. Moreover, the female to male ratio and the size distribution of shore crabs captured with each sampling method also showed marked differences. This suggests that the two sampling methods used in this study probably sampled different parts of the *C. maenas* population at Treborth. Samples of *C. maenas* located under rocks and boulders in the lower shore had a smaller mean carapace width (CW) and a larger proportion of females than those caught in baited traps (Tables 2.1-2.2). Samples of crabs collected by searching under rocks and boulders thus probably represent the proportion of the crab population that are resident in the low intertidal zone when the tide recedes. By contrast, *C. maenas* captured using baited traps had a larger mean CW and a smaller proportion of females (Tables 2.1-2.2), probably representing those individuals that migrate into the intertidal with the incoming tide, but which remain offshore during periods of low water. These results suggest that male and female crabs behave differently with regard to tidal cycles.

Further support for this idea is that both the mean density and CW of resident shore crabs showed a marked seasonal variation, indicating the strong influence of ambient temperature fluctuations on the distribution and abundance of crabs that remain onshore with the ebbing tide (Figures 2.2-2.3). The mean numbers and CW of migrating shore crabs at mid and low shore, on the other hand, did not show such a marked seasonal variation (Table 2.1). Previous studies have reported that during the summer adult shore crabs often remain onshore when the tide recedes, hiding under algae and rocks or in crevices (Atkinson & Parsons, 1973). When water temperatures fall under 8 °C, however, shore crabs migrate into deeper water, remaining there until the temperature increases again (Crothers 1968). Small juvenile crabs, by contrast, appear to remain fairly stationary on the shore throughout the year and show no rhythmical migration (Dare *et al.*, 1983; Klein Breteler, 1976; Naylor, 1962). Results from crab samples collected by hand at low water mark in the present study confirm these findings and suggest that the higher proportion of juvenile crabs (< 30 mm CW; Chapter 3) found during the winter months probably reflects the lower relative abundance of adult crabs in the intertidal region at this time of year.

The relatively higher proportion of the smallest crabs (< 10 mm CW) found from September to December (Figure 2.3), together with the highest female to male ratio, abundance of berried female crabs and mating pairs observed around April and May suggest that a reproductive peak probably occurs during the spring, and that postlarval *C. maenas* should be present in the intertidal by early summer. These findings are in accordance with what has been previously reported for this portunid species (Beukema, 1991; Crothers, 1968). However, shore crabs are known to have more than one reproductive peak each year under favourable temperature and food conditions, and larval production may even occur all year round in certain parts of British coastal waters (Ingle, 1980).

The size-frequency distribution of migratory *C. maenas* may differ across the intertidal gradient as a result of differences in the migratory behaviour of crabs of different age groups and sex (Crothers, 1968; Naylor, 1962). These variations may in turn differ from one locality to another depending on the topography and intertidal extent of each particular shore that is exposed at low water (Dare & Edwards, 1981). Results of the present study confirm these findings and suggest that the percentage of crabs in each size category varies less markedly across shores with a narrower than with a wider extent of exposed substratum between tidal marks. For example, at Gallows Point the percentage of crabs in each size category did not vary markedly with the time of year across the somewhat narrow intertidal gradient (Figure 2.6), whereas at Aberffraw crabs < 40 mm CW were found at a considerably higher percentage at high and mid shore during the warmer months of August and November, and at low shore in February (Figure 2.7). At Traeth Melynog, the sampling site with the widest and less steep intertidal zone, the percentage of crabs < 40 mm was very low throughout the year, only attaining higher values in the mid and low shore during the colder months of February and June (Figure 2.5). In addition, comparisons between the four sampling sites showed that the total number of crabs throughout the year at high, mid and low shore were similar at Treborth (Figure 2.8), a shore with a rather narrow and steep intertidal extent. By contrast, at Traeth Melynog, the number of crabs found in traps set at low shore was always larger than those set in the high and mid shore. Similar results were reported by Sanchez-Salazar (1986) at the latter site.

The abundance of *C. maenas* can also differ from one site to another due to variations in the local degree of shelter and food supply found (Crothers, 1970). Comparisons of the total number of crabs found during each sampling period showed that crabs were most abundant at Gallows Point throughout the year (Figure 2.8). Previous studies on the ecological features of *C. maenas* have demonstrated that maximum abundance of crabs is generally found on sheltered shores that offer a variety of refuge sites where crabs can hide (Edwards, 1958; Klein Breteler, 1976). The sampling area at Gallows Point is at the boundary of a large commercial mussel bed, which comprises highly diverse sources of food for crabs. When the tide recedes, extensive fucoid patches offer abundant shelter for crabs, thus combining good conditions for the successful settlement and growth of crab populations. The availability of food types and the topographic conditions at Gallows Point might also explain the considerably larger proportion of crabs < 40 mm CW captured in baited traps at this locality compared with Treborth, Aberffraw, and Traeth Melynog (Figure 2.8).

Differences in the density of *C. maenas* and *Cancer pagurus* found intertidally under rocks and boulders in the present study (Figures 2.2-2.4) probably reflect the contrasting behaviour of these two species of brachyuran crabs. Whilst *C. maenas* actively searches for food with the incoming tide and large numbers of shore crabs are expected to be left stranded as the tide recedes (Hunter & Naylor, 1993; Naylor, 1958), *C. pagurus* is a burrowing, relatively more sedentary, species that does not exhibit such a marked migratory behaviour (Brown & Bennett, 1980; Lawton, 1983). The fact that *C. pagurus* was never caught in baited traps further confirms the rather sedentary nature of this cancrid species.

Inter-specific competition for refuges has been described between North American benthic crustaceans (Jeffries, 1966; O'Neill & Cobb, 1979), and may be important in structuring European benthic crustacean communities. Spatial resources have been found to be an important factor affecting the intertidal size-frequency distribution and abundance of juvenile *C. pagurus* (Lawton, 1983). Larval production of *C. maenas* is known to be less markedly seasonal than in *C. pagurus*, and female edible crabs can carry eggs for a period of up to 7-8 months (Ingle, 1980). These reproductive characteristics in *C. pagurus* may result in the prior occupancy of intertidal refuge sites by other postlarval decapods, particularly *C. maenas* (Elner, 1981), probably reducing the success of intertidal settlement by *C. pagurus*. However, previous observations have suggested that the low intertidal zone of nearby beaches may be important as nursery areas for different sizes of juvenile *C. pagurus* (Lawton, 1983).

Along-shore movements of juvenile crabs in response to changing requirements for shelter as well as general movements into subtidal areas as crabs mature indicate that spatial resources are unlikely to be limiting for larger, adult edible crabs (Lawton, 1983). Thus, the samples of *C. pagurus* collected at low-water mark at Treborth during this study probably represent only a small proportion of the total local edible crab population, where the majority of the adult individuals are distributed subtidally.

2.4.2. Prey populations.

The size-frequency distribution and density of the *Cerastoderma edule* population at Traeth Melynog during the present study confirm some of the results reported by previous authors. Sanchez-Salazar *et al.* (1987b) found marked variations in the abundance of *C. edule* across the intertidal gradient at this same site, density being highest at intermediate shore levels and decreasing sharply towards the upper and lower tidal limits. However, these authors found large numbers of cockles < 10 mm shell length (SL), whereas, in the present study, cockles < 15 mm SL were only occasionally found in the high shore. In addition, Sanchez-Salazar *et al.* (1987b) found that cockle density was $\cong$100 m^2 in April, but increased markedly in October ($\cong$ 244 m ^{2}) following spat settlement during the late summer. Present results, however, showed that cockle density was higher in June than in November at all shore levels (Table 2.4), probably due to the general absence of cockle spat in almost all samples examined (Figure 2.10). This could be the result of using a mesh size (6.5 mm) that was not small enough for the smallest cockles to be retained, since later samples of juvenile crabs (mesh size: 1.5 mm) collected in June, 1997 included cockles down to 3.0 mm SL in substantial numbers.

Predation by shore crabs and oystercatchers, *Haematopus ostralegus*, can strongly influence the population structure and spatial distribution of *C. edule* at Traeth Melynog (Sanchez-Salazar *et al.*, 1987b). The extent to which crab predation can influence mollusc populations depends greatly on the population structure and spatial distribution of predator and prey (Whetstone & Eversole, 1978), therefore, not only seasonal fluctuations in crab population density, but those in crab size-frequency distribution will influence the predation impact on the bivalve species. Previous reports have demonstrated that juvenile shore crabs can affect recruitment success of meiofaunal prey (Gee *et al.*, 1985), and production of juvenile *C. maenas* in the Danish Wadden Sea during July and August was estimated to account for 26.1 % of the elimination of *C. edule* (Jensen & Jensen, 1985). The presence of juvenile shore crabs at relatively high densities in the current study (Table 2.3), and their co-occurrence with cockle spat at all shore levels, suggests that predation even by the smallest crabs probably plays an important role in structuring the *C. edule* population at Traeth Melynog. However, further investigation is required to accurately assess this impact, since alternative food types such as polychaete worms (e.g. *Arenicola marina*) and gastropods (e.g. *Hydrobia ulvae*) were also common in the samples collected.

The mean density and size-frequency distribution of *Mytilus edulis* differed markedly between the natural population at Aberffraw and those adjacent to the commercially reared mussel beds at Gallows Point, although, seasonal fluctuations in these population parameters could not be detected at either site (Table 2.4; Figures 2.11-2.12). Mussel population features such as growth, mortality, and recruitment can vary from one shore to another, depending on the degree of wave exposure, substratum and food supply, and the abundance of major predators (Seed, 1973). Populations from the high shore of wave-exposed sites with relatively few major predators tend to have long-lived mussels and reduced linear growth, a characteristic that is further accentuated by high mussel population densities (Seed, 1969). A combination of these environmental factors is observed at Aberffraw, where the high densities within *M. edulis* patches probably significantly reduce growth in shell length, and where the lack of a suitable substratum restricts distribution towards the sea.

Some of the differences observed between *M. edulis* populations from these two sampling sites, however, probably derive mainly from the commercial harvesting of the mussel beds at Gallows Point. *C. maenas* is a widespread and often abundant predator along the coastlines and estuaries of Europe, and has been recognised as an important pest of juvenile molluscs in many natural and cultivated fisheries (Dare *et al.*, 1983). Cultivators have reduced the risk of crab predation by seeding larger spat or using suspended cultivation methods (Laing & Spencer, 1997). Mussels < 20 mm SL were infrequent at Gallows Point, and when they were present, they were slightly more abundant in the high and mid shore than in the lower regions of the shore. These observations might result from programmed management strategies of the cultivators to minimise loss in mussel production. The fact that crab abundance was considerably higher at Gallows Point than at any other sampling site, and that crabs were always found in higher numbers in the low- than in mid- and high-shore traps (Figure 2.8), indicate the potential impact of crab predation on these relatively more vulnerable size classes of mussels. In order to substantiate such a hypothesis, a more detailed examination of the ecological features of both crab and prey populations is needed, since overall seasonal fluctuations in crab abundance were not followed by any subsequent fluctuations in the density of mussels collected between tidal marks (Figures 2.8 & 2.11).

2.5. Summary

1. The numbers of *Carcinus maenas* recorded at Treborth were strongly influenced by the sampling method, and evidence suggested that each method sampled only a portion of the total local crab population. *C. maenas* collected using a standard searching time at low water mark of spring tides were generally smaller and had proportionately more female crabs. Both the mean density and size of these resident crabs fluctuated markedly throughout the year, attaining the highest values in late summer. These samples probably

comprise the more sedentary individuals that remain in the intertidal zone when the tide recedes, and whose distribution and abundance are mostly affected by seasonal fluctuations in ambient seawater temperature. *C. maenas* collected using baited traps, by contrast, were larger and had proportionately fewer female crabs. These samples probably represent individuals that migrate into the intertidal to forage with each incoming tide. Neither the mean size nor the abundance of these migrating crabs appeared to be so strongly influenced by seasonal variations in water temperature.

2. A reproductive peak in the *C. maenas* populations at Treborth occurs during the spring, when the highest female to male ratio, and the abundance of berried females and mating pairs was observed. The higher proportion of crabs < 10 mm CW from September to December further confirmed these results and indicated that postlarval *C. maenas* are probably present in the intertidal by early summer.

3. Seasonal variations in the size-frequency distribution of migratory *C. maenas* differed across the intertidal gradient as a result of differences in the migratory behaviour of crabs of different age groups and sex. These variations, in turn, differed from one locality to another suggesting that the percentage of crabs in each size category varies less markedly across shores with a narrower than with a wider extent of exposed substratum between tide marks.

4. *C. maenas* occurred at higher population densities at Gallows Point in all samples throughout the year. The commercial mussel bed on the boundary of this sampling area, and the extensive fucoid patches, provide a high diversity of food types and abundant shelter for the successful recruitment and growth of shore crabs.

5. The differences in the relative abundance of *C. maenas* and *Cancer pagurus* found in the course of this study can be explained by the differences in the vertical distribution of these crab species on the shore, as well as by their contrasting behaviour. In addition, spatial resources appear to be important factors affecting intertidal size-frequency distribution and abundance of juvenile *C. pagurus*, but probably do not constitute a

limiting factor for the larger edible crabs. Thus, samples of *C. pagurus* collected at low-water mark during this study represented only a small proportion of the total edible crab population, where the majority of the adult individuals are distributed subtidally.

6. Variations in the density and size-frequency distributions of *Mytilus edulis* from one locality to another can be the result of biotic and abiotic environmental conditions affecting mussel growth, mortality, and recruitment. However, the differences between the natural population at Aberffraw and the commercial mussel bed at Gallows Point are mostly due to programmed management strategies of cultivators leading to increased mussel production.

Chapter 3

Chelal Morphology and Biomechanics

3.1. Introduction

Chelal morphology varies throughout the range of brachyuran crabs (Vermeij, 1977). Morphological characteristics of crab chelae can determine diet, foraging behaviour and the prey handling techniques (Brown *et al.*, 1979; Warner & Jones, 1976). Monomorphic crabs like those from the genus *Cancer* show equal facility in using both chelae to crush molluscs (Elner & Lavoie, 1983), but portunids, such as *Carcinus maenas*, with dissimilar chelal morphologies use them in distinct ways to feed on a variety of prey types (Ropes, 1968). Although it is possible to relate certain chelal features to the feeding habits of a particular species, differences in morphology are a result of several evolutionary pressures relating to defence, reproduction, burrowing or other behavioural mechanisms (West *et al.*, 1991), and direct relationships between claw form and feeding functions can sometimes be misleading (Seed, 1986a, 1993).

Crabs use chelae in several different ways throughout their feeding behaviour (Akumfi & Hughes, 1987; Jubb *et al.*, 1983; Krantz & Chamberlin, 1978), and the efficiency in the use of their claws determines to a great extent the handling methods used to open their prey. Attack methods are not specific behavioural sequences, but a consequence of crab chelae and prey morphology (Elner & Raffaelli, 1980; Rheinallt & Hughes, 1985) and thus vary with species of prey and predator. Moreover, variability in the natural diet of crabs of the same species can also be related to crab size and relative chelal strength (Choy, 1986; Paul, 1981). Therefore, differences in chelal morphology and biomechanics between and within brachyuran species can have a strong influence on prey selection, and must be taken into account in studies of foraging behaviour.

Attack methods can be a mechanical consequence of chelal morphology but the ability to open a prey item also depends on the strength, size and occluding surfaces of the claws (Elner & Jamieson, 1979). There are various ways of measuring relative chelal strength and comparisons based solely on external dimensions can underestimate potential capabilities of chelae (Seed & Hughes, 1995). The magnitude of the force a chela can exert depends on the length and arrangement of the sarcomere fibres comprising the closer muscle as well as on the amount of muscle tissue present (Warner & Jones, 1976). Furthermore, the magnitude of the force applied is altered by the claw's lever system and thus varies according to the position along the dactylus where the prey is held (Warner & Jones, 1976). Occlusive geometry has an important influence on the way the chelae are used to pinch, and it alters the magnitude of the force delivered at specific points along the claw (Brown *et al.*, 1979). Structural and geometrical variables provide for great potential diversity in occlusive design, and some of the differences in the types of shells selected by crabs can be explained by the occlusive geometry and dentition of the crab chelae (Seed & Hughes, 1997; Warner *et al.*, 1982).

Considering the relevance that handling techniques have in the study of crab foraging behaviour, this chapter will consider the morphology, occlusive geometry, and biomechanics of the chelae of *C. maenas* and *C. pagurus* over a wide range of crab sizes. Results will include comparative descriptions of allometric relationships within the chelae of *C. maenas* and juvenile *C. pagurus* from the Menai Strait, North Wales. In order to investigate the intra-specific differences between chelal morphology and strength of juvenile and adult *C. maenas*, and the way this might affect their selective feeding behaviour, comparisons over a wide size range of this species will be carried out. In a later chapter (4), this information will be related to the different methods used by crabs to evaluate, select and attack their prey.

3.2. Materials and Methods

Carcinus maenas (5-75 mm CW) and juvenile *Cancer pagurus* (10-90 mm CW) were collected by hand from the mid-low intertidal zone at Treborth (Figure 2.1, A) in November, 1994, and deep-frozen until required. Samples were selected to provide a wide range of crab sizes. Carapace width (the maximum distance between the tips of the most distal marginal teeth) of each crab was measured to the nearest 0.1 mm using vernier callipers. Both chelae were removed, and their general morphology and occlusive geometry described. Chelal height (the maximum cross sectional dimension) of each chela was measured to the nearest 0.1 mm and the apodeme plate dissected out, individually labelled, and stored in 70 % alcohol for further analysis. In order to evaluate mechanical advantage, defined as the factor by which the magnitude of the force applied to the claw's lever system is altered by it (see Warner & Jones, 1976), the lever lengths L_1 (the distance between the pivotal point of the dactylus and the point of insertion of the closer apodeme) and L_2 (the

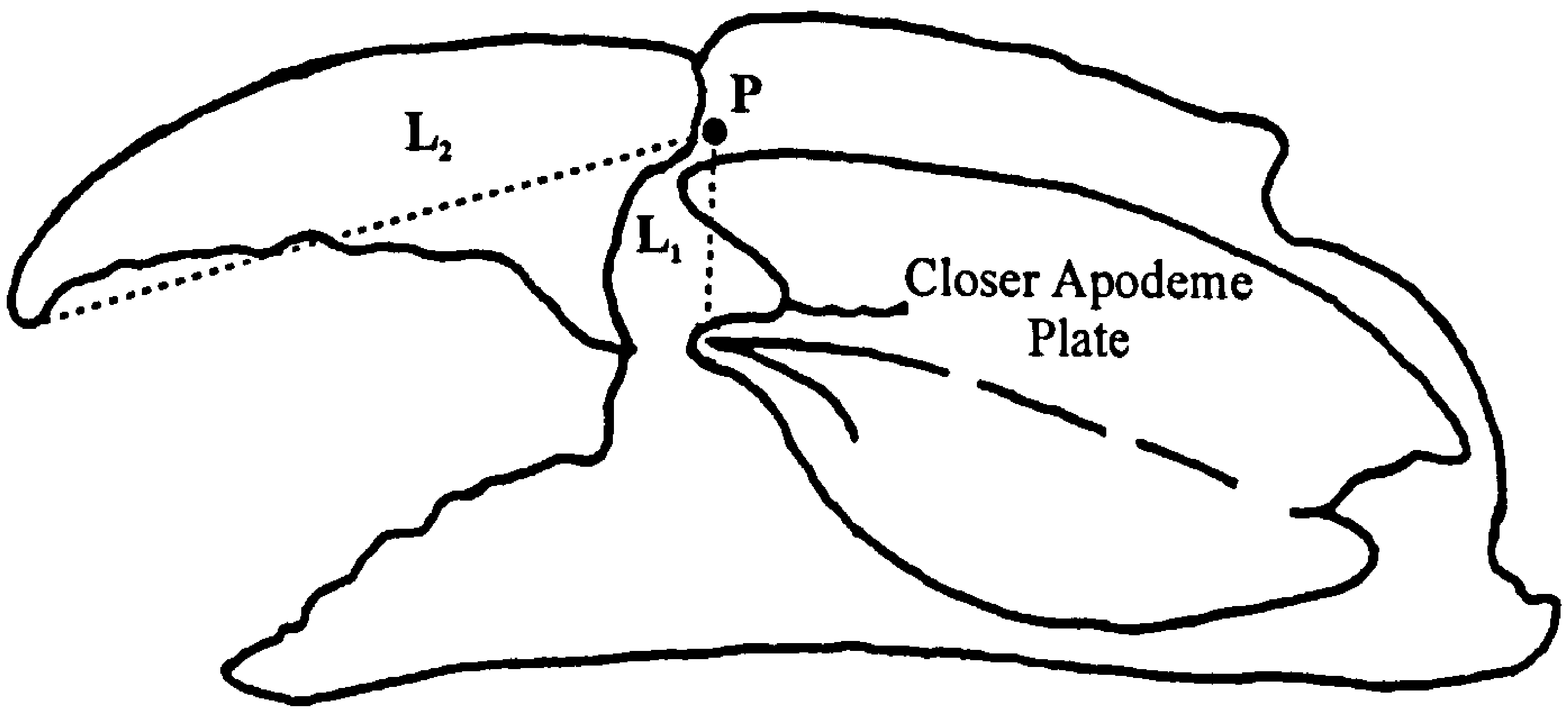


Figure 3.1. Diagrammatic view of a crab's claw showing the closer apodeme plate and the dimensions used to calculate mechanical advantage at the claw tip (L_1 / L_2); P = pivotal point of dactylus and propus.

distance between the pivot and the distal point of the dactylus; Figure 3.1) were recorded to the nearest 0.1 mm using vernier callipers for dimensions > 3.0 mm, and to the nearest 0.01 mm using a micrometric graticule and microscope for dimensions < 3.0 mm. Assuming that the chelal lever system operates on a frictionless pivot, the mechanical advantage (= grip strength) of the claw is equal to the ratio between L_1 and L_2 (Seed, 1986a). Minimum values of mechanical advantage of the chelae at the chelal tip between species and sexes were compared using two sample *t*-tests.

The apodeme plates were dried and mounted on blank 35 mm slides, projected, and their outlines traced. Areas of the drawings obtained were computed using a grid projected onto an acetate sheet (1.0 x 1.0 mm) to count the number of quadrats within each outline. Entire quadrats were counted as units and those falling on the trace were counted as half units; the appropriate magnification factor was applied in order to give the actual areas of the apodeme plates.

The relationship between any two size variables can be expressed by the allometric equation:

$$y = a x^b$$

where a and b are constants, and x and y are pairs of size variables. This equation implies that the two size variables grow relative to each other at a constant rate, defined by the parameter b, and referred to either as the relative growth rate or the level of allometry. If the simple allometric equation is expressed logarithmically it becomes

$$\log y = \log a + b \cdot \log x.$$

Thus, if log y is plotted against log x it will give a straight line whose slope has a value of b. For pairs of variables using the same units of measuring dimensions; growth is positively allometric when $b > 1$, isometric when $b = 1$, and negatively allometric when $b < 1$. For pairs of variables with area-length dimensions, growth is positively allometric when $b > 2$, isometric when $b = 2$, and negatively allometric when $b < 2$.

Carapace width (CW), chelal height (CH) and apodeme area (AA) were examined for evidence of differential growth by testing each pair of variables for their fit to the allometric equation. Fits to this equation were tested by transforming data logarithmically and applying least squares regression. Since the results of all correlation analyses were statistically significant ($p < 0.05$) and the coefficients of determination were high ($r^2 > 0.95$), simple regression analysis was considered appropriate, and the constants a and b were estimated accordingly.

To test for divergence from isometry, one sample *t*-tests were applied to the estimated values of the coeffcient b in the allometric model. To compare the allometric relationships between juvenile and adult crabs, and between species and sexes, analysis of variance was used to test differences between any two slopes (coefficient b in the allometric equation) in various combinations of size variables. For comparisons within species, *C. maenas* < 30 mm CW and > 30 mm CW were considered to be juvenile and adult crabs respectively (Lee & Seed, 1992; Hartnoll, 1978). Because the size range of *C. pagurus* studied only included juvenile crabs (Chapter 2), comparisons between small (10-40 mm CW) and large (40-90 mm CW) individuals were made for this species.

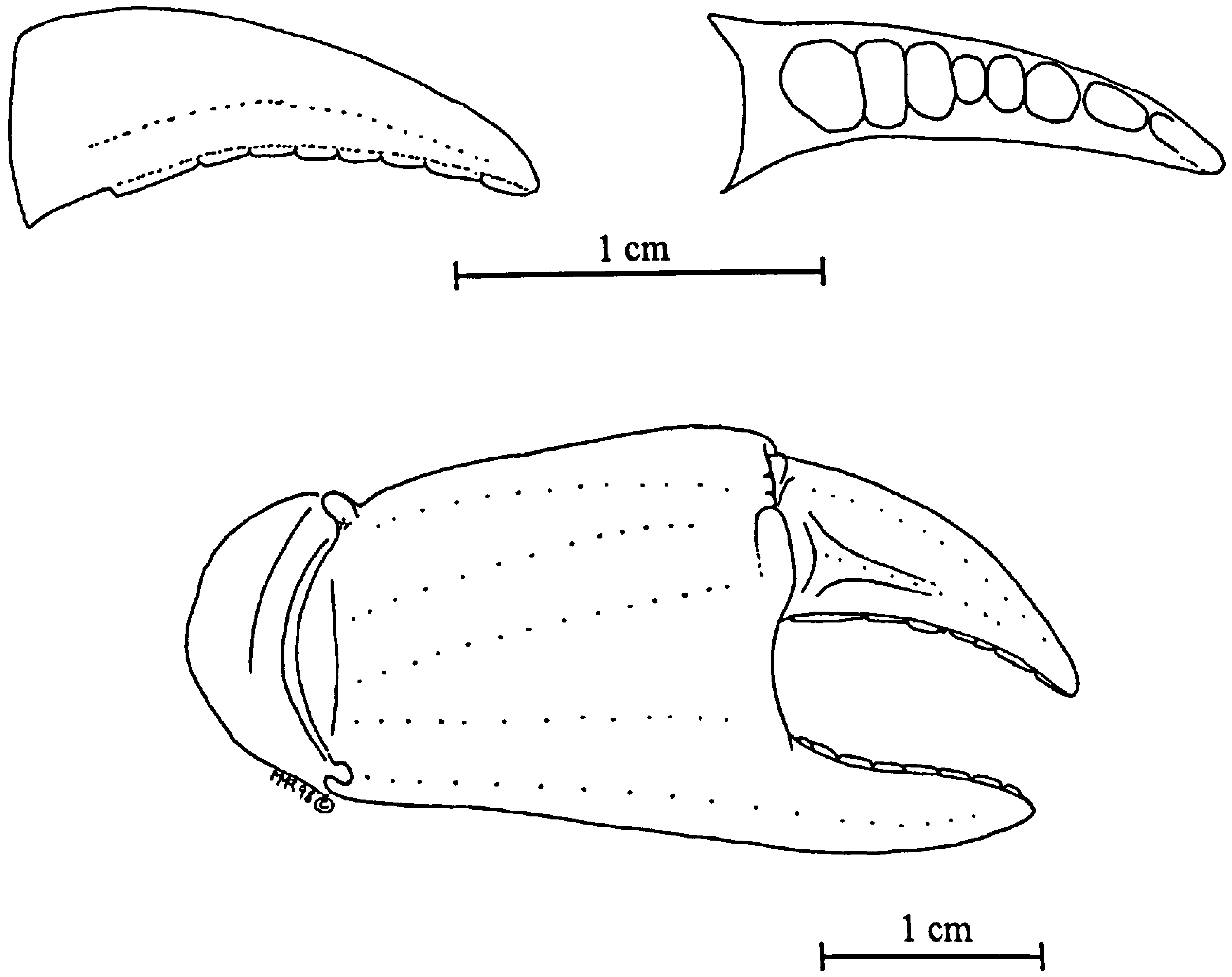
3.3. Results

The sample of 140 *Carcinus maenas* described and measured in this study comprised 70 females ranging from 6.5-62.2 mm CW (29.3 ± 14.6), and 70 male crabs ranging from 7.9-72.4 mm CW (34.5 ± 20.1). Master and minor chelae in *C. maenas* differed in their general morphology, size and occluding surfaces. The master claw was on the right side in 78.5 % of the female shore crabs ($\chi^2 = 21.1, p < 0.001$) and in 84.6 % of males ($\chi^2 = 31.2, p < 0.001$).

The sample of 52 *C. pagurus* studied, comprised 23 female and 29 male crabs, ranging from 20.7-90.5 mm (49.1 ± 17.5) and 13.4-73.3 mm CW (41.2 ± 16.7), respectively. Unlike *C. maenas*, the monomorphic chelae of *Cancer pagurus* were generally similar in their morphology. They were also of equivalent height in 56.5 % of female and 28.6 % of male crabs. The right chela in 30.4 % of the female and the left chela in 42.9 % of the male edible crabs were slightly larger, although differences were not statistically significant ($\chi^2 = 1.6, p = 0.21$ and $\chi^2 = 0.8, p = 0.37$, respectively).

Crusher Chela

A **Dactylus**



B **Propus**

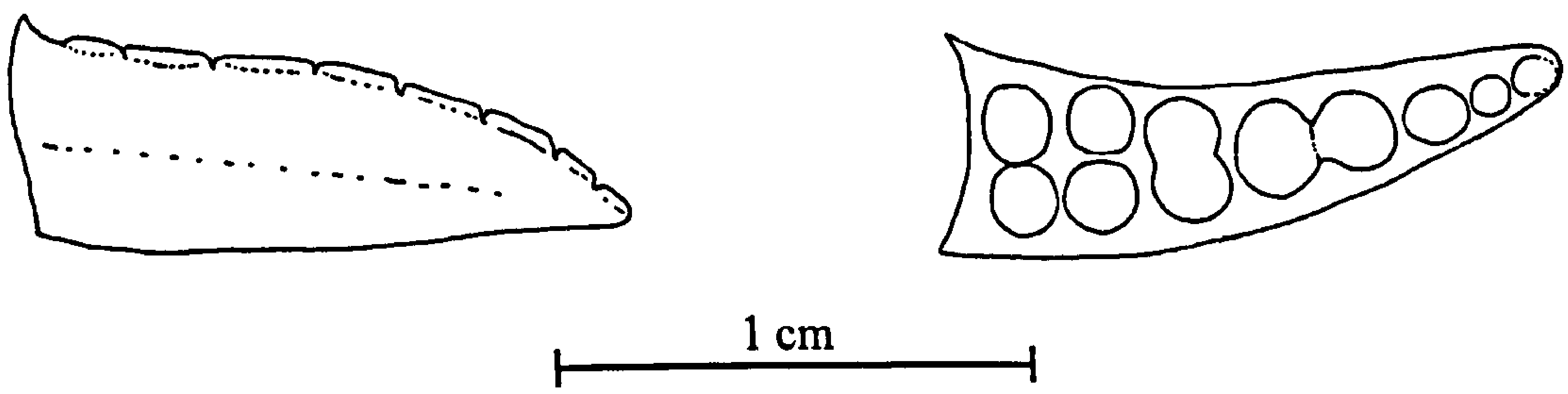
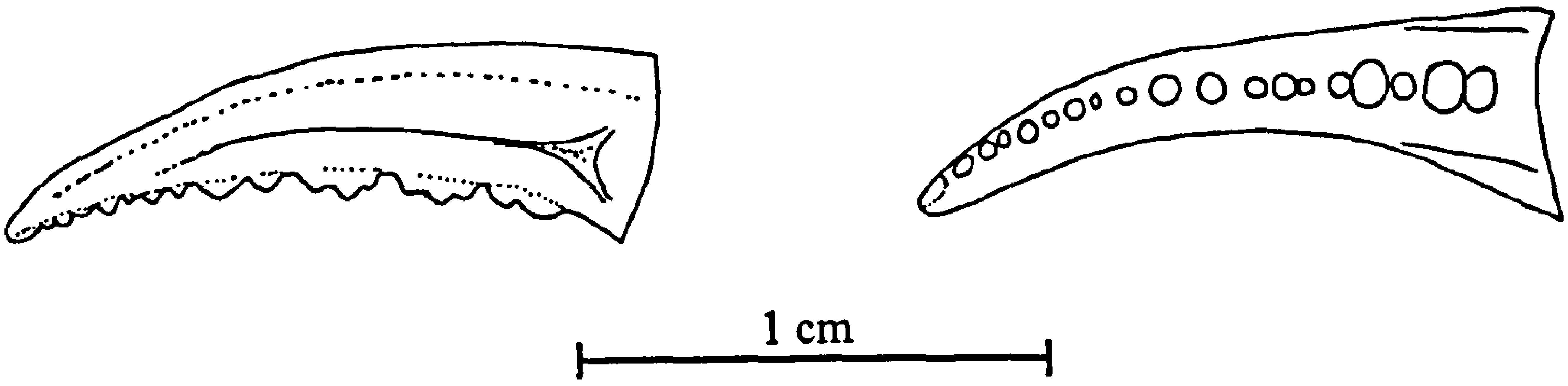
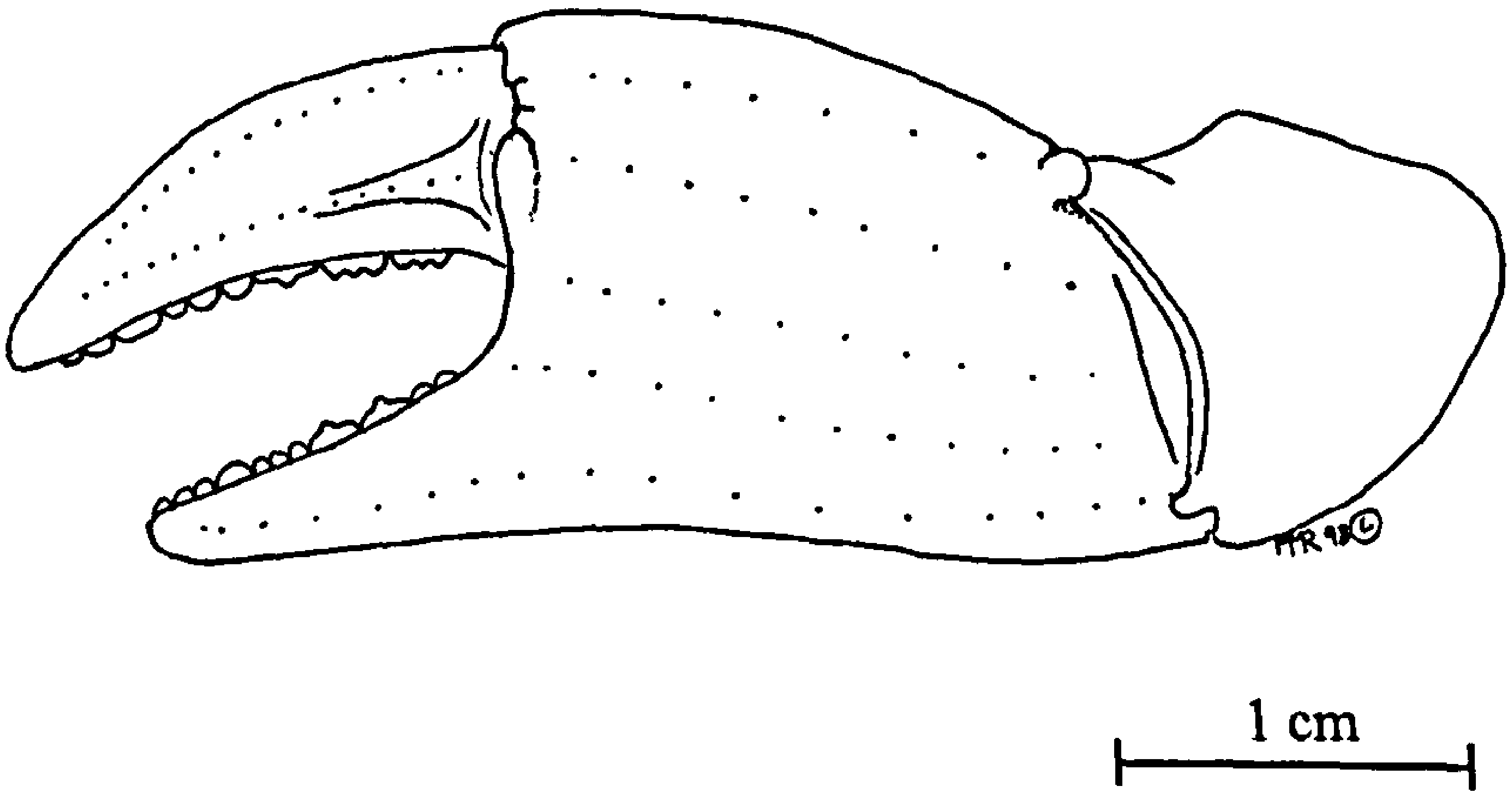


Figure 3.2a. Morphology of the crusher chela of a male *Carcinus maenas* (54 mm CW) showing the occluding surfaces of dactylus (A) and propus (B).

Cutter Chela

A Dactylus





B Propus

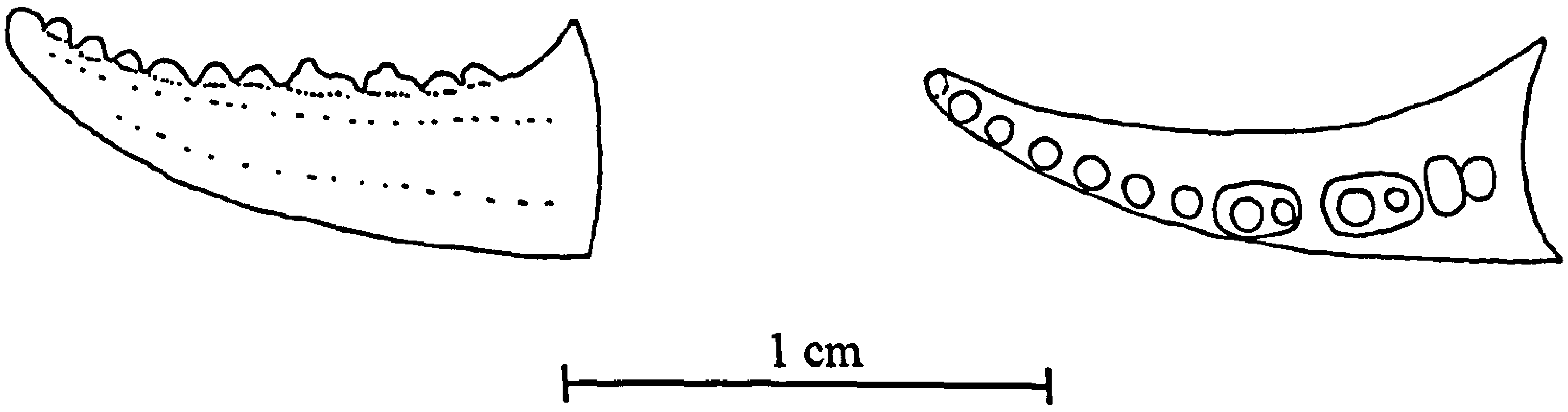


Figure 3.2b. Morphology of the cutter chela of a male *Carcinus maenas* (54 mm CW) showing the occluding surfaces of the dactylus (A) and propus (B).

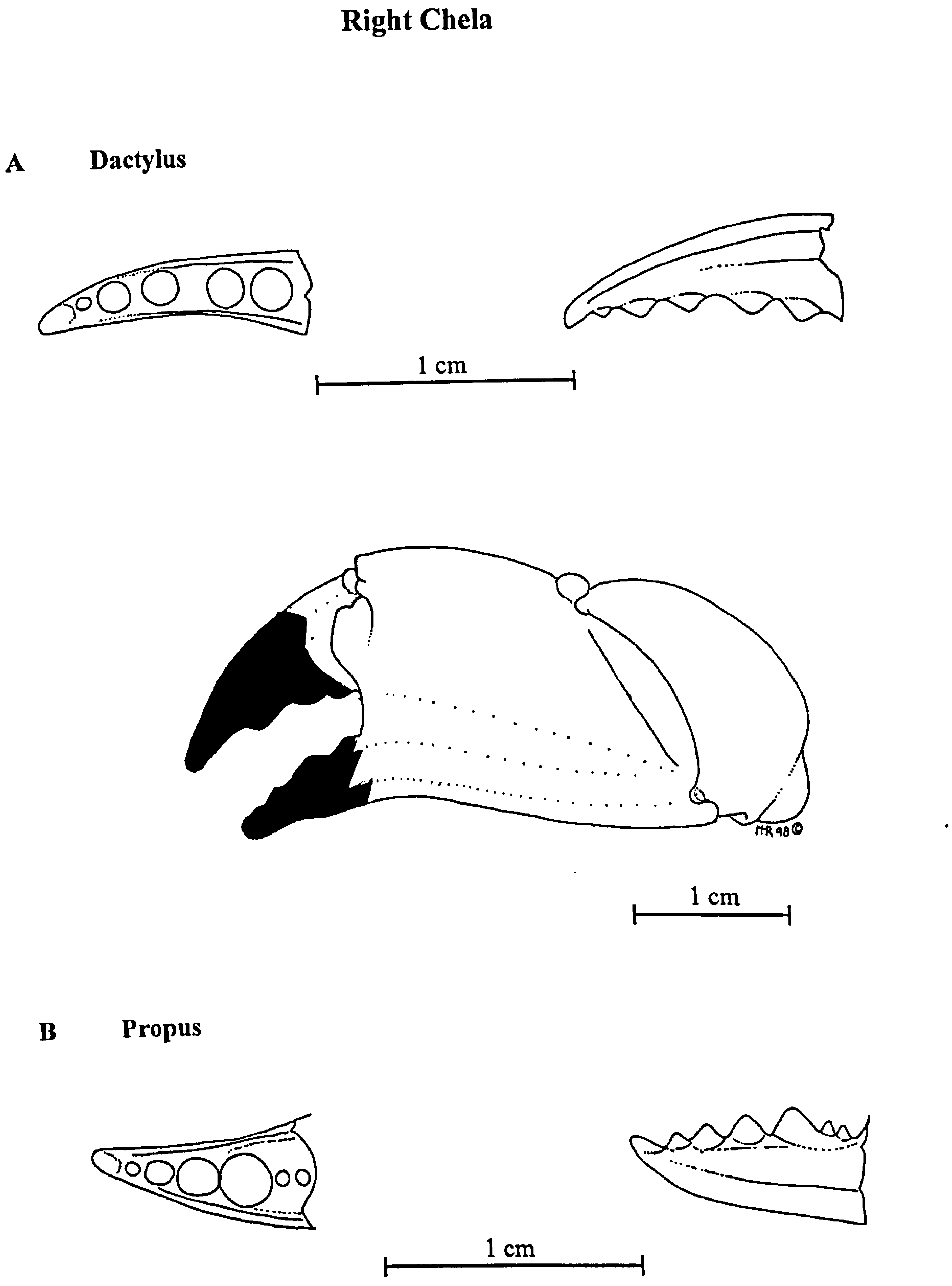


Figure 3.3. Morphology of the right chela of a juvenile *Cancer pagurus* (68 mm CW) showing the occluding surfaces of the dactylus (A) and propus (B). Since the general morphology and occluding surfaces of the left chela are very similar, these have not been represented.

Table 3.1a. Mechanical advantage (MA) corresponding to lever lengths L_1/L_2 for the chelae of *Carcinus maenas* and juvenile *Cancer pagurus*. Values are means ± se.

		Crusher/Right chela [1]		Cutter/Left chela [1]	
Species	Sex	MA	n	MA	n
C. maenas	F	0.297 ± 0.007	65	0.251 ± 0.005	64
	M	0.327 ± 0.010	60	0.269 ± 0.008	62
C. pagurus	F	0.358 ± 0.006	23	0.359 ± 0.007	22
	M	0.366 ± 0.007	22	0.365 ± 0.007	24

[1] Crusher and cutter chelae refer to the heterochelous *C. maenas*; right and left chelae refer to the monomorphic *C. pagurus*.

Table 3.1b. Mechanical advantage (MA) corresponding to lever lengths L_1/L_2 for the chelae of juvenile (< 30 mm CW) and adult (> 30 mm CW) *Carcinus maenas*. Values are means ± se.

		Crusher chela		Cutter chela	
Size	Sex	MA	n	MA	n
Juveniles	F	0.289 ± 0.009	41	0.244 ± 0.007	40
	M	0.312 ± 0.013	39	0.263 ± 0.012	38
Adults	F	0.314 ± 0.007	24	0.261 ± 0.006	24
	M	0.355 ± 0.008	21	0.279 ± 0.005	24

3.3.1. Chelal morphology and occlusive geometry.

The occluding surfaces of the robust master claw in *C. maenas* (Figure 3.2a) consist of a series of broad molariform teeth along the propus that become smaller and more rounded towards the distal region. These are opposed by a similar series of slightly narrower teeth on the dactylus that provide a blunt surface for crushing. When the claw is closed, there is a gap or disjointed area in the middle region of the claw where the propus and dactylus do not meet. However, the distal tips of the master claw meet each other in all but the largest specimens, where the rather curved tips overlap. The propus and dactylus of the minor chela (Figure 3.2b) have interlocking occluding surfaces that consist of a linear series of smaller conical teeth, providing sharp edges for cutting or shearing. The occluding surfaces of the propus and dactylus of this slimmer, more slender claw do not meet along the whole of their length, although the gap formed is much narrower than in the master chela.

Overall chelal morphology did not vary markedly amongst juvenile and adult *C. maenas*, although smaller shore crabs had less distinctive differences between the crusher and cutter chelae. Whilst adults had a chelal dentition with a rather polished and worn appearance, juvenile chelae were less heavily worn and the limits to each tooth were more obvious. Right and left chelae in *C. pagurus* are both robust and heavy. The occluding surface of the propus consists of a series of large molariform teeth that are only slightly sharper on the smaller chela. The opposing surface of the dactylus is arranged with a corresponding series of more narrow rounded teeth, providing a suitable crushing surface. The overall curved shape of both chelae make the occluding surfaces gape in the middle region and the most distal tips overlap (Figure 3.3).

3.3.2. Mechanical advantage.

Mechanical advantage values for crusher and cutter chelae in *C. maenas*, and for right and left chelae in *C. pagurus* are summarised in Table 3.1a. For *C. maenas*, mean mechanical advantage of the crusher chela was significantly higher than that of the cutter in males ($t = 4.75, p < 0.001$) and in females ($t = 5.76, p < 0.001$). The crusher chela in male shore crabs, was also at a significantly higher mechanical advantage than that of females ($t = 2.56, p < 0.05$), but no significant differences in mechanical advantage of the cutter chelae

Table 3.2. Coefficients for the linear regressions between various combinations of size parameters from a size range of *Carcinus maenas* and juvenile *Cancer pagurus*; CW: carapace width; CH: chelal height; AA: apodeme area; (r^2) coefficient of determination; number of observations (n) as in Table 3.3.

C. maenas	Crusher chela			Cutter chela		
Size parameters	Intercept	Slope	r^2	Intercept	Slope	r^2
Females						
CW-CH	-0.70	1.04	0.97	-0.74	1.02	0.98
CW-AA	-1.39	1.83	0.95	-1.64	1.87	0.96
CH-AA	-0.16	1.76	0.94	-0.25	1.76	0.93
Males						
CW-CH	-0.90	1.21	0.98	-0.82	1.08	0.97
CW-AA	-1.97	2.28	0.96	-1.88	2.05	0.96
CH-AA	-0.27	1.85	0.95	-0.37	1.94	0.96

C. pagurus	Right chela			Left chela		
Size parameters	Intercept	Slope	r^2	Intercept	Slope	r^2
Females						
CW-CH	-0.78	1.06	0.99	-0.75	1.03	0.99
CW-AA	-1.62	1.94	0.97	-1.80	2.04	0.97
CH-AA	-0.14	1.79	0.97	-0.33	1.98	0.98
Males						
CW-CH	-0.75	1.04	0.99	-0.79	1.07	0.99
CW-AA	-1.79	2.04	0.95	-1.67	1.98	0.98
CH-AA	-0.33	1.98	0.97	-0.22	1.87	0.98

Table 3.3. Growth coefficient (slope: b) of the regressions between various combinations of size parameters from a size range of *Carcinus maenas* and juvenile *Cancer pagurus*; CW: carapace width; CH: chelal height; AA: apodeme area; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns = no significant departure from isometry.

C. maenas	Crusher chela				Cutter chela			
Size parameters	b	*t*-test	*p*	n	b	*t*-test	*p*	n
Females								
CW-CH	1.04	1.05	ns	50	1.02	0.73	ns	48
CW-AA	1.83	-2.06	ns	45	1.87	-1.71	ns	44
CH-AA	1.76	-2.81	**	44	1.76	-2.43	*	44
Males								
CW-CH	1.21	4.57	***	61	1.08	1.74	ns	62
CW-AA	2.28	2.48	*	59	2.05	0.43	ns	57
CH -AA	1.85	-1.16	ns	61	1.94	-0.53	ns	55

C. pagurus	Right chela				Left chela			
Size parameters	b	*t*-test	*p*	n	b	*t*-test	*p*	n
Females								
CW-CH	1.06	5.63	***	22	1.03	3.02	**	22
CW-AA	1.94	-1.08	ns	21	2.04	0.63	ns	20
CH-AA	1.79	-4.25	***	20	1.98	-0.42	ns	20
Males								
CW-CH	1.04	2.89	**	27	1.07	5.41	***	28
CW-AA	2.04	0.42	ns	26	1.98	-0.52	ns	26
CH-AA	1.98	-0.32	ns	26	1.87	-2.67	*	26

between the sexes could be detected. The mechanical advantage of left and right chelae in *C. pagurus* proved to be statistically indistinguishable, and both were significantly higher than that of crusher chelae of male ($t = 3.28$, $p < 0.01$), and female ($t = 7.16$, $p < 0.001$) *C. maenas*. No significant difference in mechanical advantage between male and female *C. pagurus* was detected ($t = -1.05$; $p = 0.30$). Mechanical advantage varied amongst juvenile and adult *C. maenas* (Table 3.1b), but remained remarkably constant throughout the size range of *C. pagurus* measured. Adult male and female shore crabs had crusher chelae which operated at a significantly higher mechanical advantage than those of juvenile males ($t = -2.78$, $p < 0.01$) and females ($t = -2.22$, $p < 0.05$), respectively, but no significant differences were detected between the cutter chelae in either of the sexes (Table 3.1b). Thus, when the whole range of crabs was considered, mechanical advantage increased significantly through the sequence - cutter chela in male and female *C. maenas* - crusher chela in female *C. maenas* - crusher chela in male *C. maenas* - all chelae in *C. pagurus*.

3.3.3. Allometric relationships between chelal size parameters.

The coefficients (using logarithmically transformed data) of the allometric equations describing the relationships between chelal height, apodeme area and carapace width for both chelae in *C. maenas* and *C. pagurus* are summarised in Table 3.2. Size variables throughout the entire range of crabs examined showed a high degree of correlation as indicated by the high values of the coefficients of determination (r^2).

Results of the one sample *t*-tests applied to the estimated values of slopes (coefficient b in allometric equation) to evaluate divergence from isometry are presented in Table 3.3. In *C. maenas* only chelal height ($t = 4.57$, $p < 0.001$) and apodeme area ($t = 2.48$, $p < 0.05$) of the crusher chela in male crabs are positively allometric with respect to carapace width, indicating that this claw grows proportionately larger and stronger as male crabs increase in their body size. There was no significant departure from isometry for chelal height and apodeme area with respect to carapace width in either female chelae, or in the male cutter claw. Apodeme plate area in both male claws increases isometrically with respect to chelal height thus maintaining geometric similarity amongst all size classes of crabs. However, apodeme areas in both crusher ($t = -2.81$, $p < 0.01$) and cutter chelae ($t = -2.43$, $p < 0.05$) in female crabs are negatively allometric with respect to chelal height, suggesting that increase

Table 3.4. Analysis of variance for various combinations of size parameters between the chelae of juvenile (< 30.0 mm CW) and adult (> 30.0 mm CW) *Carcinus maenas*, and small (< 40.0 mm CW) and large (> 40.0 mm CW) juvenile *Cancer pagurus*; CW: carapace width; CH: chelal height; AA: apodeme area; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns = no significant differences.

C. maenas	Crusher chela		Cutter chela	
Size parameters	*F* (slope)	*F* (intercept)	*F* (slope)	*F* (intercept)
Females				
CW-CH	1.48 ns	1.08 ns	0.65 ns	0.26 ns
CW-AA	2.47 ns	2.67 ns	0.40 ns	0.68 ns
CH-AA	0.00 ns	0.00 ns	0.01 ns	0.17 ns
Males				
CW-CH	25.26 ***	21.95 ***	5.65 *	4.08 *
CW-AA	2.42 ns	2.30 ns	0.40 ns	0.21 ns
CH-AA	0.34 ns	0.29 ns	0.29 ns	0.50 ns

C. pagurus	Right chela		Left chela	
Size parameters	*F* (slope)	*F* (intercept)	*F* (slope)	*F* (intercept)
Females				
CW-CH	0.23 ns	0.31 ns	0.06 ns	0.01 ns
CW-AA	0.14 ns	0.06 ns	0.01 ns	0.02 ns
CH-AA	0.07 ns	0.00 ns	0.21 ns	0.13 ns
Males				
CW-CH	0.01 ns	0.01 ns	4.62 *	3.62 ns
CW-AA	0.47 ns	0.52 ns	4.16 ns	3.64 ns
CH-AA	1.18 ns	1.36 ns	1.91 ns	1.72 ns

Table 3.5a. Analysis of variance for carapace width (independent variable) and chelal height (dependent variable) between chelae of male and female crabs of both species; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns = no significant differences.

	Crusher/Right chela [1]		Cutter/Left chela [1]	
Comparisons between:	F (slope)	F (intercept)	F (slope)	F (intercept)
sexes in *C. maenas*	11.61 **	6.64 *	1.08 ns	0.73 ns
sexes in *C. pagurus*	0.08 ns	0.07 ns	3.50 ns	3.30 ns
males of both species	6.73 **	0.88 ns	0.61 ns	0.79 ns
females of both species	0.00 ns	0.50 ns	0.06 ns	0.01 ns

Table 3.5b. Analysis of variance for carapace width (independent variable) and apodeme area (dependent variable) between chelae of male and female crabs of both species; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns = no significant differences.

	Crusher/Right chela [1]		Cutter/Left chela [1]	
Comparisons between:	F (slope)	F (intercept)	F (slope)	F (intercept)
sexes in *C. maenas*	9.55 **	7.41 **	2.41 ns	2.12 ns
sexes in *C. pagurus*	0.61 ns	0.62 ns	0.00 ns	0.01 ns
males of both species	1.25 ns	0.13 ns	0.00 ns	0.13 ns
females of both species	0.31 ns	0.71 ns	2.11 ns	0.69 ns

Table 3.5c. Analysis of variance for chelal height (independent variable) and apodeme area (dependent variable) between chelae of male and female crabs of both species; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns = no significant differences.

	Crusher/Right chela [1]		Cutter/Left chela [1]	
Comparisons between:	F (slope)	F (intercept)	F (slope)	F (intercept)
sexes in *C. maenas*	2.24 ns	2.89 ns	0.78 ns	1.05 ns
sexes in *C. pagurus*	1.11 ns	1.17 ns	0.18 ns	0.19 ns
males of both species	0.95 ns	0.32 ns	0.21 ns	0.16 ns
females of both species	1.39 ns	0.48 ns	2.49 ns	0.40 ns

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[1] Crusher and cutter chelae refer to the heterochelous *C. maenas*; right and left chelae refer to the monomorphic *C. pagurus*.

in apodeme area of both claws occurs significantly more slowly than increase in chelal height.

Chelal height of both right and left claws in male and female *C. pagurus* are positively allometric with respect to carapace width (Table 3.3), indicating that all claws in this monomorphic species grow proportionately larger as the crabs increase in size. However, the apodeme plates of these claws grow isometrically with respect to carapace width. Whilst the left apodeme plate in female *C. pagurus* and right one in males grow isometrically with respect to chelal height, growth of the apodeme plates in the right female ($t = -4.25, p < 0.001$) and the left male chelae ($t = -2.67, p < 0.05$) was negatively allometric with respect to this size parameter, indicating that these chelae do not become proportionately stronger as they increase in height.

Results of the analysis of variance comparing the allometric relationships of chelal size parameters between juvenile and adult crabs are summarised in Table 3.4. In male *C. maenas*, significant differences between juvenile and adult crabs were found for the regressions of both crusher (slope: $F = 25.26, p < 0.001$; intercept: $F = 21.95, p < 0.001$) and cutter chelal heights (slope: $F = 5.65, p < 0.05$; intercept: $F = 4.08, p < 0.05$) with respect to carapace width, indicating that the chelae of adult male crabs grow at a faster rate relative to overall body size than those of juvenile males. No significant differences between the growth of juvenile and adult male crabs were found for the regressions of apodeme area with respect to either chelal height or carapace width. Amongst female *C. maenas*, no significant differences between juvenile and adult crabs were found in any of the compared regressions.

In general, there were no significant differences between either the slopes or intercepts amongst small (10-40 mm CW) and large (40-90 mm CW) *C. pagurus* for any of the combinations of chelal size parameters (Table 3.4), indicating that throughout the size range studied these size parameters grow at a relatively constant rate. The only exception was that for the height of the left chela of small male crabs which appears to grow at a faster rate relative to carapace width than in large male crabs (slope: $F = 4.62, p < 0.05$; intercept: $F = 3.62, p = 0.07$).

The results of the analysis of variance on the regressions for various combinations of size parameters in the chelae of *C. maenas* and *C. pagurus* are summarised in Table 3.5a-c, and indicate that male shore crabs possess a significantly larger crusher chela ($F = 11.61, p <$

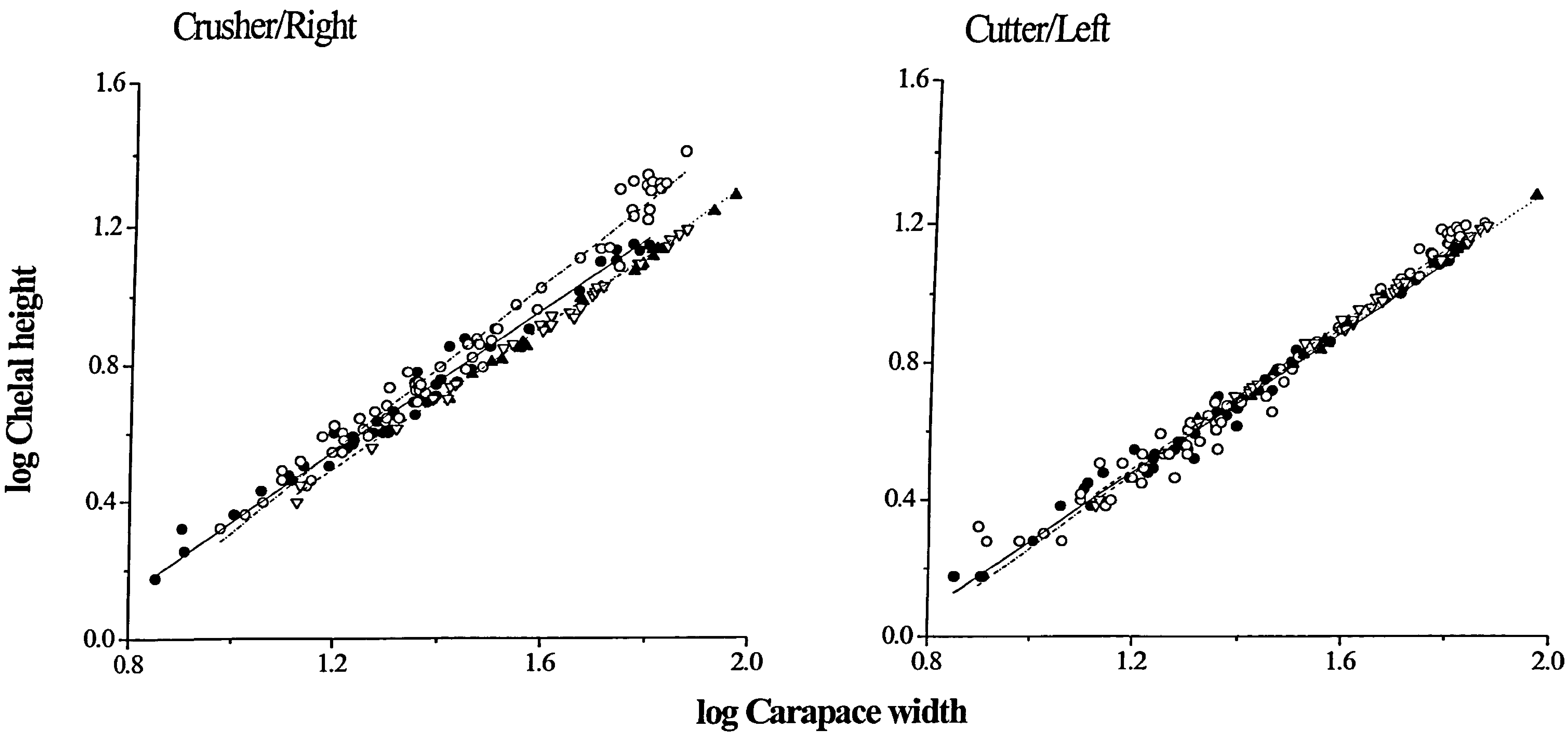

Figure 3.4. Relationships between chelal height and carapace width in the crusher and cutter chelae of female (●) and male (○) *Carcinus maenas*, and the right and left chelae of female (▲) and male (▽) *Cancer pagurus*. Regression lines for female (——) and male (-------) *C. maenas* and for female (·······) and male (-·-·-·-) *C. pagurus* were fitted using the parameters presented in Table 3.2.

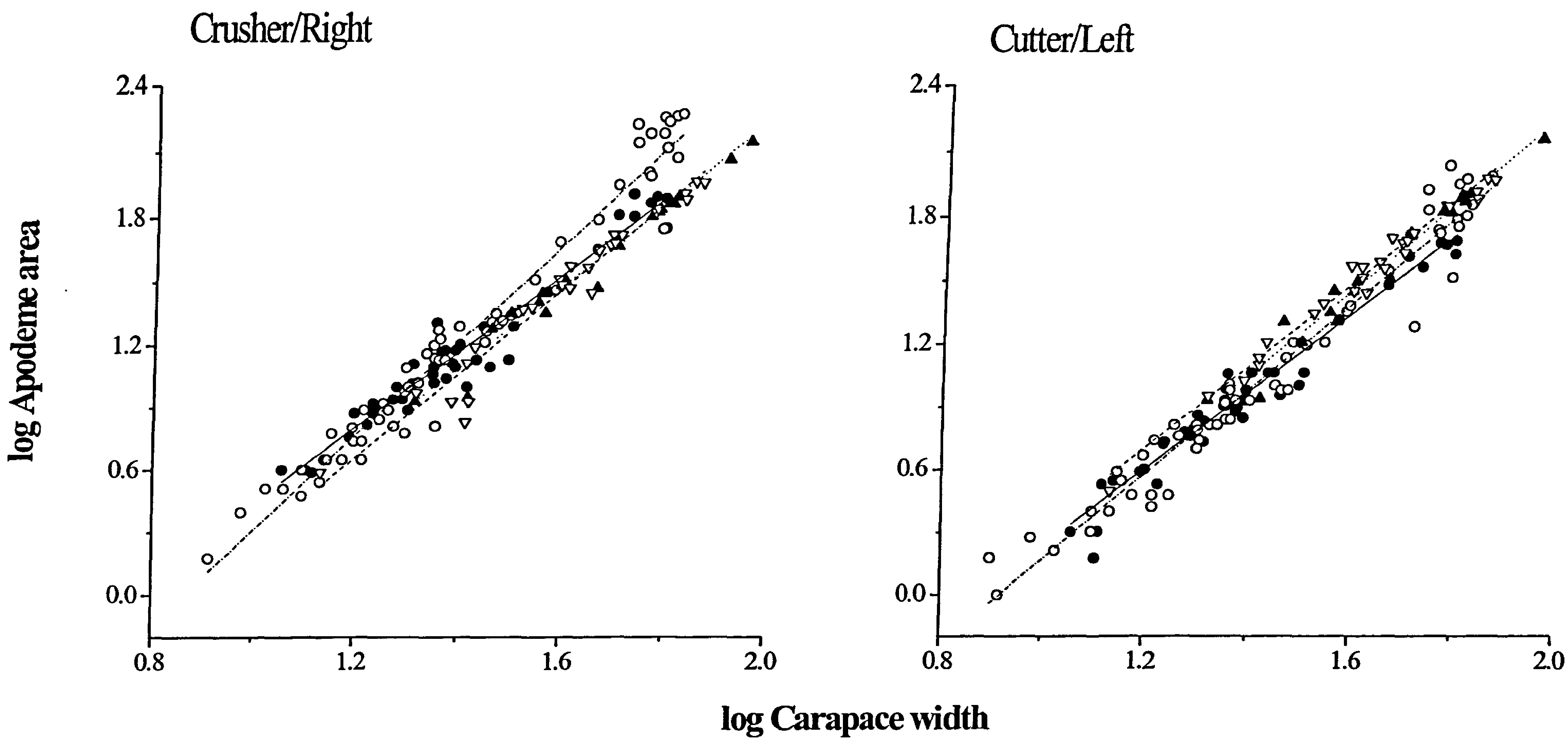

Figure 3.5. Relationships between apodeme area and carapace width in the crusher and cutter of female (●) and male (○) *Carcinus maenas*, and the right and left chelae of female (▲) and male (▽) *Cancer pagurus*. Regression lines for female (——) and male (-------) *C. maenas*, and for female (·········) and male (-·-·-·-) *C. pagurus* were fitted using the parameters presented in Table 3.2.

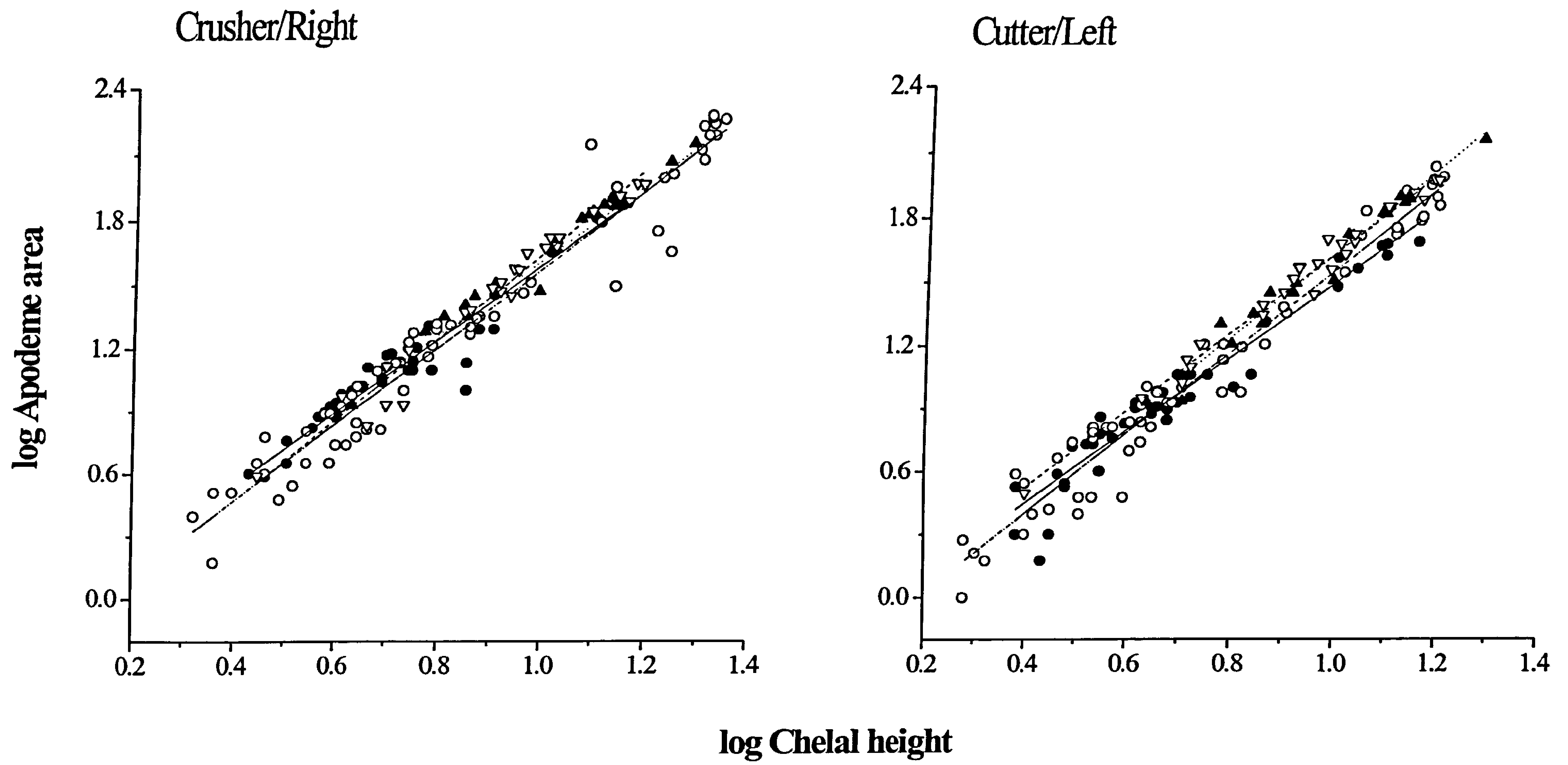

Figure 3.6. Relationships between apodeme area and chelal height in the crusher and cutter of female (●) and male (○) *Carcinus maenas*, and the right and left chelae of female (▲) and male (▽) *Cancer pagurus*. Regression lines for female (——) and male (-------) *C. maenas*, and for female (··········) and male (-·-·-·-) *C. pagurus* were fitted using the parameters presented in Table 3.2.

0.01), with a larger apodeme plate ($F = 9.55$, $p < 0.01$) than female shore crabs of comparable body size, although there were no significant differences between the cutter chelae of male and female crabs (Table 3.5a-b). Both the slopes and intercepts of the regression lines for crusher chelal height and carapace width and for crusher apodeme area and carapace width of male shore crabs were significantly different (Table 3.5a-b), indicating that these regression lines for males intersect those for females (Figures 3.4-3.5). Females smaller than approximately 30.0 mm CW (1.4 on the log scale) thus have a slightly larger crusher chela and apodeme plate than males of similar body size. In order to establish whether these differences were statistically significant, further analysis of variance on the regressions of juvenile male and female crusher chelal height (CH) and apodeme area (AA) against carapace width (CW) were carried out. Results revealed no significant differences between either the slopes (CW-CH: $F = 0.00, p = 0.98$; CW-AA: $F = 1.63, p = 0.21$) or the intercepts (CW-CH: $F = 0.11, p = 0.74$; CW-AA: $F = 1.57, p = 0.22$) of either regressions, suggesting that crusher claws are statistically indistinguishable in their size and strength amongst juvenile crabs (< 30 mm CW) of both sexes.

Male shore crabs have a significantly larger ($F = 6.73, p < 0.01$) crusher chela than edible crabs of comparable carapace width, but their respective apodeme plates had similar areas ($F = 1.25, p = 0.27$; Table 3.5a-b, Figures 3.4-3.5), suggesting that male *C. maenas* have a larger, but not stronger crusher chela than *C. pagurus* of comparable carapace width. No significant differences between male and female *C. pagurus* were found in any combination of size parameters, indicating that chelal size and apodeme area are similar for male and female crabs of similar body size in this monomorphic species (Table 3.5a-c, Figures 3.4-3.6). Similarly, no significant differences in the apodeme areas of either chelae amongst crabs of equivalent chelal height could be demonstrated (Table 3.5c; Figure 3.6).

Because of the significant differences in allometric relationships between juvenile and adult male *C. maenas* (Table 3.4), analysis of variance to compare all size parameters between species and sexes were applied to data sets excluding juvenile crabs. Results of these tests were similar to those that included juvenile crabs.

3.4. Discussion

Authors in the past have suggested that crab chelae act as templates upon which feeding behaviour and prey preferences are determined (Elner, 1978), and that morphological characteristics of the chelae need to be included in any comprehensive study of crab foraging behaviour (Boulding, 1984; Davidson, 1986; Elner, 1980). Variations in chelal morphology amongst brachyuran species and their relationship to feeding preferences have also been used to explain biogeographical patterns of species occurrence (Vermeij, 1977; West, *et al.*, 1991). In the present study, there were marked differences between the massive monomorphic chelae of *Cancer pagurus*, and the dimorphic chelae of *Carcinus maenas* which possess a more robust crusher claw and a slimmer cutter claw (Figures 3.2-3.3). As in other molluscivorous crabs (Warner & Jones, 1976; Blundon & Kennedy, 1982a; Lee & Seed, 1992), the chelae of female *C. maenas* were less strongly dimorphic than their male counterparts, although in both sexes the crusher was more frequently the right claw. Right-handedness in *C. maenas* might have evolved as a response to the predominantly dextral coiling of marine gastropods, as it has been suggested for calappid crabs (Ng & Tang, 1985).

Diversity in occlusive design and regional specialisation within chelipeds suggests that crab chelae are polyfunctional and thus exhibit structures that are probably determined by an interplay of several selective forces (Lee & Seed, 1992). Bearing in mind that potential functional capabilities of claws can be underestimated (Brown *et al.*, 1979), two general morphological types of chelae which are likely to represent adaptations to feeding were found in the course of this study. The series of broad molariform teeth found in both chelae of *C. pagurus* and in the crusher chela of *C. maenas* (Figures 3.2a & 3.3) make the occluding surfaces of these claws especially well designed for crushing hard-shelled prey. Teeth were wider and larger in the most proximal region of the claw, providing a blunt surface for crushing prey at the region where mechanical advantage is highest. They became smaller and more rounded towards the distal region, at which end the tips of the propus and dactylus meet each other providing effective pincers for holding prey shells and pinching flesh. These rather curved claws result in the occluding surfaces gaping in the middle region, where only relatively voluminous items of prey can be held whilst smaller prey items are easily dropped. In contrast, the cutter chela in *C. maenas* had smaller and sharper teeth and the gape in the middle region was narrower. This suggests that the cutter chela is better adapted for cutting and shearing, and is used for keeping prey in position, rather than for applications of force.

Direct relationships between occluding design and the specific performance of claws while handling prey have been suggested for other portunids (e.g. Du Preez, 1984; Seed, 1980), and the contrasting dentition of crusher and cutter chelae in *C. maenas* allow for similar relationships to be suggested.

Chelal strength and occlusive geometry are closely related to handling techniques, and this relationship can partly explain crab preferences for certain types and sizes of prey (Davidson, 1986). Morphological differences between chelae are related to the way various species of crabs use their chelae throughout a variety of handling methods (Rheinallt, 1982). Whilst *C. maenas* generally used the master chela for crushing and the minor chela for holding prey, *C. pagurus* used both chelae indiscriminately for these purposes. These results verify previous observations on the feeding behaviour of *C. maenas* (Elner, 1977; Elner & Raffaelli, 1980), and are also consistent with the distinct use of claws in the handling techniques of other heterochelous species (Elner & Jamieson, 1979; Du Preez, 1984; Hughes & Seed, 1981; Seed, 1980). Studies on cancrids, on the other hand, have reported a lack of any apparent specialisation of the two virtually identical claws (Boulding, 1984; Juanes & Hartwick, 1990; Lawton & Hughes, 1985), and are therefore considered unusual amongst molluscivorous crabs (Seed & Hughes, 1995; Vermeij, 1977).

Evidence of a significant increase in mean mechanical advantage values through the sequence - cutter chela in male and female *C. maenas* - crusher chela in female *C. maenas* - crusher chela in male *C. maenas* (Table 3.1a) further supports what has been found in other studies of dimorphic crabs (Brown *et al.*, 1979; Seed, 1993; Vermeij, 1977), where the master or crusher claw is potentially stronger, and thus used more frequently than the cutter claw for crushing prey items. Although adult male *C. maenas* possess a higher crusher chela than juvenile *C. pagurus* of comparable carapace width, the fact that mechanical advantage of the monomorphic claws of both male and female *C. pagurus* were the highest of all crabs measured suggests that both claws in the edible crab are potentially stronger than the crusher claw in *C. maenas*, and can be used indiscriminately when feeding on hard-shelled molluscs. Moreover, this study only examined juvenile *C. pagurus*, and like the chelae of *C. maenas*, these probably increase allometrically with respect to carapace width, resulting in adult *C. pagurus* to have larger and stronger chelae than adult *C. maenas*.

Table 3.6. Mean mechanical advantage ± 1 SD of the crusher and cutter chelae of several portunids.

Species	Sex	Crusher chela	Cutter chela	Source
Thalamita	M	0.330 ± 0.020	-	Seed, 1986a
crenata	F	0.321 ± 0.018	0.220 ± 0.007	
Thalamita	M	0.295 ± 0.032	0.216 ± 0.011	Seed, 1986a
danae	F	0.276 ± 0.026	0.220 ± 0.014	
Callinectes	M	0.230 ± 0.024	0.178 ± 0.017	Blundon & Kennedy, 1982a
sapidus	F	0.232 ± 0.018	0.185 ± 0.020	
Carcinus	M	0.327 ± 0.044	0.264 ± 0.023	Lee & Seed, 1992
maenas	F	0.282 ± 0.027	0.251 ± 0.025	
Liocarcinus	M	0.247 ± 0.027	0.224 ± 0.027	Lee & Seed, 1992
holsatus	F	0.222 ± 0.029	0.215 ± 0.025	

Mean mechanical advantage values in both chelae of male and female *C. pagurus* were not significantly different (Table 3.1a), and are similar to those reported in previous studies (e.g. 0.329 ± 0.01; Warner & Jones, 1976). They also fall within the range of values given for other cancrids, which range from 0.394 (*Cancer borealis*) to 0.268 (*Cancer magister*; e.g. Lawton & Elner, 1985; Seed & Hughes, 1995). The massive chelae of *C. pagurus*, which operate at a relatively high mechanical advantage, are clearly related to the fact that these crabs typically feed on slow-moving hard-shelled molluscs, although it has been suggested they could also constitute an adaptation for deep burrowing (Lawton & Elner, 1985).

Results in the present study showed that mechanical advantage of the cutter chelae was similar in both male and female *C. maenas*, whereas the mean value for the crusher chela in males was significantly higher than in females (Table 3.1a). Mean mechanical advantage values for both crusher and cutter chelae in *C. maenas* observed in the present study (Table 3.1a) are similar to those reported previously for this species (Table 3.6). Moreover, comparisons with mean mechanical advantage values given for other portunids (Table 3.6) suggest that male *C. maenas* are able to generate greater compressive forces than both male and female *Thalamita danae*, *Callinectes sapidus* and female conspecifics, but similar forces to those generated by male and female *Thalamita crenata*. Female *C. maenas*, *T. danae* and *C. sapidus* are able to generate similar forces, as indicated by the mean mechanical advantage values of their crusher chelae.

Information regarding the mechanical advantage and chelal morphology of *C. maenas* suggests that the common shore crab is a somewhat more heterochelous species, with a relatively more robust crusher chela, than other portunids such as *Ovalipes catharus* (Davidson, 1986) and *Necora puber* (Rheinallt & Hughes, 1985). Seed and Hughes (1997) found that male *Callinectes sapidus* was no more heterochelous than female conspecifics, with ratios between crusher and cutter chelae height of 1.22 ± 0.12 and 1.22 ± 0.05, respectively. In the present study, male *C. maenas* had a crusher to cutter chelal height ratio of 1.25 ± 0.02, whilst in females the ratio was 1.18 ± 0.01. Although the confidence intervals given for these values do not allow for significant differences between *C. maenas* and *C. sapidus* to be distinguished, the difference in the crusher to chelal height ratios between sexes in *C. maenas* proved to be statistically significant ($t = 3.47$, $p < 0.001$). These figures indicate that male *C. maenas* are more heterochelous than female conspecifics thus confirming the results of previous reports on the sexual dimorphism in this brachyuran species (Lee & Seed, 1992).

Differences in mechanical advantage between portunid species account for the different potential forces and use of the chelae during the development of certain handling techniques (Rheinallt, 1982; Seed, 1980). While the force produced by the system increases with mechanical advantage, the speed of the resultant movement and the distance moved decrease proportionately (Warner & Jones, 1976). The relatively narrow, long master chela, characteristic of most swimming crabs, has a relatively low mechanical advantage in order to increase speed of movement. This type of chela is better adapted for attacking fast moving prey such as juvenile crabs, prawns, and even fish, and allows greater dexterity when manipulating these prey. The slower but stronger master chelae of *C. maenas* are better suited for generating compressive forces on large prey items that can only be crushed at a relatively higher mechanical advantage, making them successful predators of slow-moving, resistant prey such as bivalves and gastropods (Rheinallt & Hughes, 1985; Seed & Hughes, 1995). Although it is tempting to draw conclusions from evident correlations between chelal strength and natural diet, it is essential to bear in mind that a causal relationship between the mechanical advantage of crab chelae and their diet could be misleading (Lee & Seed, 1992). Studying the natural diet of *Scylla serrata*, Hill (1979) found that crabs had difficulty catching fish and penaeid shrimps. Although *S. serrata* is considered to be unusual amongst portunids in that it possesses a relatively robust, yet fast claw, it was not able to catch highly mobile prey.

Crab success in opening prey while developing a certain attack method can also depend on the muscle strength and size of claws relative to body size (Brown *et al.*, 1979). Comparative measures of the sarcomere length of the closer apodeme muscle in monomorphic and dimorphic species showed that although the robust, heavy claws of *C. pagurus* had consistently longer fibres (generally associated with slowly contracting, strong 'tonic muscles') than those in the dimorphic *Liocarcinus depurator* (short fibres, associated with rapidly contracting, weak 'phasic muscles'), there were no differences between the length of sarcomeres from the major and minor claws of this swimming crab (Warner & Jones, 1976). The authors suggest that differences in the forces from the two chelae were due to differences in mechanical advantage and the amount, rather than the type, of muscle present.

The cross-sectional area of the closer apodeme muscle located within the propus is a measure of the quantity of sarcomere fibres comprising the muscle, and can be indirectly estimated from the apodeme plate area onto which it is inserted (Warner & Jones, 1976). Apodeme area is expected to increase with crab size and more directly with chelal height; at the same time crab size and chelal height are also highly correlated (Hughes & Seed, 1981). These relationships can be described by allometric or isometric models, depending on chelal type, and crab sex and species (Hartnoll, 1978). In the present study, analysis of the allometric equations describing growth relationships between chelal height, apodeme area and carapace width (Table 3.3), indicates that the crusher claw in male *C. maenas* grows proportionately larger and stronger with increasing total body size. However, the lack of significant departure from isometry in the regression between the crusher apodeme area and chelal height, indicates that these two size parameters grow at the same relative rate thus confirming the direct relationship between them. In contrast, the chelal heights and apodeme areas in both female chelae and in the male cutter chela are isometric with respect to overall body size, but the apodeme plates in both crusher and cutter female chelae are negatively allometric with respect to their corresponding chelal heights. This suggests that females, unlike males, do not become proportionately stronger even though the size of their chelae grow at the same relative rate as their carapace width. Similar differences between master and minor chelae (Seed, 1980), as well as between sexes have been shown in other heterochelous and sexually dimorphic species. Such differences have been explained in terms of increasing sexual dimorphism with increasing age and variations in feeding and general behaviour between the sexes (Lee & Seed, 1992), as well as to the different uses of these chelae when handling prey (Elner, 1978; Ropes, 1968). Male crabs typically use the master chela for other activities related to defence and sexual behaviour that can account for larger and stronger claws than those in females (Hartnoll, 1974; Hughes & Seed, 1981; Seed 1990). For example, in male *Thalamita danae* a positive allometric equation best described the relationship between carapace width and both crusher and cutter chelal heights and apodeme areas. Female *T. danae* did not deviate significantly from isometry for either crusher or cutter heights with respect to carapace width, but revealed a negatively allometric relationship between cutter apodeme area and chelal height (Seed, 1986a).

In *C. pagurus*, both chelae become proportionately higher as crabs increased in body size, but these chelae increase in strength at the same relative rate as carapace width (Table 3.3). Similar results have been found for *Cancer productus*, where chelal strength (measured with a strain gauge) increased proportionately with carapace width (Boulding, 1984). This could indicate that chelal strength in some cancrid species is more related to their typical burrowing behaviour than to chelal feeding functions. While chelal height and strength increased proportionately with each other in the right male chela and the left female chela, the right chela in females and the left in males did not become proportionately stronger, although chelal height increased proportionately with respect to carapace width (Table 3.3). This discrepancy might be the consequence of 30.4 % of female *C. pagurus* having the right, and 42.9 % of male crabs having the left chela slightly larger, although differences in handedness in both sexes were not statistically distinguishable. Right female and left male chelae being larger, but with a smaller amount of muscle inserted on the apodeme plates, may constitute a mechanism for reducing the energy spent on the maintenance of such massive claws, that could cause disproportionate increments in metabolic rates during periods of high activity, as suggested by previous authors (Hartnoll, 1974; Lee & Seed, 1992).

Throughout this study, differences in mechanical advantage between crabs of the same species were associated with variations in the distance from the pivot to the point of insertion of closer apodeme, rather than in the distance from the pivot to the tip of the dactylus. Although the occlusive design of the chelae did not vary markedly amongst juvenile and adult *C. maenas*, significant differences in mechanical advantage suggested that claw strength varies due to changes in the growth pattern of chelal height and apodeme area relative to carapace width throughout the range of crabs measured. These results are in accordance with those previously reported for this and other portunids (Blundon & Kennedy, 1982a; Seed, 1986a, Warner *et al.*, 1982), and indicate that mechanical advantage is strongly influenced by the cross-sectional dimension of claws.

When comparing growth patterns of several size parameters between juvenile and adult *C. maenas* (Table 3.4), it was found that the rate of increase in both crusher and cutter chelal height relative to carapace width had a significant change in slope when male, but not female crabs, reached a body size of approximately 30 mm CW. Lee and Seed (1992) also found changes in the slope of the regression between chelal height and carapace width of male *C. maenas* at a body size of 30 mm CW, and associated this with the puberty moult. These results suggest that chelal height in both male claws grows at a faster relative rate in adults than it does in juvenile crabs, as indicated by the slopes for the regressions which in male adults (crusher: $b = 1.45$; cutter: $b = 1.22$; Table 3.4) are significantly higher than those in juveniles (crusher: $b = 1.07$; cutter: $b = 0.95$; Table 3.4). Intra-specific variations in these size parameters are in accordance with changes in sexual and competitive behaviour of juvenile crabs as they grow into the adult stage (Hartnoll, 1974; 1978). Feeding habits can also influence claw size (Smith & Palmer, 1994), and marked differences in natural diet between juvenile and adult crabs (Choy, 1986; Elner, 1981; Paul, 1981; Ropes, 1968) could result in short-term adaptive changes in the growth pattern of certain size parameters as a response to food availability. These variations, in turn, could account for the limited size range of prey accessible to juvenile crabs, since small crabs will be restricted by body to claw size ratio (Boulding, 1984; Rangeley & Thomas, 1987).

By contrast, the lack of significant changes in the slopes of the regressions for female *C. maenas* (Table 3.4), suggests that the rate of increase in chelal size and strength with respect to carapace width remains relatively constant as juvenile females grow into the adult stage. These results can be explained by the distinctly different roles of the two sexes during courtship, and constitute further evidence to support that sexual selection is a major driving force controlling sexual dimorphism in cheliped size (Lee & Seed, 1992). In addition, claws in female crabs probably have a more restricted use for feeding than in male conspecifics (Vermeij, 1977), where the display of large chelipeds has an important influence in the outcome of sexual and agonistic encounters. Thus, it is reasonable to consider that, as crabs become sexually mature, male individuals direct part of their energy to cheliped growth, whilst female crabs channel it towards diverse metabolic needs, such as egg production (Warner, 1977).

The fact that the slopes of the regressions of chelal height, apodeme area and carapace width amongst *C. pagurus* did not change significantly throughout the size range of crabs measured (Table 3.4) suggests that all the edible crabs described in this study were probably juvenile. In a monographic work on the fisheries of *C. pagurus* in British waters, Edwards (1979) found that most male *C. pagurus* attained sexual maturity at an average size of 110 mm CW and approximately 3 years of age, while females became sexually mature between 127-152 mm CW. Most of the samples analysed by Edwards came from commercial catches taken offshore, where the reproductive stock is extensively distributed. The crabs studied in the present work were all found in the low intertidal zone and the largest male and female crabs were 73.3 mm and 90.5 mm CW, respectively.

Comparisons between the growth patterns of the chelae of male and female *C. maenas* (Table 3.5a-c; Figures 3.4-3.6) showed that male crabs had a larger and stronger crusher claw than females of similar size, although the cutter chelae were not statistically different. Whilst this was true for shore crabs larger than approximately 30 mm CW, chelae in juvenile male and female crabs were statistically indistinguishable. Therefore, male and female juvenile shore crabs are potentially able to open prey of similar size. However, when these crabs reach a carapace width of approximately 30 mm, the male crusher chela becomes more powerful, allowing for sexual differences in shell-breaking potential to increase markedly with crab size. These results further support the sexual differences in a strong heterochelous species like *C. maenas* (Elner, 1980; Hartnoll, 1978), and are also consistent with what has been found for other portunids (e.g. Seed, 1986a), where sexual dimorphism becomes more conspicuous with increasing age.

Comparisons between the growth patterns of the chelae of male and female *C. pagurus* showed no statistical differences (Table 3.5a-c), therefore, all edible crabs of comparable body size had chelae of similar size and strength (Figures 3.4-3.6). No sexual differences in prey handling capability have been detected for juvenile *C. pagurus* in previous studies (Lawton, 1983; Lawton & Hughes, 1985;), further supporting the equivalent potential that young individuals of both sexes have to open hard-shelled molluscs.

Comparisons between species (Table 3.5a-c; Figures 3.4-3.6) suggest that male *C. maenas* have larger crusher chelae than *C. pagurus* of similar size, but the apodeme plates in both chelae in *C. pagurus* are similar to that of the crusher claw in male *C. maenas*. Crab chelal strength can be measured in a variety of ways, and the use of a single descriptor can lead to unrealistic conclusions (Brown *et al.*, 1979). In the present study, several morphological features in the chelae of *C. maenas* and juvenile *C. pagurus* have been analysed, and results suggest that the monomorphic chelae of juvenile *C. pagurus* are potentially stronger than those of *C. maenas*. Thus it can be suggested that a juvenile *C. pagurus* can potentially open larger prey items than a male *C. maenas* of comparable body size. It is important to note, however, that the ability to open bivalve prey is not only determined by claw strength, but is also influenced by other morphological and behavioural features. Higher dexterity, generally associated with heterochelous species, may enable crabs to handle smaller prey without dropping them (Seed, 1980; Seed & Hughes, 1997), and the use of more elaborate handling techniques allows them to feed on larger prey which otherwise could not be opened successfully. Because handling techniques vary with prey species, size and strength (Lawton & Hughes, 1985; Elner & Jamieson, 1979), and relative chelal size influences shell breaking times, chelal strength and morphology are still important factors that determine, at least in part, the feeding strategy and behaviour of crabs.

3.5. Summary

1. Two distinct morphological types of chelae which are likely to represent adaptations to feeding were found in the course of this study: large, rather curved claws with a series of broad molariform teeth that provide an occluding surface especially well designed for crushing hard-shelled prey; and small, relatively narrow chelae with sharp teeth, better adapted for cutting and shearing than for applications of force. The first morphological type was represented by both chelae in *Cancer pagurus* and the more robust crusher claw in *Carcinus maenas*, whereas the second morphological type was represented by the slimmer cutter claw in the latter, heterochelous, species.

2. Marked differences were observed between the massive monomorphic chelae of *C. pagurus* and the dimorphic chelae of *C. maenas*. Both claws of male and female *C. pagurus* were at a significantly higher mechanical advantage than the crusher and cutter claws of both male and female *C. maenas*. These differences suggest that *C. pagurus* can exert greater compressive forces than *C. maenas* of similar size, and may enable *C. pagurus* to open prey of a larger size than *C. maenas*. However, the ability to open bivalve prey is not only determined by claw strength, but can also be influenced by other morphological and

behavioural features, such as differences in chelal dexterity, or the use of elaborate handling techniques that allow crabs to feed on prey items than those that could be crushed outright.

3. Sexual dimorphism in chelal size, relative growth, and biomechanics was evident in the size range of *C. maenas* examined in this study. The significant differences between the crusher to cutter chelal height ratio of male and female *C. maenas* indicated that the chelae of female crabs were less strongly dimorphic than those of their male counterparts. These differences suggest that sexual dimorphism in cheliped size is not an exclusive consequence of the feeding habits of a particular species, but the evolutionary result of a variety of driving forces, amongst which sexual selection is probably one of greatest importance. Mean mechanical advantage of the cutter claw was similar in male and female *C. maenas*, but the crusher claw of male *C. maenas* was at a significantly higher mechanical advantage than that of female crabs. Allometric equations describing growth relationships between chelal height, apodeme area and carapace width showed that the crusher claw in male *C. maenas* grows proportionately larger and stronger with respect to total body size. By contrast, both chelae in female *C. maenas*, and the cutter claw in males, increase in size and strength at the same relative rate as carapace width. Comparisons between relative growth patterns of the chelae in male and female *C. maenas* showed that male crabs had a larger and stronger crusher chela than females of similar body size, although the cutter chelae were statistically indistinguishable. This suggests that male *C. maenas* can potentially open more robust prey than female crabs of similar carapace width.

4. The occlusive geometry of chelae did not vary markedly amongst juvenile and adult *C. maenas*. However, both male crusher and cutter chelae were larger relative to carapace width in adults than in juvenile crabs. These intra-specific differences in chelal size parameters are related to changes in the sexual and competitive behaviour of juvenile crabs as they grow into adults. Likewise, differences in the natural diet of juvenile and adult *C. maenas* can result in short term adaptive changes in the growth patterns of certain chelal size parameters as a response to food availability.

5. Amongst *C. maenas* < 30 mm CW, chelal height and strength in male crabs was similar to that in females of comparable carapace width, indicating that male and female juvenile crabs are potentially capable of opening prey of similar size. When crabs reach a carapace width of approximately 30 mm, the male crusher becomes more powerful, allowing for sexual differences in shell breaking potential to increase markedly with crab size.

6. The intertidal *C. pagurus* population examined in this study was comprised only of juvenile crabs. The largest male and female *C. pagurus* recorded were 73.3 and 90.5 mm CW, respectively, whereas the size at sexual maturity reported for *C. pagurus* populations in British waters is 110 and 127 mm CW for males and females, respectively. In addition, there was no sexual dimorphism in chelal size over the size range of crabs studied. Mean mechanical advantage in the chelae of male and female *C. pagurus* were statistically indistinguishable. The monomorphic chelae in both male and female *C. pagurus* became proportionately larger as crabs increase in carapace width, although they increased in strength at the same relative rate as overall body size. Comparisons between relative growth patterns of the chelae in *C. pagurus* revealed no significant differences, suggesting the lack of sexual differences in prey handling capabilities amongst juvenile edible crabs.

Chapter 4

Prey Morphology and Handling Techniques

4.1. Introduction

Many studies have shown that crabs are versatile predators eating a wide spectrum of food types (Hill, 1976; Leber, 1985; Raffaelli *et al.*, 1989). In general terms, they are considered omnivorous predators feeding preferentially on slow-moving or sessile macroinvertebrates (Seed, 1993), though crabs in some brachyuran families (e.g. Portunidae) have been reported to attack successfully highly mobile prey (Lawton, 1989; Paul, 1981). Various kinds of hard-bodied prey, such as bivalve molluscs and gastropods have been found in the gut contents of different species of crabs, whilst soft-bodied organisms (e.g. annelids, juvenile fish and crustaceans in postmoult stages) also form an integral part of their natural diet (Choy, 1986; Wear & Haddon, 1987). Although crabs are predominantly carnivorous, plant remains have been found in their stomach content, especially in small juveniles and intermoult stages (Ropes, 1968).

Whilst crab predation on soft-bodied organisms proceeds by simple breaking up the flesh, many of the methods used to open hard-shelled prey such as molluscs involve a variety of specialised tactics (Rheinallt & Hughes, 1985). Crabs can use their chelae to tear individual prey items from clusters (Lin, 1991), to drill holes (Krantz & Chamberlin, 1978), to chip and peel away pieces of shell (Du Preez, 1984; Hughes & Seed, 1981), and for the application of force at points where the shell is weakest (Boulding, 1984; Cunningham & Hughes, 1984; Elner, 1978). They can also use their mouthparts for holding, severing and chewing flesh (Hill, 1979), and they can detect and evaluate food items through chemical stimuli using their antennae or chemosensory organs on the dactyli of the walking legs (Akumfi & Hughes, 1987; Jubb, *et al.*, 1983).

The methods used by crabs to open hard-shelled prey range from outright crushing, which requires a substantial structural investment in the form of powerful chelae, to complex shell opening behaviour and specialised claw morphology, which may compensate for limited crushing power (reviewed in Seed & Hughes, 1995). Sometimes the specialisation of claw morphology and crab behaviour is such that predator identification can be established simply by observing patterns of shell destruction and shell fragments (Elner & Lavoi, 1983; Hughes & Elner, 1989).

Predatory techniques not only vary with morphological and behavioural mechanisms in brachyuran species, but also change substantially when the same species of crab feeds on different types of molluscan prey (Lawton & Hughes, 1985; Rangeley & Thomas, 1987). Thus, it appears that the use of a particular attack method is a consequence of the interplay between shell strength, shape and size of prey, and crab morphology and behaviour (Elner & Raffaelli, 1980).

The limits to the range of prey sizes and species a crab can open are to a certain extent determined by the amount of time the crab spends breaking open the prey shell. The limit to the minimum size is strongly related to the capacity of the predator to find and hold an individual prey item, since very small prey can easily slip from the chelae (Rheinallt & Hughes, 1985). The limit to the maximum size, on the other hand, is less strongly related to the crushing power of the crab, since bivalves that are too large to fit into the chelae can be opened using other methods that take an order of magnitude longer (Elner & Hughes, 1978). Shell-breaking times and other characteristics of handling time curves can be explained in terms of variations in handling techniques (Rheinallt & Hughes, 1985). Therefore, the use of certain attack methods will have a strong influence on prey selection (Boulding, 1984). Moreover, because attack methods often depend on the size and strength of the prey relative to the crab (Seed, 1993), the use of handling techniques and the frequency with which they are used can vary within crab species, thereby explaining, at least in part, the differences in prey preference and foraging behaviour between crabs of different size and sex.

Considering the relevance that handling techniques have in the study of crab foraging behaviour, this chapter will describe the different methods used by the common shore crab, *Carcinus maenas*, and the European edible crab, *Cancer pagurus*, to evaluate, select and attack their prey. Results will include comparative descriptions between the handling techniques used by crabs when allowed to forage on the mussel, *Mytilus edulis*, the flat oyster, *Ostrea edulis*, the Pacific oyster, *Crassostrea gigas*, and the cockle, *Cerastoderma edule*. Differences between the contrasting morphological features of the shells of these bivalves will be described and related to the handling methods exhibited by crabs feeding on them.

Because little is known about the prey handling methods used by juvenile shore crabs, and given the importance of their potential effects on bivalve populations,

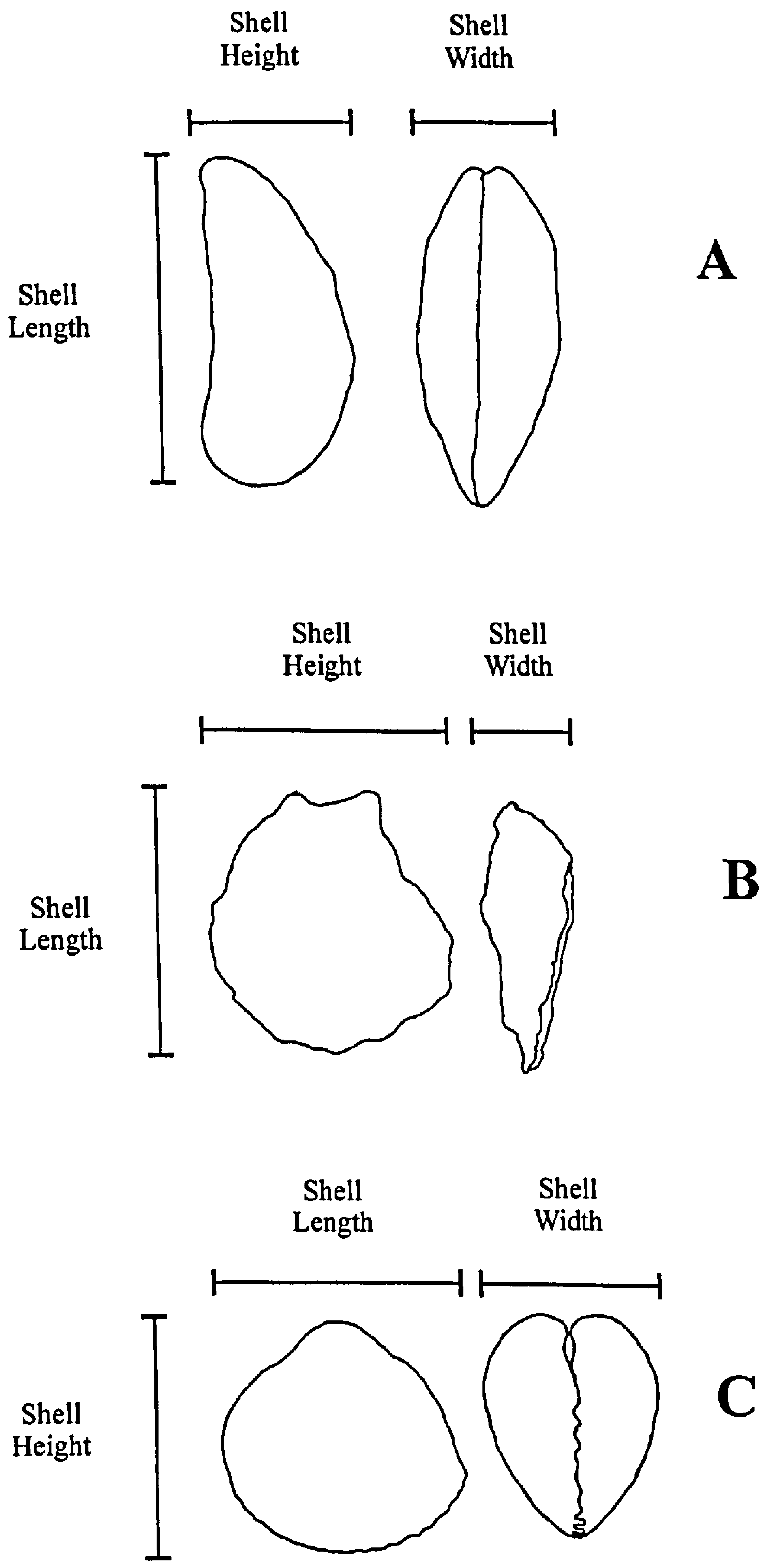

Figure 4.1. Terminology used in the present study to describe prey shell dimensions in:A)*Mytilus edulis;* B) *Ostrea edulis* and *Crassostrea gigas*; and C) *Cerastoderma edule.*

comparisons between juvenile and adult *C. maenas* will also be undertaken. Differences in the handling methods within the size range of shore crabs will help to establish whether different size ranges of crabs use distinct handling methods on these bivalves, and the way these might affect their selective behaviour.

4.2. Materials and Methods

Nine juvenile (5-35 mm CW) and eight adult (40-70 mm CW) *Carcinus maenas* and nine juvenile *Cancer pagurus* (10-40 mm CW) were collected by hand from the shore at Treborth (Figure 2.1, A) and kept individually in plastic aquaria (30 x 20 cm) filled to a depth of 10 cm with running sea water. Only male crabs were used in experiments in order to avoid any potential bias due to sexual dimorphism. Intertidal mussels, *Mytilus edulis* (Plate 1, A) were obtained from Aberffraw (Figure 2.1, D) by scraping them off the rock; cockles, *Cerastoderma edule* (Plate 1, D) were obtained from Traeth Melynog (Figure 2.1, C), whilst oysters, *Ostrea edulis* (Plate 1, B) and *Crassostrea gigas* (Plate 1, C) were obtained from the CEFAS oysterbeds at Brynsiencyn (Figure 2.1, ⊗) in North Wales, Anglesey. All prey were kept in plastic trays with running seawater, and fed a mixture of microalgae (*Rhinomonas reticulata, Skeletonema costatum, Tetraselmis chui, Pavlova lutheri*) once a day. Prior to trials, undamaged prey were chosen and any epizoic organisms removed from their shells.

4.2.1. Prey morphology.

Because the morphological features of the shells of the bivalves studied differ markedly (Plate 1, A-D) the relationships between several measures of their shell dimensions were compared. Samples each consisting of 35 *M. edulis* (4-45 mm SL), 35 *O. edulis* (7-48 mm SL), 42 *C. gigas* (9-52 mm SL), and 35 *C. edule* (2-40 mm SL) were cleaned of any fouling organisms, and the shell length (SL: maximum dimension of the shell), shell height (SH: maximum dimension of the axis perpendicular to SL), and shell width (SW: minimum dimension of the shell) of each individual was measured to the nearest 0.1 mm with vernier callipers. The terminology used is illustrated in Figure 4.1. Flesh and shells were separated by brief immersion in boiling water. They were then damp-dried on absorbent paper and dried to constant weight at 60°C. Dry tissue weights (W) were then determined to the nearest 0.01 mg on a top loading balance.

Relationships between SW, SH, W and SL were best described by power functions:

$$y = a \cdot x^b$$

where b is the rate of increase in the variable y relative to the variable x, and a is the value of y when $x = 0$. Linear relationships between SW, SH, W and SL were obtained by least square regressions on logarithmically transformed data. In order to reveal differences between the four prey species, regression lines were compared using analysis of variance. Pairwise comparisons between the regression slopes and intercepts were then performed using Tukey's method.

4.2.2. Handling techniques.

Experiments were carried out by offering one crab in each of several size categories a prey of known shell length, and recording in detail the way each crab handled and attacked the prey item. If a crab was successful in the attack, a prey item of a larger size was presented; if, on the contrary, an item was abandoned, it was immediately replaced with another one of smaller size. In cases where crabs were reluctant to eat, they were starved for 1-3 days until hunger levels were recovered for experiments to be continued. The size ranges and number of each prey species offered to each size category of crabs are give in Appendix B1. Experiments were terminated only after each crab had eaten a wide size range of each prey species and the handling methods had been extensively described. Water temperature throughout the trials ranged from 12-18°C. The time each crab spent handling each prey item was also recorded, but a more detailed analysis of handling and breaking times, and their relationship to prey value is presented in Chapter 6.

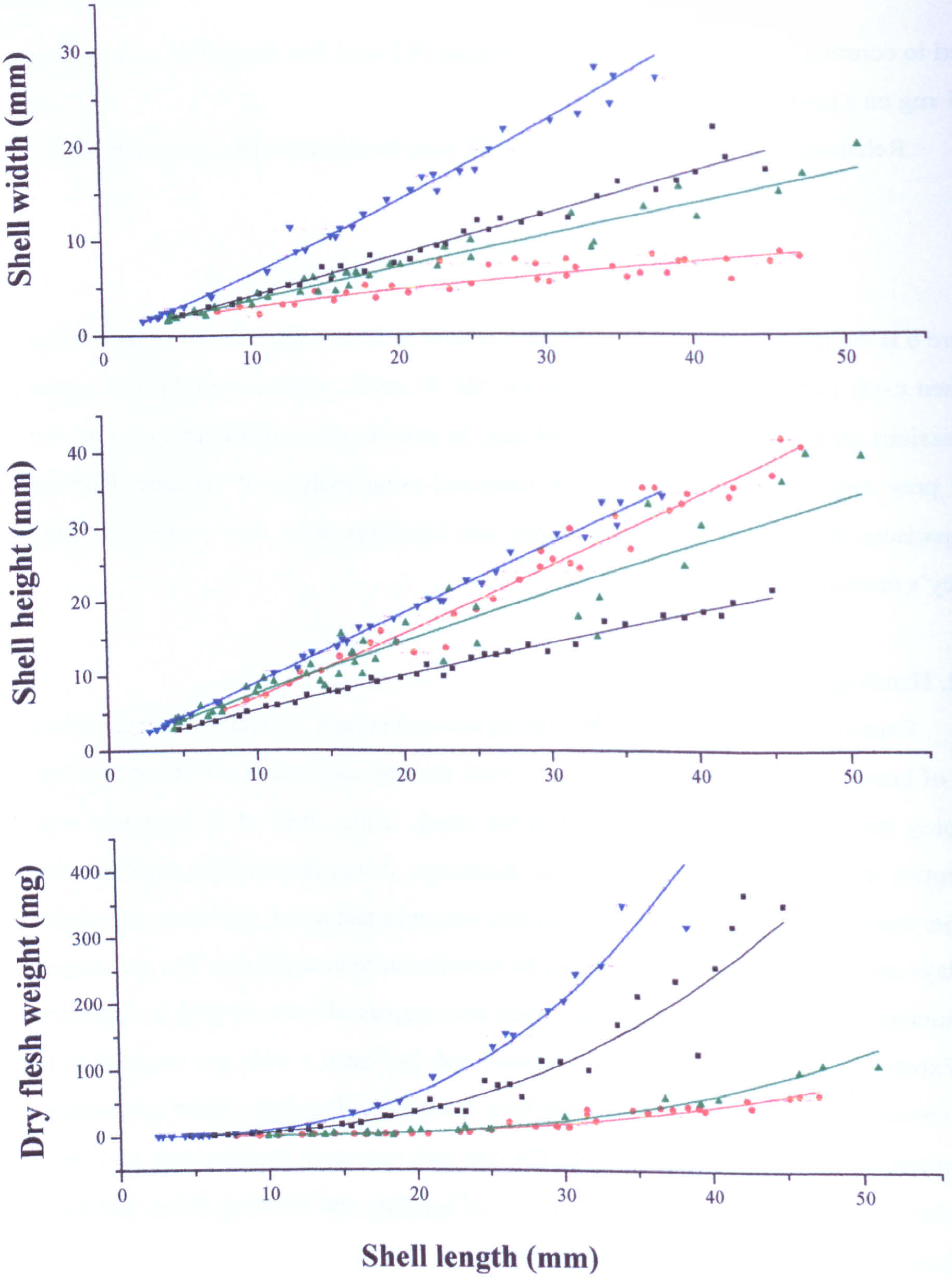

Figure 4.2. Relationships between shell width (mm), height (mm), length (mm) and dry flesh weight (mg) of a wide size range of *Mytilus edulis* (▪), *Ostrea edulis* (●), *Crassostrea gigas* (▲) and *Cerastoderma edule* (▼). The parameters of the linear equations between logarithmically transformed data are presented in Table 4.1.

Table 4.1. Equation coefficients of the allometric relationships between shell width (SW), shell height (SH), dry flesh weight (W) and shell length (SL) in *Mytilus edulis*, *Ostrea edulis*, *Crassostrea gigas*, and *Cerastoderma edule*. Coefficients a and b in the linear model ($y = a + b x$) were obtained by least square regressions on the logarithms of the shell parameters; r^2 is the coefficient of determination.

	Mytilus edulis				*Ostrea edulis*			
Parameters	a	b	r^2	n	a	b	r^2	n
log SW (mm) - log SL (mm)	-0.42	1.03	0.99	35	-0.23	0.70	0.82	35
log SH (mm) - log SL (mm)	-0.13	0.88	0.99	35	-0.26	1.12	0.98	35
log W (g) - log SL (mm)	-4.94	2.69	0.99	35	-5.99	2.89	0.96	35
	Crassostrea gigas				*Cerastoderma edule*			
	a	b	r^2	n	a	b	r^2	n
log SW (mm) - log SL (mm)	-0.39	0.96	0.97	42	-0.35	1.15	0.99	35
log SH (mm) - log SL (mm)	-0.02	0.91	0.94	42	-0.04	1.00	0.99	35
log W (g) - log SL (mm)	-6.50	3.30	0.95	22	-4.86	2.82	0.99	25

Table 4.2. Results of Tukey's pairwise comparison tests performed on the regression coefficients (slopes\ intercepts) of allometric relationships between shell width (SW), shell height (SH), dry flesh weight (W) and shell length (SL) in *Mytilus edulis, Ostrea edulis, Crassostrea gigas* and *Cerastoderma edule*; * $p < 0.05$, ns = not significantly different.

		Comparison of slopes		Comparison of intercepts	
		M. edulis	*O. edulis*	*C. gigas*	*C. edule*
SW (mm) - SL (mm)	*M. edulis*		4.74 *	0.83 ns	2.05 ns
	O. edulis	11.27 *		4.41 *	3.37 ns
	C. gigas	2.97 ns	9.34 *		1.32 ns
	C. edule	-4.86 *	16.35 *	8.45 *	
SH (mm) - SL (mm)	*M. edulis*		3.34 ns	3.83 *	3.25 ns
	O. edulis	-8.79 *		6.94 *	6.37 *
	C. gigas	-1.50 ns	8.02 *		0.70 ns
	C. edule	-5.45 *	4.48 *	4.23 *	
W (g) - SL (mm)	*M. edulis*		10.74 *	15.09 *	0.99 ns
	O. edulis	2.77 ns		4.45 *	11.88 *
	C. gigas	7.80 *	4.83 *		16.17 *
	C. edule	1.98 ns	1.03 ns	6.19 *	

4.3. Results

4.3.1. Prey morphology.

Relationships between shell width (SW), height (SH), dry flesh weight (W) and shell length (SL) in *Mytilus edulis*, *Ostrea edulis*, *Crassostrea gigas*, and *Cerastoderma edule* are plotted in Figure 4.2, and the coefficients of the corresponding linear equations are shown in Table 4.1. The coefficients of determination (r^2) in all four prey species were high, showing the significant correlation between the shell dimensions that were measured. Analysis of variance revealed significant differences between the slopes (F = 34.12; $p < 0.001$) and intercepts ($F = 2.87$; $p < 0.05$) of the regressions of log SW against log SL of the four species examined. Pairwise comparisons between the slopes of the regression lines showed that the slope for *C. edule* was significantly greater than for the other species (Table 4.2). Regression slopes for *M. edulis* and *C. gigas* were similar, and were both significantly greater than for *O. edulis* (Table 4.2). These results suggest that as prey increase in shell length, *C. edule* increase in shell width more rapidly than *M. edulis* and *C. gigas*, which in turn increase in shell width more rapidly than *O. edulis* (Figure 4.2). Thus, amongst prey < 8 mm SL the shell width of the four bivalves is approximately similar. However, amongst larger prey, *C. edule* have a significantly wider shell than both *M. edulis* and *C. gigas* of comparable shell length, and *O. edulis* have the narrowest shell of the four species.

Results of the analysis of variance on the logarithms of SH and SL revealed significant differences between the slopes ($F = 11.5$; $p < 0.001$) and the intercepts ($F = 6.88$; $p < 0.001$). Pairwise comparisons between regression slopes showed that the slope for *O. edulis* was significantly greater than for *C. edule*, which in turn was significantly greater than for both *M. edulis* and *C. gigas* (Table 4.2). No significant differences were found between the regression slopes or intercepts for *M. edulis* and *C. gigas* (Table 4.2). These results suggest that as prey increase in shell length, *O. edulis* increase in shell height more rapidly than *C. edule*, which in turn increase more rapidly than both *M. edulis* and *C. gigas* (Figure 4.2). Thus, amongst prey < 8 mm SL the shell height of the four bivalves is approximately similar. However, amongst larger prey, *O. edulis* and *C. edule* have a significantly higher shell than both *M. edulis* and *C. gigas* of comparable shell length.

Results of the analysis of variance on the logarithms of W and SL revealed significant differences between the slopes ($F = 6.82$; $p < 0.001$) and intercepts ($F = 46.92$; $p < 0.001$) of the four regression lines. The regression slope for *C. gigas* was significantly

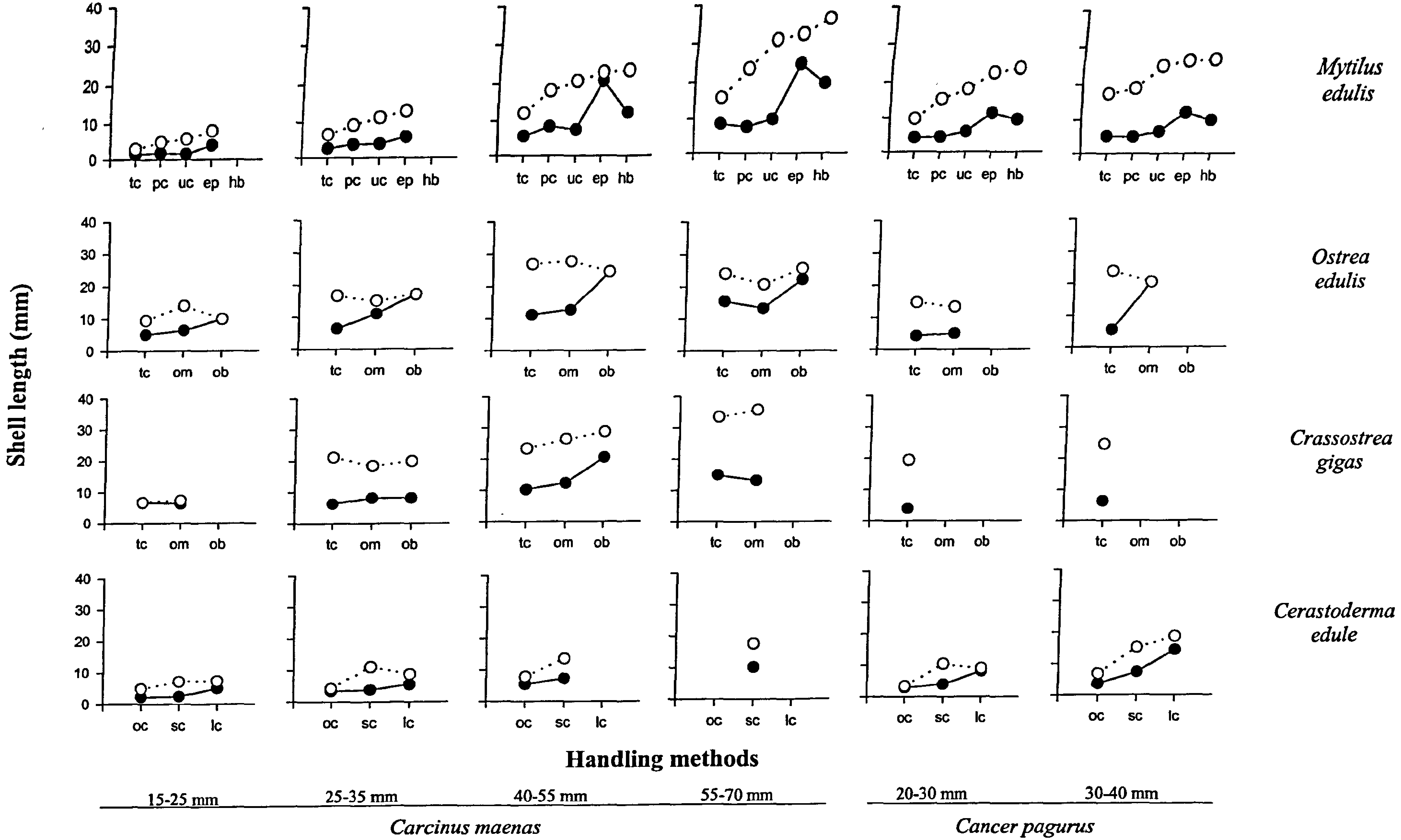

Figure 4.3. Maximum (open symbols) and minimum (shaded symbols) shell length of *Mytilus edulis, Ostrea edulis, Crassostrea gigas*, and *Cerastoderma edule* that were successfully opened by several size categories of *Carcinus maenas* and *Cancer pagurus* using different attack methods: mussels: **tc** (total crushing), **pc** (posterior crushing), **uc** (umbone crushing), **ep** (posterior edge-chipping), and **hb** (hinge-boring); oysters: **tc** (total crushing), **om** (margin-biting), and **ob** (hole-boring); cockles: **oc** (outright crushing), **sc** (crushed with several force applications), and **lc** (localised crushing).

greater than those for *M. edulis*, *O. edulis* and *C. edule*, which in turn were statistically indistinguishable from each other (Table 4.2). Whilst the intercepts of the regression lines for *M. edulis* and *C. edule* were similar, they were both significantly greater than for *O. edulis*, which in turn was significantly greater than that for *C. gigas*. Thus, the regression lines for *M. edulis* and *C. edule* are similar, and are both higher and parallel to the regression line for *O. edulis*, suggesting that *M. edulis* and *C. edule* of comparable shell length have similar biomass, and they both have significantly more biomass than any *O. edulis* of comparable shell length. By contrast, the regression line in *C. gigas* intersects those of the other three species, suggesting that amongst small prey sizes Pacific oysters have less biomass than mussels, cockles and flat oysters. As prey increase in size, however, the biomass in *C. gigas* increases more rapidly than in the other bivalve species (slope: 3.30 ± 0.34). Thus, amongst prey > 50 mm SL, *C. gigas* can have more flesh than *M. edulis*, *C. edule* and *O. edulis* of comparable shell length (Figure 4.2).

4.3.2. Handling techniques.

Feeding experiments showed that each foraging bout was prefaced by vigorous movements of the mouthparts with the crab actively moving around the aquarium. Prey appeared to be detected mostly either visually (items being lowered into the water), or physically, by encountering a prey item with the chelipeds or the dactyli of the walking legs. If prey were not encountered immediately in one of these ways, then prey that started to gape appeared to be detected by chemoreceptors present on the crab's antennae.

Mussels

Both *Carcinus maenas* and *Cancer pagurus* of all size categories opened *M. edulis* using broadly the same type of techniques. These were:

(i) Total crushing (**tc**): mussels opened using this method ranged from 1.3-17.3 mm in shell length (SL), depending on crab size (Figure 4.3). Crabs did not usually manipulate prey for an extended period of time, but very quickly positioned the prey between the outer maxillipeds with the posterior end of the shell facing outwards. Force was applied across the umbone once, or, at the most twice, by the mandibles or the chelipeds without moving the position of the prey, and the shell crushed. In most cases crabs did not use the chelae to hold prey while gleaning flesh from the shell, but were able to manipulate the shell fragments

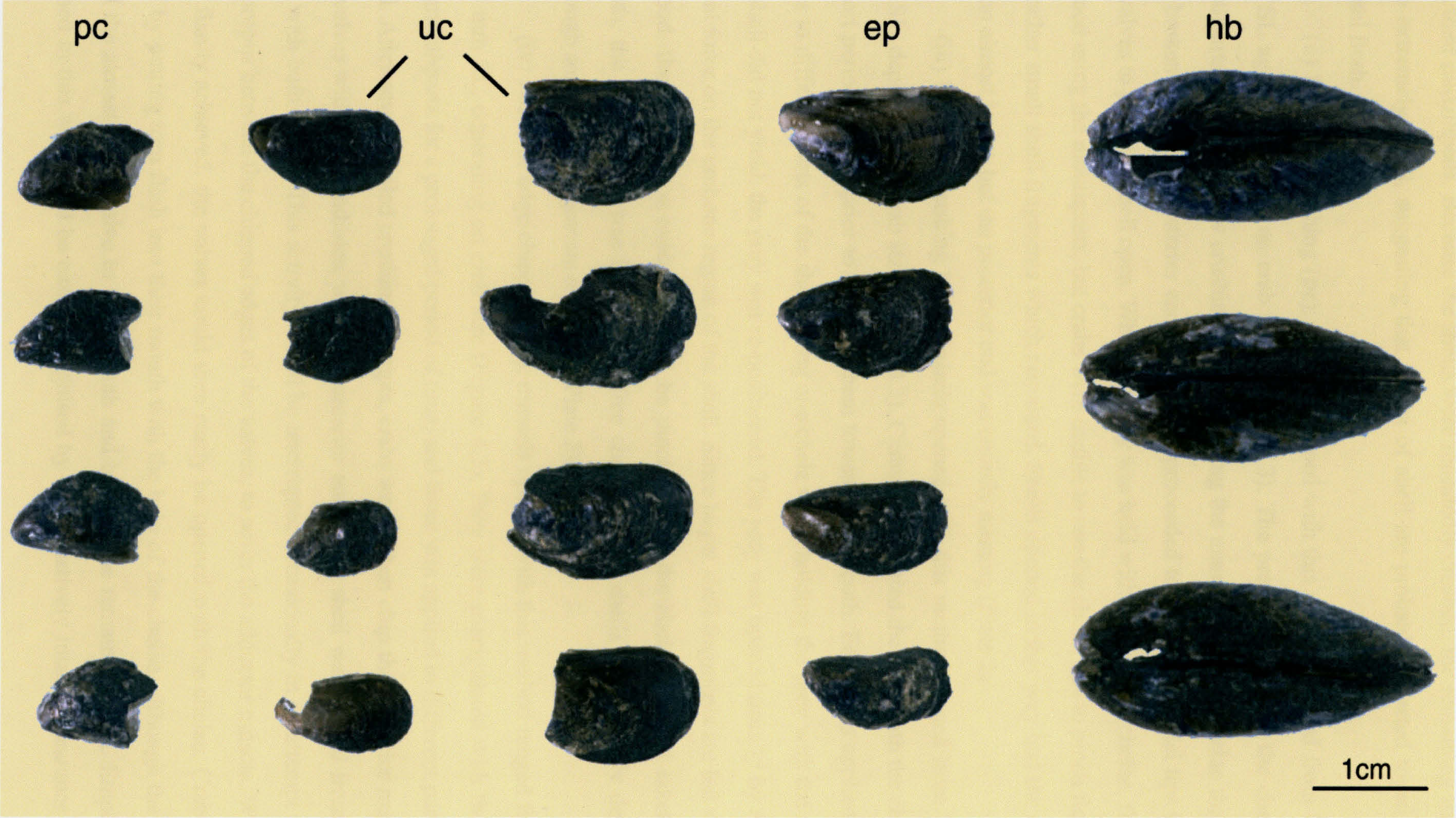

Plate 2. *Mytilus edulis* shells opened by *Carcinus maenas* and *Cancer pagurus* using the posterial crushing (pc), umbone crushing (uc), posterior edge-chipping (ep) and hinge -boring (hb) methods.

with their maxillipeds. Because the shells were repeatedly crushed, the remaining fragments were extremely small, suggesting that pieces of shell are probably ingested together with mussel flesh.

(ii) Posterior crushing (**pc**): mussels opened with this method ranged from 1.9-23.7 mm SL again depending on crab size (Figure 4.3). The prey was held by the chelae and mouthparts and after a few crushing attempts, using the mandibles or the chelae the mussel was broken across the posterior end. Crabs then proceeded to insert the chelal tips between the valves to prise the shell open. While the prey was held with one or both chelae, flesh was gleaned using the mouthparts, but crabs were unable to use the chelal tips to pinch flesh from the rather small shell fragments which remained. Shells opened in this way had the umbone region almost intact, but the posterior end was entirely missing (Plate 2).

(iii) Umbone crushing (**uc**): mussels opened with this method ranged from 1.7-31.1 mm SL, depending on crab size (Figure 4.3). Crabs manipulated the prey with the chelae for a short period of time prior to drawing them towards the mouth. Force was applied several times to different parts of the shell, using one chela while holding the prey with the other. If the shell did not yield, the prey was re-positioned. The prey was opened usually by applying lateral force on the umbone region of the shell. Since larger shell fragments are left with this method, the flesh, once exposed, could be pinched with the chelal tips and taken to the mouth, the other valve was held in the free chela. Empty shells were largely destroyed, although some large fragments remained (Plate 2).

(iv) Posterior edge-chipping (**ep**): mussels opened with this method ranged from 3.9-32.7 mm SL, depending on crab size (Figure 4.3). Prey were manipulated with the chelae and mouthparts for a prolonged period of time, and force was applied to different parts of the shell. After several failed crushing attempts, crabs would then chip the posterior margins of the valves with the mandibles, while the anterior end of the shell was moved from side to side with both chelae. This activity would be interrupted occasionally in an attempt to insert the propus between the chipped edges of the valves, to sever the adductor muscle. When this was finally achieved, the valves could then easily be opened with the chelae. Crabs would feed by putting torn flesh into their mouth with the help of the chelae, although they would hold the almost entire valve to their mouth and bite off the remaining flesh. Empty shells opened in this way could be easily recognised by their relatively intact appearance and the chipped condition of the posterior margins (Plate 2). When using this method, crabs would sometimes persist longer with a particular mussel irrespective of its size.

(v) Hinge-boring (**hb**): mussels opened with this method ranged from 8.4-36.8 mm SL, depending on crab size (Figure 4.3). Crabs which failed to crush mussels or to open them using the edge-chipping method would attempt to insert the tip of the propus between the valves at the hinge region by making a small hole that became progressively wider as the propus was repeatedly inserted. Once a larger hole had been established, crabs were able to insert the propus of the chela and prise the mussel open. Crabs would eat the flesh using both chelae as well as the maxillipeds. Although shells opened in this way remained virtually intact, the hole was readily visible when the empty valves were put together (Plate 2).

Overall *C. maenas* and *C. pagurus* of the same size category took a similar amount of time to open mussels using the three crushing methods described above (methods **tc**, **pc**, **uc**), although there was a trend towards longer breaking times as larger mussels were attacked (Chapter 6). The edge-chipping method (**ep**) took considerably longer than any crushing methods, but took a similar amount of time as the hinge-boring method (**hb**).

Both *C. maenas* and *C. pagurus* used the same types of mussel opening techniques, although some differences in the way these methods were performed by each crab species were noted. For example, juvenile *C. maenas* did not usually use the hinge-boring technique, whereas *C. pagurus* of similar carapace width used this method frequently. In addition, *C. maenas* used their dimorphic chelae in a clearly distinctive way. The crusher chela was systematically used to pick up and crush prey, and the propus of this claw was generally inserted between the valves. The cutter chela was generally used to hold prey in different positions. Shore crabs mostly used the crusher claw to hold the open shell while removing flesh with the cutter, but the use of these chelae could be reversed for this particular purpose. Even though *C. pagurus* tended to use either chela throughout any handling method, they frequently used the right chela as the 'crusher' and the left as the 'cutter'.

C. maenas were voracious and persistent with a particular prey item, and were not easily disturbed by the presence of the observer. *C. pagurus*, by contrast were generally less active, much slower in their movements, and would very frequently stay motionless in a corner of the aquarium holding the prey against their abdomen. *C. pagurus* would not readily abandon prey that could not be opened with the first crushing attempts, but generally persisted more than *C. maenas*. If this happened, crabs had less chance to encounter prey again, since edible crabs move around the aquaria less readily. While eating, *C. pagurus* tended to crush the shell into smaller fragments than did *C. maenas*. Shore crabs were ready to eat at any time of day, while edible crabs preferred to feed late in the evening.

When *C. maenas* were manipulating the larger mussels of the size ranges offered they used the first pair of walking legs to hold the prey item against the aquarium floor, unlike large *C. pagurus* which unusually used the walking legs when handling prey. In *C. maenas*, all walking legs played an important role in keeping the body balanced, especially when attempting to insert the chelae between the edges of the valves. Inserting the chelae was the part of the feeding procedure that took the longest time, and crabs would sometimes stop completely and hold the mussel vertically or slightly leaning towards the aquarium floor. Occasionally the tip of the propus would become trapped between the valves, and crabs would spend a prolonged period of time trying to insert the chela completely or free themselves.

Comparisons between juvenile and adult *C. maenas* showed that adult crabs (> 30 mm CW) seemed to have difficulty both locating and manipulating mussels < 7 mm SL, but were able to alternate two or more techniques on large prey items. Adult shore crabs used their mouthparts more frequently than juveniles throughout the different handling methods described earlier. When feeding on larger mussels, adult *C. maenas* often used the hinge-boring technique (**hb**), and were able to insert the propus of the crusher chela through the anterior or even the most ventral region of the valves. Since crabs using this method spent a long time repeatedly loading the prey, it seemed that the shell was weakened until the crab was able to crush the valves. By contrast, juvenile *C. maenas* were never observed using the hinge-boring method. Unlike juveniles, adult *C. maenas* would sometimes apply compressive forces at the umbone region in a dorso-ventral as well as in a lateral direction. Adult shore crabs also seemed to be more persistent than juveniles, since they would frequently drop a mussel several times, but pick it up again before rejecting it completely or proceeding with the attack.

Although crabs of different size used similar prey opening techniques, the size of mussels that could be opened with each particular technique increased with increasing size of crab. Whilst the maximum size of mussels opened by crabs in the same size category

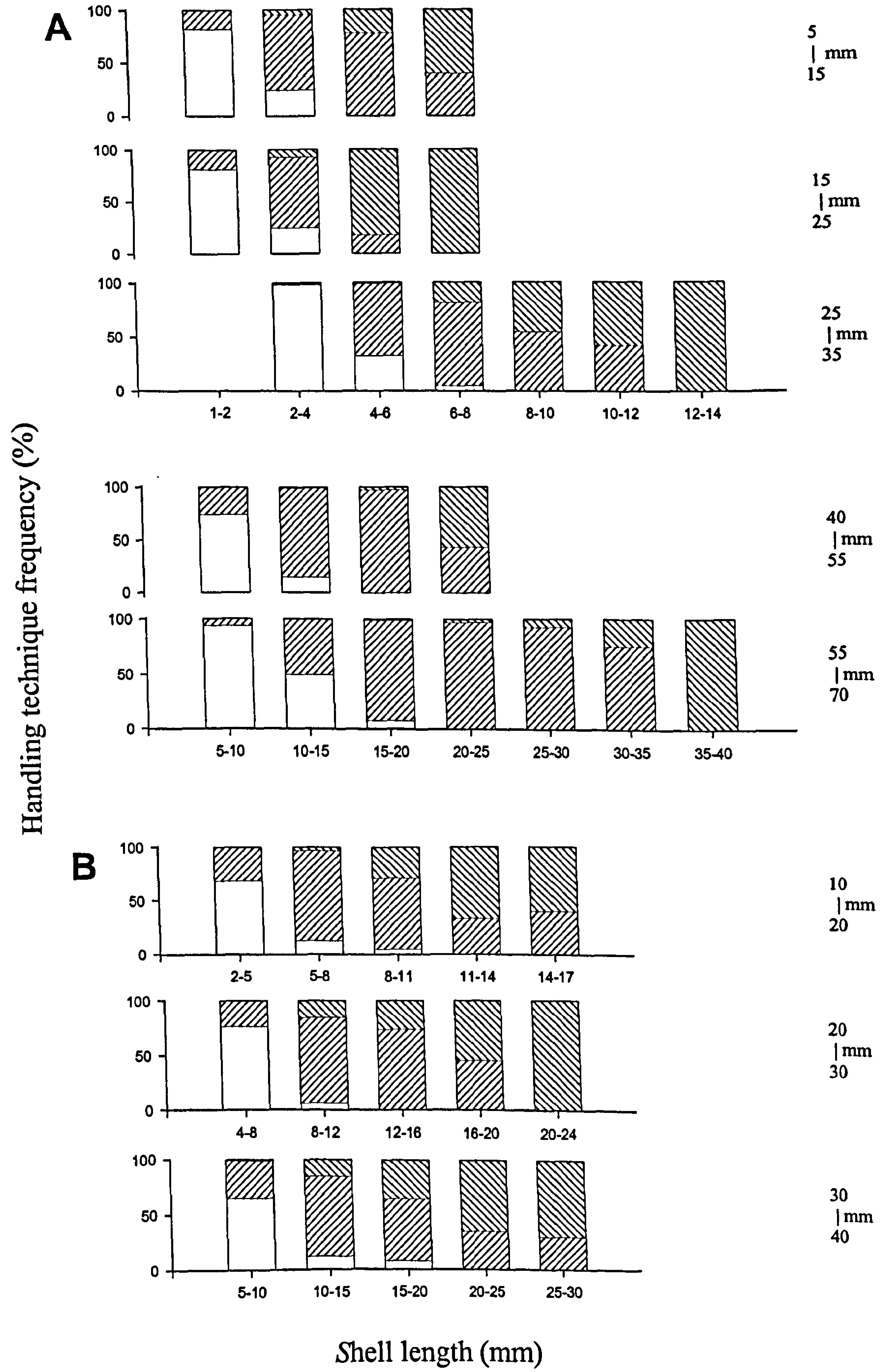

Figure 4.4. Frequency of the attack methods used by different size ranges of *Carcinus maenas* (**A**) and *Cancer pagurus* (**B**) on a wide size range of *Mytilus edulis*. Values are the percentages of mussels of each size class that were opened using each method:

☐ total crushing (tc)
▨ posterior and umbone crushing (pc-uc)
▧ hinge-boring and edge-chipping (ep-hb)

increased as attack methods became more complex, the minimum size did not always increase in the same manner (Figure 4.3). Thus, the size range of mussels opened by any one method overlapped with that of another technique, and the degree of overlap increased as methods became more complex. The only exception to this was that the minimum size of mussels opened with the edge-chipping method (**ep**) was markedly larger than the minimum size opened with any of the crushing methods (**tc**, **pc** or **uc**). This resulted in a relatively distinct size range of mussels that were attacked by posterior edge-chipping.

The techniques used by crabs to open mussels were quite prey-size specific, and the frequency with which each technique was used varied with size and strength of the prey relative to that of the crab. The patterns of variation, however, were remarkably constant amongst crabs of different size and species. The frequency in the use of each handling method, expressed as the percentage of mussels in each prey size category that were opened with a particular method, are shown in Figure 4.4. While total crushing (**tc**) occurred at high frequency amongst the smallest prey size classes offered to each size category of crab, it rapidly decreased with increasing prey size. The reverse was true for edge-chipping (**ep**) and hinge-boring (**hb**), which were used more frequently on the largest size classes of mussels offered, although crabs occasionally attacked relatively small mussels with this technique. The methods where prey were crushed at specific regions of the shell i.e. posterior end (**pc**) and umbone crushing (**uc**), were used on all but the very largest prey items; however, the highest frequency of use was found amongst the medium-sized mussels (Figure 4.4).

Oysters

Handling techniques used by both crab species on *O. edulis* and *C. gigas* were very similar, and the somewhat small differences between the way these two oyster species were opened are probably due to differences in their shape, rather than to any distinctive opening method used by crabs on either prey species.

Three different methods for opening oysters were observed: outright crushing (**tc**), margin-biting (**om**), and hole-boring (**ob**). Different code letters are used here in order to distinguish them from those methods used with mussels. Although both crab species developed the same oyster-opening techniques, it should be noted that here again *C. pagurus*

Plate 3. *Ostrea edulis* and *Crassostrea gigas* opened by *Carcinus maenas* and *Cancer pagurus* using the umbone crushing (uc), margin-biting (om) and hole-boring (ob) methods.

did not use its powerful monomorphic chelae in any distinctive way, while *C. maenas* used the crusher chela to crush oysters and cutter chela to hold the prey in place.

Crabs would take oysters from the edges or margins of the shell using both chelae and hold the hinge towards the mouth. Forces were then applied with the crusher chela across the umbone region at different angles, while holding the prey with the cutter chela. In most cases the shell was successfully crushed when the force was applied along a line perpendicular to the sagittal axes of the shell, as if crabs were 'cutting off' the anterior tip of the shell (method **tc**). Once the shell was crushed, crabs would take flesh with the cutter chela or with their maxillipeds. The only conspicuous shell fragments left with this method were the posterior shell margins.

After a few unsuccessful attempts to crush an oyster, crabs would hold the prey with one or both chelae and bite around the margins or lips of the shell valves with the mandibles, until the prey was substantially reduced in size (method **om**). Normally they alternated margin-biting with further attempts to crush the shell, whose altered shape seemed to be more suitable for gripping. Although this method improved crushing success, on some occasions crabs would persist on inserting the propus of the crusher chela between the valves at any point along the shell margins in order to sever the adductor muscle and separate the two valves. This last option often left large shell fragments, very obviously bitten around the edges (Plate 3). Otherwise shells were completely destroyed.

Oysters that could not be opened using any of the above techniques had shells whose typically irregular aspect had been smoothed due to the constant handling by the crab. This seemed to leave weaker spots on the shell through which the crab could easily insert the propus of the crusher chela at different points over the dorsal valve (method **ob**). By cutting the adductor muscle, crabs could then open the prey without difficulty and remove the flesh with the chelae. This opening method resulted in the discarded shells being smooth and having a small round hole in the dorsal valve (Plate 3).

C. maenas spent less time crushing oysters (method **tc**) than it spent opening oysters with either of the other two methods, but hole-boring (**ob**) was clearly the most time consuming of all the techniques used (Chapter 6). The time spent by *C. pagurus* opening oysters was more strongly related to the size of the prey than to the types of methods applied, and was overall longer than the time spent by *C. maenas*. All large fragments of oyster shells

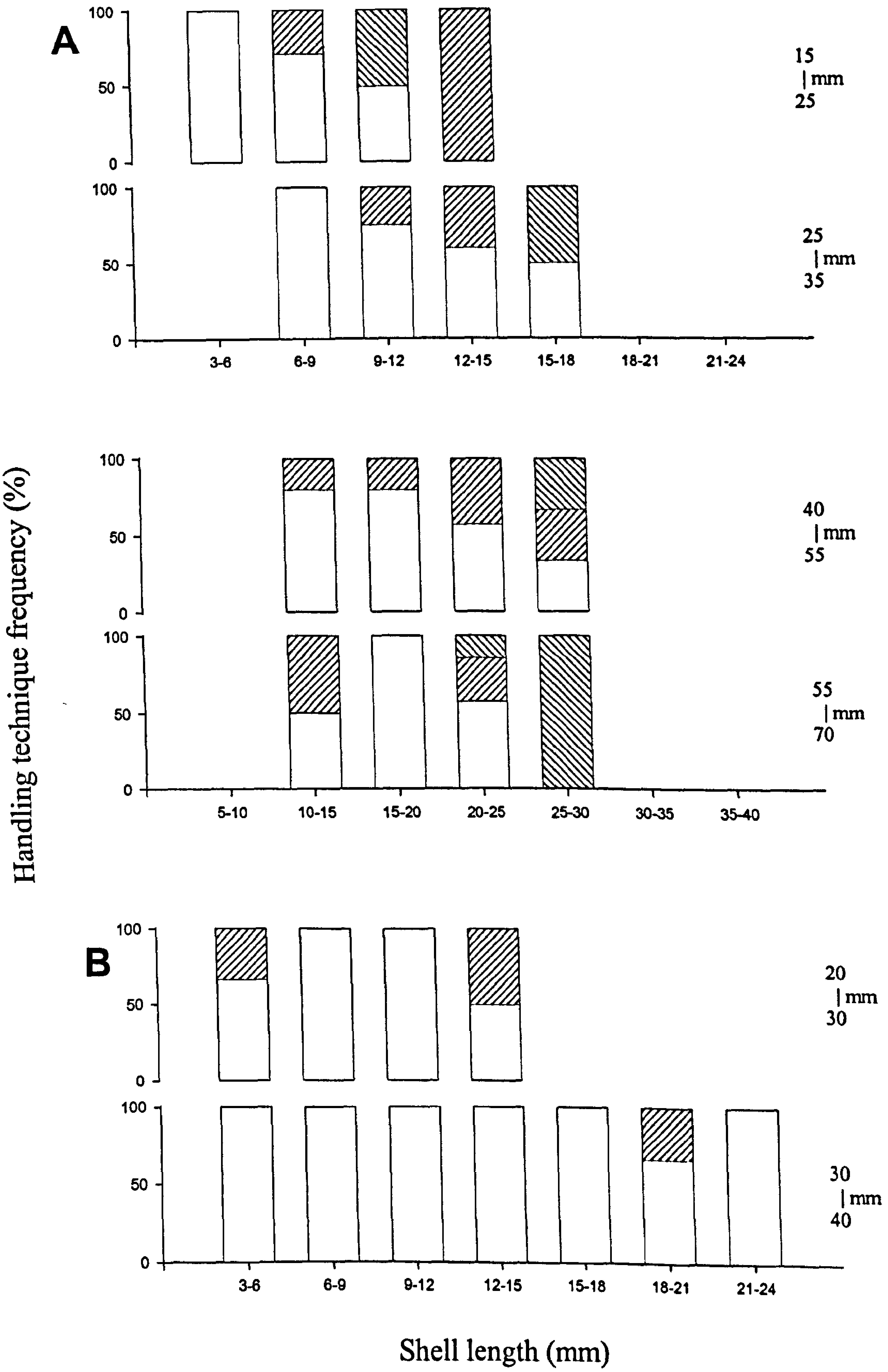

Figure 4.5. Frequency of the attack methods used by different size ranges of *Carcinus maenas* (**A**) and *Cancer pagurus* (**B**) on a wide size range of *Ostrea edulis*. Values are the percentages of oysters of each size class that were opened using each method:

▭ total crushing (tc)
▨ oyster margin-bitting (om)
▧ oyster hole-boring (ob)

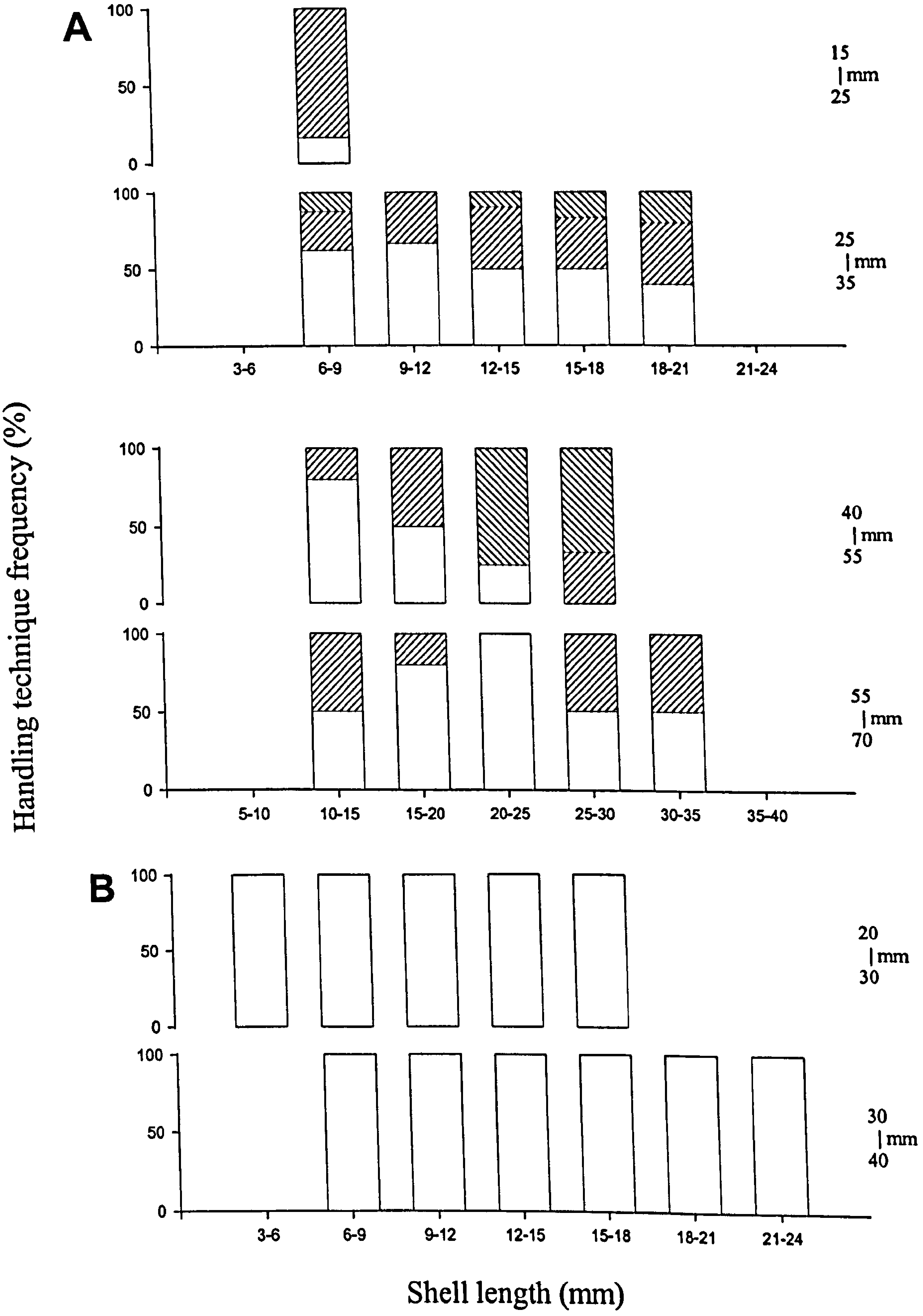

Figure 4.6. Frequency of the attack methods used by different size ranges of *Carcinus maenas* (A) and *Cancer pagurus* (B) on a wide size range of *Crassostrea gigas*. Values are the percentages of oysters of each size class that were opened using each method:

- ▭ total crushing (tc)
- ▨ oyster margin-bitting (om)
- ▧ oyster hole-boring (ob)

were gleaned more efficiently than mussel shell fragments, but in general oyster shells were completely destroyed more often than mussel shells.

Attack methods used on oysters were generally not as size-specific as the mussel opening techniques and, although the size ranges of oysters opened with each method overlapped (Figure 4.3), a trend towards using more elaborate methods on larger oysters could be established. The total crushing and margin-biting methods were used by all sizes of *C. maenas* on almost every size of oysters (**tc**: 3.9-33.4 mm and **om**: 5.0-35.7 mm SL), while the hole-boring method (**ob**) was specially used by medium and large shore crabs (40-70 mm CW) on all but the smallest (< 10 mm SL) oysters. *C. pagurus* used the crushing (**tc**) and margin-biting (**om**) methods to manipulate *O. edulis* of similar size ranges to those attacked by *C. maenas*, but was only seen to crush open specimens of *C. gigas*, and never used the hole-boring method (**ob**) on either species of oyster.

The frequency with which these oyster-opening methods were used on different sizes of *O. edulis* and *C. gigas* are shown respectively in Figures 4.5 and 4.6. Although *C. maenas* used almost all opening methods on oysters irrespective of their size, certain patterns in the way in which the frequency of attack methods varied with prey size were evident. Outright crushing (method **tc**) was more frequently used by *C. maenas* on small rather than large *O. edulis*, but this prey-size related variation was less evident when feeding on *C. gigas*. The frequency with which the margin-biting method (**om**) was used did not vary markedly amongst the larger size ranges of either *O. edulis* or *C. gigas*, although juvenile *C. maenas* did not use this method on the smallest *O. edulis*. The use of the hole-boring technique (**ob**) showed a slight tendency towards higher frequencies amongst the larger oysters, but was used by *C. maenas* of 15-25 mm CW throughout the size range of *C. gigas* offered. By contrast, *C. pagurus* only used the crushing method (**tc**) when feeding on *C. gigas*, but small edible crabs (20-30 mm CW) occasionally used the margin-biting technique on small and large but not on medium sized *O. edulis*. Both species of crabs were generally reluctant to eat oysters. Although individual oysters were repeatedly offered, in some cases crabs could successfully open as few as one oyster, particularly where methods **om** and **ob** were applied. For this reason, percentage values can be misleading, since few oysters may have actually been opened.

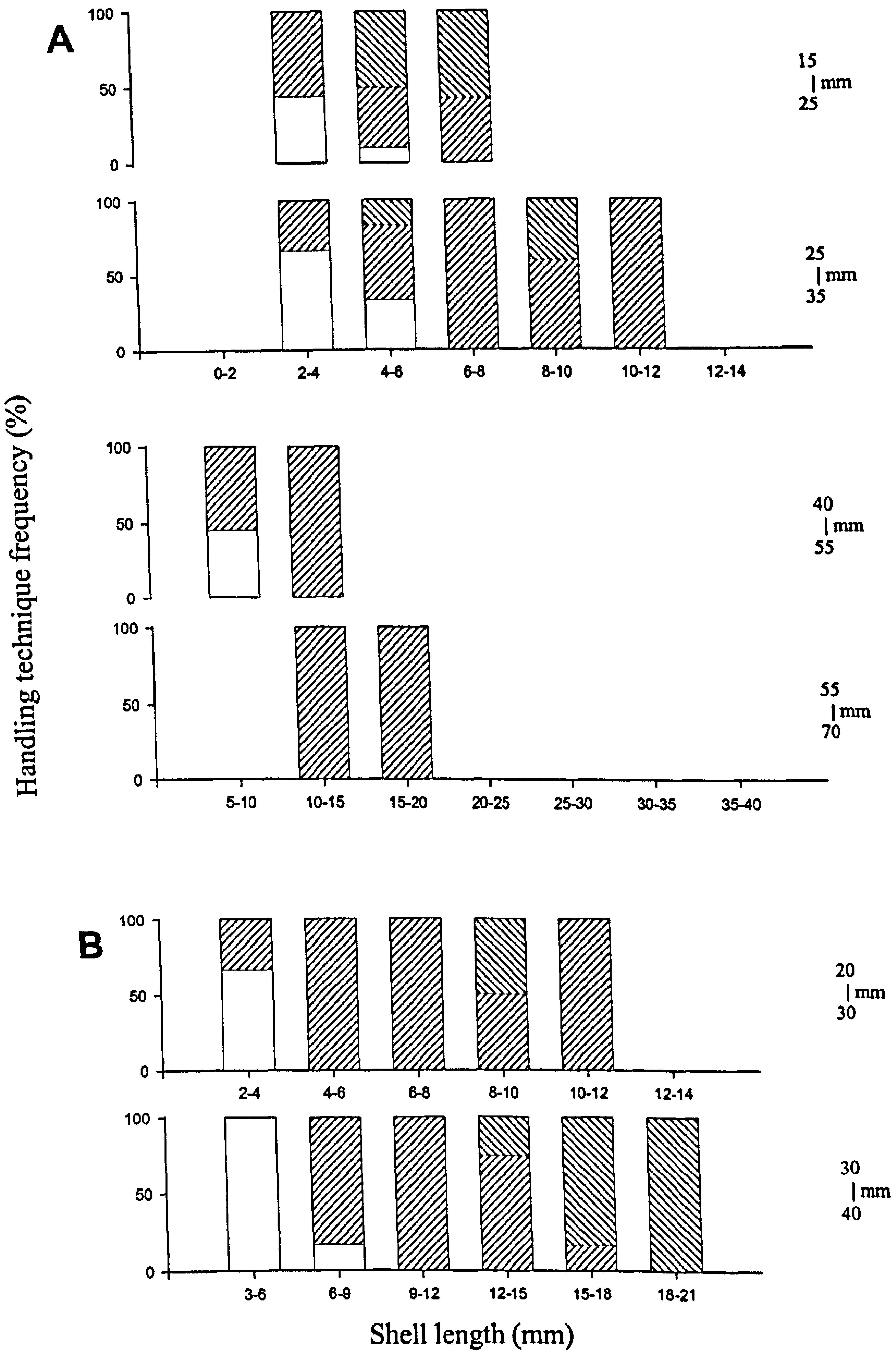

Figure 4.7. Frequency of the attack methods used by different size ranges of *Carcinus maenas* (A) and *Cancer pagurus* (B) on a wide size range of *Cerastoderma edule*. Values are the percentages of cockles of each size class that were opened using each method:

☐ outright crushing (oc)
▨ crushing after repeated attempts (sc)
▧ localised crushing (lc)

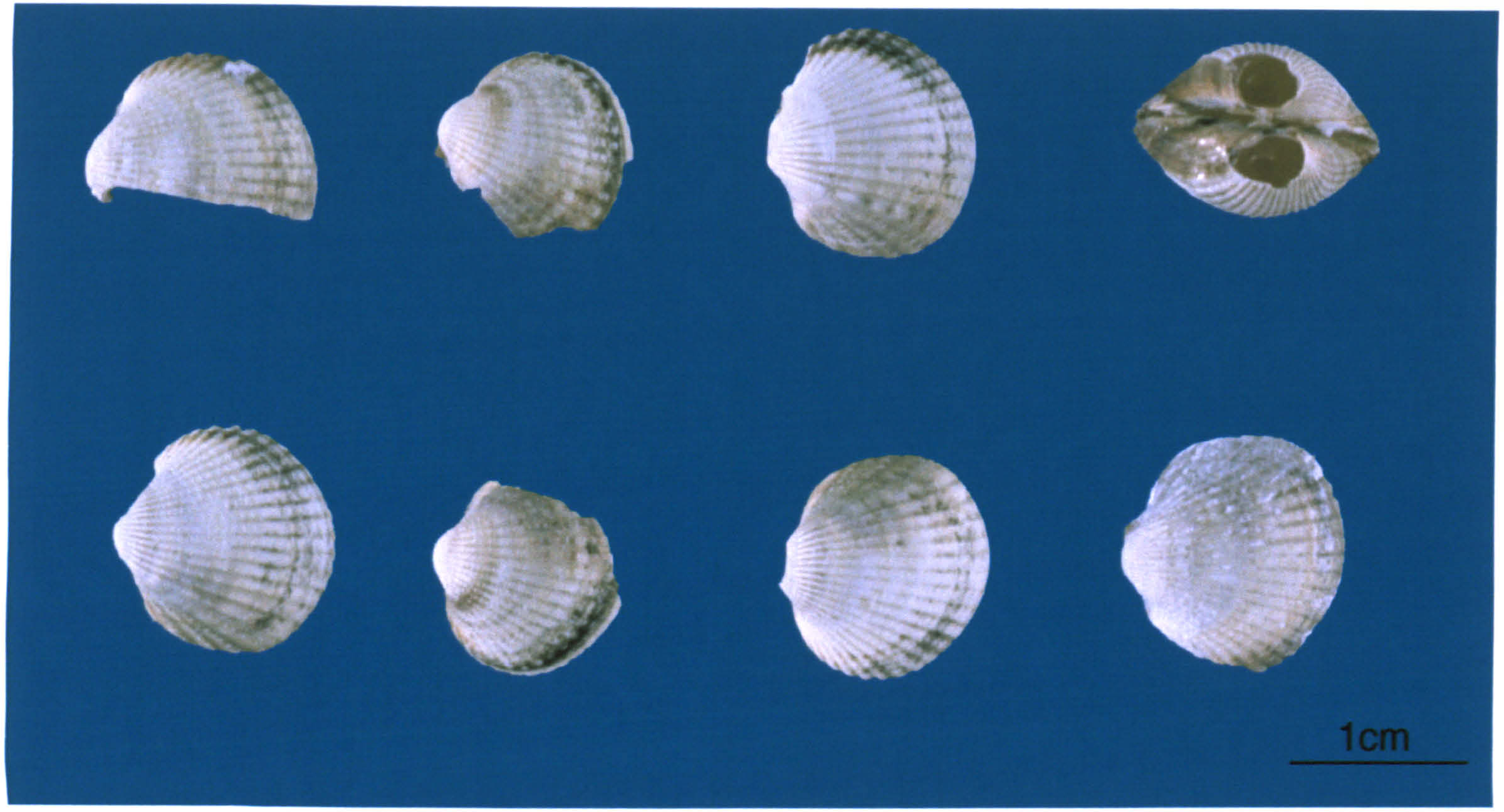

Plate 4. *Cerastoderma edule* shells opened by *Carcinus maenas* and *Cancer pagurus* using the localised crushing (lc) method.

Cockles

Crabs took cockles quite readily, and immediately brought them towards the mouth using the chelae and first pair of walking legs. Small cockles were crushed outright between the mandibles (method **oc**), and the flesh eaten voraciously; prey that did not yield to this first attempt were manipulated in the chelae and mouthparts, and a series of forces applied to different points of the shell in a dorso-ventral direction, especially on larger prey, or a lateral direction, more typically on smaller prey, until the shell was broken. Crabs would then start by biting the flesh with their mouthparts, subsequently separating the valves with the chelae and using the cutter claw to bring food towards the mouth (method **sc**). This was the most generalised opening method, and prey that could not be opened in this way were almost always abandoned. Only occasionally did crabs attempt to insert the propus of the crusher chela between the interlocking valves. This was never successful, although crabs were sometimes able to break the shell at a relatively localised point near the posterior edges of the valves (Plate 4); this method was then classified as localised crushing (**lc**). All crabs handled cockles in a similar way, and no major differences were observed between or within species apart from those described above. Of all the prey species used in these trials, cockle shells were gleaned the most efficiently and large fragments of shells were always found except for those opened by outright crushing (**oc**).

The time spent by crabs opening cockles was less for the first two methods described (**oc** and **cu**), but tended to be longer for the localised crushing method (**lc**), since crabs spent more time attempting to break different parts of the shell. All opening methods used on cockles took considerably less time than any of the more complex techniques described for the other bivalve species in this study (Chapter 6).

The maximum size of cockles opened by both crab species increased dramatically from the outright crushing method (**oc**) to the method where repeated forces were applied (**sc**), but the minimum size of cockles opened was similar for all methods (Figure 4.3). This was not observed for the localised crushing method (**lc**), although the relatively few data obtained for this method should be noted.

The frequency with which the different opening methods for cockles were used varied with prey size, and the patterns of variation were similar for all size ranges and both crab species (Figure 4.7). The outright crushing method (**oc**) was more frequently used on the smallest size groups of cockles. The method where repeated crushing attempts were directed on the umbone region (method **sc**) was used on all prey sizes. Although several small and large items could be crushed across the umbone region, the frequency of this attack method was highest on medium-sized cockles. The method where the shell was broken at a localised point near the posterior edges of the valves (method **lc**) was used more frequently on the largest items offered in each crab size category, except for adult *C. maenas*, where this method was never adopted.

4.4. Discussion

According to Lau's (1987) division of decapod predatory techniques, all the handling methods observed during the present study would fall into the category of those for which chelae are essential. In general terms they varied from techniques where the success of the attack basically relied on the strength and crushing power of the chelae, to those where certain characteristics in claw morphology allowing higher dexterity, together with specialised crab behaviour were required for opening the prey shell.

The techniques used by predatory crabs to open molluscan prey have been extensively documented, and results in this study broadly conform to what has been found in previous studies (e.g. Boulding, 1984; Bisker & Castagna, 1987; Davidson, 1986; Du Preez, 1984; Heller, 1976). All of these studies agree that crabs hunt for food using chemical stimuli received by sense organs on the antennae and walking legs (Ache, 1982; Jubb *et al.*, 1983). They are not primarily visual hunters and do not generally scan large areas to estimate overall prey availability (Elner & Hughes, 1978), although some species like *Callinectes sapidus* can use vision to pursue mobile prey (Seed & Hughes, 1997). Crabs in the present study generally detected prey items by contact using the dactyli of the pereiopods and through chemical stimuli. However, they were also capable of locating items when these were lowered into the aquarium. Hughes and Seed (1995) showed that *C. sapidus* only attacked fiddler crabs if they moved. Results in the present and other studies suggest that visual response in brachyuran crabs is restricted to movement (Hughes, 1989).

Both *Carcinus maenas* and *Cancer pagurus* normally used several behavioural techniques until the prey was either opened or abandoned; it seemed that prey was assessed in terms of its size, and decisions appeared to be influenced by the crabs experience with the previous prey offered. A similar behaviour has been previously observed in *C. maenas* feeding on mussels (Elner, 1977), and other authors (Akumfi & Hughes, 1987) have reported that this species manipulates prey to operate a mechanism of size assessment based on recent experience.

Following an initial period of manipulation, both *C. maenas* and *C. pagurus* would attempt to crush prey items (mussels, oysters and cockles) in different positions that varied with the size and shape of the shell. For small mussels and cockles, crabs would hold the prey items with their chelae and crush them with the mandibles, a procedure which is in accordance with the specific functions and active use of mouth appendages described in previous works (Davidson, 1986; Hill, 1979; Rheinallt & Hughes, 1985; Seed, 1982). *C. maenas* has been reported to crush small mussels totally, with the mandibles or the master chela, but it can also crush relatively weak regions of the shell when opening slightly larger mussels (Cunningham & Hughes, 1984; Elner, 1978). In the present study, both *C. maenas* and *C. pagurus* used the umbone crushing method on slightly larger mussels than those where the posterior crushing method was used (Figure 4.3). Attempts to crush the umbone region of these slightly larger items were more successful than those used to crush the much higher, but less wide posterior end. This was probably because during umbone crushing items were held in a position in the chelae where force is magnified by a higher mechanical advantage. These results confirm the findings of previous reports (Boulding, 1984; Rheinallt & Hughes, 1985; Warner & Jones, 1976) in that the way the prey shell fits into the chelal grip can significantly influence the magnitude and direction of the force it receives, and can partly determine the success rate of the attack. If the frequency with which the attack method used is related to breaking success (Hughes & Elner, 1979), then an appropriate match between shell and chelal geometry can explain the frequency with which certain crushing methods are used on specific types and sizes of molluscan prey.

If prey did not yield with the first crushing attempts, then crabs would rapidly re-orientate the prey item and reapply force on a different shell position. Previous studies have shown that repeated loading of the shell can generate microfractures that weaken its resistance and augment its vulnerability to further crushing (Boulding & LaBarbera, 1986). It has been suggested that crabs are able to detect when a prey item that is held in their claws is yielding, and that microfractures are probably important cues in further decisions regarding the time the predator will persist on a particular prey item (Elner, 1978). With the exception of outright crushing, all other crushing methods described in the present study included this repeated crushing procedure. The crushing methods described here for *Cerastoderma edule* are a particularly clear example of the way shells of increasing size and strength yield with an increasing number of crushing attempts. Sanchez-Salazar *et al.* (1987a) described three different methods that *C. maenas* used when feeding on *C. edule*: a) crushing with a single application of force; b) repeated applications of force on a prey item that was re-orientated after each crushing attempt; and c) attempts to insert the tips of both dactyli between the edges of the shell valves. Whilst *C. maenas* and *C. pagurus* in the present study used the first two methods described by Sanchez-Salazar *et al.* (1987a), only shore crabs occasionally attempted to insert the dactyli between the valves, though they were never seen to be successful (Figures 4.3 & 4.7). The valves at the posterior end of the cockle shell close at a very steep angle, resulting in a plane surface that is unsuitable for edge-chipping, and crabs find great difficulty inserting the dactyli between the tightly interlocking valves (Plate 1, D). When attempting to insert the dactyli between the valves, shore crabs would occasionally break one of the edges of the valves and continue to peel off remaining pieces of the shell. Breaking the posterior edge of the valves appears to be a result of either an initially damaged shell (Boulding & LaBarbera, 1986) or an inherent weakness in this particular shell region (Du Preez, 1984). Thus, this somewhat fortuitous breaking method should not be regarded as a specific method of attack, but rather a particular case of general crushing methods where repeated forces are applied on the shell.

When handling *Crassostrea gigas*, both *C. maenas* and *C. pagurus* would crush the most anterior region of the shell as if they were 'cutting off' the protruding umbone. The use of this variation of shell crushing was not frequently observed with the flat oyster, *Ostrea edulis*, and thus seems to be associated with the specific shell shape of *C. gigas*. Similar methods have been observed in *C. maenas* (Elner & Raffaelli, 1980; Hughes & Elner, 1979) and *Ovalipes punctatus* (Du Preez, 1984) feeding on periwinkles and whelks, respectively, where crabs would grasp the lip or columella with the minor chela, whilst the shell apex was completely removed with the master chela. These findings further support that specific attack methods are a mechanical consequence of the morphology of the chelae and the prey shell.

Shell crushing methods used on all four bivalves were broadly similar, and varied only with the position in which prey items were held within the claws, and the number of crushing attempts they received before the flesh was exposed. However, more complex methods like edge-chipping and hinge- and hole -boring, were used specifically on each prey species. This supports the idea that crushing methods are rather generalised amongst those brachyuran crabs which feed on various hard-shelled prey (Bisker & Castagna, 1987; Blundon & Kennedy, 1982a; Ebling *et al.*, 1964; Moody & Steneck, 1993; Whetstone & Eversole, 1978; Yamada *et al.*, 1993; Zipser & Vermeijj, 1978), while specific, relatively complex opening methods are more strongly influenced by the contrasting shapes of each molluscan species (Du Preez, 1984; Hughes & Elner, 1979; Hughes & Seed, 1981; Lawton & Hughes, 1985; Seed, 1982). Crabs chipped the posterior edge of mussel valves in order to insert the chelal tips between the valves (method **ep**), a time consuming but otherwise generally successful method. However, crabs biting the margins of oyster shells (method **om**) appeared to be attempting to reduce the size of the shell in order to be able to grip it more firmly within the chelae. Consequently, almost all oysters attacked in this way were eventually opened by crushing. The velvet swimming crab, *Necora puber* was reported to crush the shell of *Littorina rudis* only after it had been reduced in size, thus allowing the shell to fit in the back of the chelae where mechanical advantage is maximal (Rheinallt & Hughes, 1985). These results suggest that crabs bite the margins of oyster shells in order to improve their crushing success, rather than to attempt to insert the chelae between the valves, a technique used specifically on mussels (Hughes & Seed; 1981). Further support for this idea is the fact that the outright crushing method (**tc**) used on oysters was more strongly related to maximum shell length in *O. edulis* than it was in *C. gigas*. Outright crushing was more frequently used on small *O. edulis* than on large ones, but was used with a similar frequency in all sizes of *C. gigas* (Figures 4.5-4.6). Within a certain size range of prey, differences between the handling methods used by crabs on the two oyster species could be related to the contrasting shapes of their shells. Whereas *O. edulis* has a flat, more circular disc-like shell, the shell in *C. gigas* is more elongate, with a relatively more voluminous anterior region (Figure 4.2). In this way, small *O. edulis*, with an overall smaller diameter than large ones, and all sizes of *C. gigas* could be easily crushed within the chelae, without the need to reduce the overall height of the shell.

Edge-chipping (**ep**), whereby pieces of the shell of larger mussels are gradually chipped away from the posterior edge until the dactylus can be wedged into the gap to sever the adductor muscle, has previously been described by Hughes and Seed (1981) in *Callinectes sapidus*, but its consistency in several portunids (Elner, 1978; Davidson, 1986; Seed, 1982;), its complexity and effectiveness, suggest that this is a specific method for opening mussels in various crab species (Seed & Hughes, 1995). The comparatively fewer studies of cancrid crabs, however, have reported that their powerful monomorphic chelae allow them to usually adopt crushing methods when opening hard-shelled prey (Vermeij, 1977). The fact that the *C. pagurus* examined in the present study were small juvenile crabs, hence weaker than those examined elsewhere (e.g. Richardson *et al.*, 1993), might help to explain why they were frequently observed to open large mussels with the edge-chipping method. The differences between the edge-chipping method used on mussels and the margin-biting method used on oysters, together with the similarities in the way both crab species used these handling techniques, provide further evidence to support the specificity in the application of the edge-chipping method to open large mussels.

The slower hinge-boring method (**hb**) used on mussels has previously been observed in shore crabs by Akumfi and Hughes (1987). These authors described how crabs press the propus of the master chela against the ligament area, a region of the shell that appears to give a firm support for the pressing and twisting motions of the propus. Once a small hole has been created, the sawing action of the teeth of the chelae enlarge the hole and sever the anterior adductor muscle that holds the valves together. A similar procedure should be expected to be used on oysters if crabs could find a similarly firm depression on the irregular surface of the dorsal valve. In the present study, shore crabs using the hole-boring techniques on oysters (**ob**) alternated crushing attempts with what appeared to be an active search of local depressions in the shell into which the propus of the master chela could be steadily pressed. After a hole has been bored, crabs could rapidly separate the two shell valves. These results further confirm the reports of previous authors in that the hole-boring method constitutes a general procedure used by shore crabs when feeding on larger bivalves (Davidson, 1986; Du Preez, 1984; Krantz & Chamberlin, 1978), and suggest that its effectiveness depends on specific morphological features in the shell.

The attack methods employed by *C. maenas* and *C. pagurus* to open *Mytilus edulis* were generally in a characteristic sequence, allowing a wide size range of prey to be opened. Because opening success is related to mussel shell length, the maximum size of mussel that could be opened by each size range of crab increased as the attack method became more complex (Figure 4.3). Occasionally, however, crabs were unable to open a relatively small mussel using methods that would normally be effective on that size range of prey, and they would proceed to apply methods further in the sequence. The consequence of this is that the minimum size of mussels successfully opened did not increase significantly, but remained more or less constant as attack methods became more complex. A possible explanation is that natural variability in the strength between mussels of similar shell length results in crushing efficiency varying with characteristics other than shell size (Du Preez, 1984; Lawton & Hughes, 1985; Seed & Hughes, 1995).

Although the maximum size of mussels opened by the edge-chipping (**ep**) and hinge-boring (**hb**) methods were similar, the minimum size of mussels opened with the edge-chipping method was markedly larger than the minimum size opened with any other method (Figure 4.3). This underlines what has been found in other crab foraging studies regarding the rather restricted use of this method to open only large mussels relative to crab size and corroborates its specificity (Seed, 1982; Seed & Hughes, 1995). In a similar way, the increase in the maximum size of *C. edule* opened using the outright crushing method (**oc**) compared with the methods where multiple forces were applied (**sc** and **lc**, Figure 4.3), suggests that only very small cockles can be opened with the first crushing attempt. However, the relatively marked overlap between the sizes of cockles opened with the methods where multiple forces were applied, strongly support the idea that these are simply two variants of the same crushing method, as discussed earlier (see page 64).

The close relationship between attack method and the maximum linear dimension of mussels and cockles becomes more evident when the frequency with which the attack method is used is plotted against prey size. Figures 4.4 and 4.7 show the consistency in the pattern of variation amongst crabs of different size and species. This, however, is less evident in the oyster opening techniques (Figures 4.5-4.6), where the frequency with which attack methods are used remains the same, regardless of total oyster shell length. The lack of prey-size specificity in the attack methods used on oysters, particularly *C. gigas*, can be explained by the wide degree of variability in the shell shape of this particular bivalve. Lawton and Hughes (1985) found that the maximum sizes for crushing *Nucella lapillus* and *Littorina littorea*, beyond which *C. pagurus* used apertural breakage, depended on the shape of shells and sizes of the apertures rather than on the strength of the shell. Thus, it is possible that shell height, width (relative to the maximum chelal gape) and thickness in these oysters are more closely related than shell length to the frequency with which crabs use the various attack methods. All crabs experienced some difficulty holding *O. edulis* in any position, and they dropped and eventually rejected *O. edulis* more often than *C. gigas*. *C. pagurus* used the crushing methods on oysters more frequently than did *C. maenas* (Figures 4.5-4.6). Detailed observations indicate that regardless of differences in chelal strength and mechanical advantage between *C. maenas* and *C. pagurus*, *O. edulis* was consistently handled with more difficulty than was *C. gigas*, since the shell of the former is too high to fit into the widest aperture of the chelae, and too flat to be firmly grasped in a dorso-ventral position (Figure 4.2).

Prey size and strength have been identified as a potential refuge from crab predation (Blundon & Kennedy, 1982a; Boulding, 1984; Seed, 1982) and size-limited predation is thought to be important in permitting close coexistence of predator and prey (Paine, 1976). Results in the present study suggest that shell shape might influence crab predation, by reducing the efficiency of certain attack methods. The geometric shape of four mollusc species influenced the time required by *Cancer novaezelandiae* to open successfully and eat prey, regardless of prey size (Creswell & McLay, 1990). If prey shape can determine its vulnerability, and hence the crabs' preference for certain types of food, then it might constitute an important factor controlling prey-predator relationships between various crabs and molluscs within marine communities.

Whilst differences in handling methods between crabs of different size were largely determined by the size of prey relative to predator claw size and strength, differences between crab species also involved variations in claw morphology, occlusive geometry and crab behaviour. Studies on crabs with dimorphic chelae (such as *C. maenas*) have confirmed the distinct use of the master chela for crushing shells in a lateral as well as a dorso-ventral direction, while the minor chela generally holds the prey vertically, with either the posterior or the anterior end of prey uppermost. Once the shell valves are crushed or torn apart, heterochelous crabs use the master chela for holding the shell, while tearing and cutting pieces of flesh with the minor chela (Du Preez, 1984; Elner, 1980; Elner & Jamieson, 1979; Seed, 1980; 1982). By contrast, monomorphic crabs (such as *C. pagurus*) use either chela with equal facility to hold or break the prey shells (Lawton, 1983; Vermeij, 1977), although the chela used initially to pick up the prey is frequently the one used for crushing (Lawton & Hughes, 1985). Results in the present study confirm these findings, but other differences in general behaviour between *C. maenas* and *C. pagurus* could also be detected. *C. pagurus* was more difficult to observe feeding than *C. maenas*, and would frequently remain motionless even after having detected and grasped a prey item. In addition, *C. pagurus* was more persistent than *C. maenas*, since it would frequently interrupt an opening attempt that could be re-initiated up to 2 hours later, during which time the prey item was grasped in the chelae. Lengthy persistence times when feeding on large prey items have previously been reported in *C. pagurus* by Lawton and Hughes (1985), and appear to be a characteristic behaviour in other cancrids (Boulding, 1984), especially when compared to portunids, where crabs seldom persist with prey items that have been abandoned (Hughes & Elner, 1979; Hughes & Seed, 1981; Rheinallt, 1986). *C. pagurus* is abundant in the lower regions of the shore and is frequently found buried in the soft sediment beneath rocks and boulders (Edwards, 1979; Hall *et al.*, 1993). Its persistence and reluctance to feed whilst being observed might be related to its general, retiring habit, a behaviour often associated with cancrid crabs.

In the present study, adult *C. maenas* always used the walking legs to hold large mussels in place. All but the smallest *C. pagurus*, however, showed less frequent use of the first and second pair of pereiopods than *C. maenas* while handling prey. Previous studies have shown that when feeding on gastropods, *C. pagurus* manipulated small prey with the maxillipeds and chelae, but used the first and second pair of pereiopods to provide additional support for larger prey (Lawton & Hughes, 1985). The use of walking legs as a means of keeping the body balanced and the prey in position is associated with the size of prey relative to the chelal strength and total body size of the crab, and is expected to be used more frequently on larger and stronger prey items, on which crabs need to exert greater crushing forces.

While *C. maenas* used several oyster-opening techniques, *C. pagurus* used the crushing (**tc**) and margin-biting (**om**) methods to manipulate *O. edulis* of size ranges similar to those opened by *C. maenas*, and only opened *C. gigas* by crushing them (Figures 4.3, 4.5-4.6). Hughes and Seed (1981) found that the methods used by *Callinectes sapidus* to open progressively larger marsh mussels, *Geukensia demissa*, were similar to those used by *C. maenas* to open progressively larger *M. edulis* (Elner, 1978). The authors found, however, that *C. sapidus* seemed always to adopt the posterior edge-chipping method to open larger mussels, whereas *C. maenas* used alternative methods (Hughes & Seed, 1981). Comparative studies have shown that some crab species can use more specific opening methods than others, probably due to differences in the power and occlusive geometry of their chelae (Davidson, 1986; Du Preez, 1984; Rheinallt & Hughes, 1985). Small crabs with quicker, more dextrous claws exhibit a greater diversity of shell opening techniques than large species that more generally use crushing methods (Bertness & Cunningham, 1981; Elner & Jamieson, 1979; Hughes, 1989).

Differences in chelal morphology and biomechanics between *C. pagurus* and *C. maenas* suggested that *C. pagurus* is potentially capable of crushing larger prey items than *C. maenas* (Chapter 3). Results in the present chapter show that *C. pagurus* is capable of opening larger mussels (Figure 4.4), but not oysters (Figures 4.5-4.6) than *C. maenas* of comparable carapace width, and that both crab species are able to open similar sizes of cockles (Figure 4.7). The chelipeds of *C. maenas*, while deficient in strength, possess greater manipulatory ability and are, therefore, more efficient in holding, rotating and applying force more precisely than *C. pagurus*. Consequently, the relatively more specialised dimorphic chelae in *C. maenas* might allow for more complex handling techniques to be performed more efficiently on larger prey items, whereas the less specialised but more powerful set of monomorphic chelae in *C. pagurus* makes crushing items at a higher mechanical advantage a more efficient method for certain prey sizes and species. Similar findings have been demonstrated for a number of crab species with contrasting chelal morphology (Creswell & McLay, 1990; Whetstone & Eversole, 1978; Hughes, 1989; Seed & Hughes, 1995). These differences in chelal strength and dexterity between decapods allow for crab species to be classified according to the feeding behaviours they exhibit. Nevertheless, care should be taken when these classifications are made on a taxonomic basis, since crabs may be more appropriately divided into functional groups based on feeding capabilities and behaviour rather than on their phylogenetic affinities (Moody & Steneck, 1993).

In both *C. maenas* and *C. pagurus*, the maximum and minimum sizes of prey opened using any given method increased as crabs increased in size (Figure 4.3). Moreover, the prey size-related patterns of variation in the frequency with which attack methods are used on mussels and cockles were comparable for crabs of similar body size regardless of species (Figures 4.4 & 4.7). These results support the findings of previous works where the maximum size of prey opened by a given method is a function of prey shell strength relative to that of chelae (Hughes, 1989). Larger crabs seemed to have difficulty both finding and taking small prey, but were able to alternate two or more techniques on a large prey item. By contrast, smaller crabs could easily handle and glean the smallest prey, but were restricted to the use of only one method when feeding on larger prey (Figure 4.3). In addition, adult *C. maenas* seemed to be more clumsy, but also more persistent than juvenile conspecifics, since they would frequently drop a prey item several times, but pick it up again before finally rejecting it or succeeding in the attack. These observations can be explained by a proportional increase in chelal strength and gape, and a resultant decrease in chelal dexterity as crabs increase in size and their chelae grow proportionately larger relative to carapace width (Chapter 3).

Differences in the use of handling methods between crabs of different size have previously been related to the maximum chelal gape (Boulding, 1984), as well as to variations in dexterity associated with size and strength of chelae relative to crab body size (Creswell & McLay, 1990; Rheinallt, 1986). The time spent handling prey is an accelerating function of prey size, and for a given sized prey is longer amongst smaller than larger crabs (Lawton & Hughes 1985). Thus, if smaller, weaker crabs were to persist with larger prey, they would increase foraging time, hence the risk of being predated. Hughes and Seed (1981) suggested that minimisation of the time that *Callinectes sapidus* spends feeding on mussels constitutes an optimising foraging strategy, since it reduces the risk of being predated. In order to compensate for the limited power of their chelae (Rheinallt, 1986), smaller crabs that are able to open a narrower size range of prey than adults, will consequently consume more small prey items thus including a wider diversity of food types in their natural diet (Choy, 1986; Hill, 1979; Rangeley & Thomas, 1987; Ropes, 1968).

Differences in the handling techniques between crabs of the same species, but from different locations suggest that learning of predatory skills may be involved (Elner, 1978; Hughes & Seed, 1981). Experiments have demonstrated the acquisition of predatory skills through changes in the speed and number of successful attacks of *C. maenas* when feeding on mussels and dogwhelks (Cunningham & Hughes, 1984). The authors suggested that the marked reduction in the number of attempts to break an individual prey as crabs become more experienced with that particular prey was due to an increased effectiveness of the attack methods, since handling times decreased with experience. Whether juvenile crabs can learn to apply alternative opening methods as their claws become stronger has not yet been established, and constitutes an interesting topic for future research.

4.5. Summary

1. Differences in the relative growth of shell width and height with respect to shell length between the four bivalves examined suggest that inter-specific differences in shell morphology increase as prey increase in size. Amongst prey > 8 mm SL, *Cerastoderma edule* has a significantly wider shell than both *Mytilus edulis* and *Crassostrea gigas* of comparable shell length, and *Ostrea edulis* has the narrowest shell of the four species. Similarly, *O. edulis* and *C. edule* have a significantly higher shell than both *M. edulis* and *C. gigas* of comparable shell length. The biomass in *M. edulis* and *C. edule* of comparable shell length are similar, and are both significantly greater than in *O. edulis*. Amongst small prey sizes, Pacific oysters have less biomass than mussels, cockles, and flat oysters. However, because the biomass in *C. gigas* increases significantly more rapidly with respect to shell length than in the other bivalve species, amongst prey > 50 mm SL, Pacific oysters have more flesh than mussels, cockles and flat oysters of similar length.

2. Crabs mainly detected prey items by contact using the dactyli of the pereiopods and through chemical stimuli, but they were also capable of locating items when these are lowered into the aquarium. This confirms that visual response in brachyuran crabs is probably restricted to movement.

3. Following an initial period of manipulation, crabs would attempt to crush prey items in various positions. Shell crushing methods used on all four bivalves were broadly similar and varied only with the position in which prey items were held within the claws, and the number of crushing attempts they received before crabs succeeded in their attack. The way the prey shell fits into the chelal grip significantly influences the magnitude and direction of the force it receives, therefore partly determines the duration and success of the attack. Crabs had more difficulty grasping the relatively flat, disc-like shape of the shell in *O. edulis*, than the more narrow, irregular shell in *C. gigas*. Both mussels and cockles were readily accommodated within the chelae, manipulated and opened with less difficulty than either oyster species. However, the globular shell in *C. edule*, especially in cockles of a larger size, required a series of crushing attempts before the flesh was exposed.

4. When the shell did not yield after a certain number of crushing attempts, crabs used more complex attack methods. These were specifically used on each prey species and were more strongly influenced by the contrasting shapes of the various bivalve shells than any of the observed crushing methods. Amongst them is the edge-chipping method, specifically used by crabs to open large *M. edulis*.

5. These results confirm that with both the relatively simple crushing methods and the more elaborate prey handling techniques, an appropriate match between shell and chelal morphology can explain the frequency and success of the different handling methods used by *Carcinus maenas* and *Cancer pagurus* to open specific types and sizes of bivalve prey.

6. The opening success of each handling method was broadly related to prey size. However, the correlation was not perfect, and there was a certain degree of overlap between the size ranges of prey on which each method was successful. This can be explained by the natural variability in strength amongst prey of similar shell length, which results in opening efficiency varying with characteristics other than shell size. Moreover, the correlation between opening efficiency of each handling method and prey size was less evident amongst oysters, whose irregular shape makes fracture resistance less directly related to shell length, than amongst the more regular shaped mussels and cockles.

7. Differences in handling methods between crab species involved variations in claw morphology, biomechanics, and crab behaviour. *C. maenas* used its master chela for crushing the shell, while the minor chela holds the prey in position. By contrast *C. pagurus* used either chelae with equal facility to hold and break the prey shells. The relatively more specialised dimorphic chelae in *C. maenas* probably allows for more complex handling techniques to be performed more efficiently on larger prey items, whereas the less specialised but more powerful set of monomorphic chelae in *C. pagurus* makes crushing items at a higher mechanical advantage a more effective method for certain prey sizes and species. In addition, *C. pagurus* was more difficult to observe feeding and persisted on a prey item for longer periods than *C. maenas*. This persistence and reluctance to feed can be related to the general retiring habit often associated with cancrid crabs.

8. Differences in handling methods between crabs of different size were largely determined by the size of prey relative to predator claw size and strength. Large crabs had difficulty both finding and taking small prey, but were able to alternate two or more techniques on a large prey item. By contrast smaller crabs could easily handle and glean the smallest prey, but were restricted to the use of a single method when feeding on larger prey. These observations can be explained by a proportional increase in chelal strength and gape, and a resultant decrease in dexterity as crabs increase in size and their chelae grow proportionately larger relative to carapace width. In order to compensate for the limited power of their chelae, small crabs that are restricted to a narrower size range of prey than adults, will consequently include more small prey items of a wider diversity in their natural diets.

Chapter 5

Crab Foraging Behaviour

5.1. Introduction

The importance of decapod predation in structuring bivalve populations has resulted in research objectives during the last decades being directed towards a better understanding of the foraging behaviour of various crab species (Beukema, 1991; Dare & Edwards, 1976; Ebling *et al.*, 1964; Kent & Day, 1983; Muntz *et al.*, 1965; Virnstein, 1977). Prey size and species selection is a major aspect within this topic, given the direct influence selective predation has on the dynamics of bivalve populations. Selective predation results in the removal of a certain type of prey from the natural environment, thus making it more scarce, and influencing the abundance and distribution of other species in the system that are related to it (Akumfi & Hughes, 1987). Size and species selection can also have an effect on the dynamics of crab populations, since it can reduce inter- and intra-specific competition by partitioning food resources amongst predators (Hughes, 1980; Lawton, 1989; Seed, 1980). Information concerning the way crabs choose their diet from a variety of prey types can be very useful for a better understanding of community dynamics, as well as for the adequate management of natural resources (Bisker & Castagna, 1987; Peterson, 1990).

Previous studies have suggested that the reluctance of crabs to eat certain sizes and species of prey could be due to morphological and mechanical characteristics of their chelae (Blundon & Kennedy, 1982a). Given the inter-specific differences in chelal strength, occlusive design (Chapter 3), and in the way different species of crabs use their chelae while feeding on bivalves (Chapter 4), preferred prey items can vary from one species of crab to another (see also Lawton, 1983; Lawton & Hughes, 1985; Rheinallt, 1982; 1986). Not only predator species, but also predator size is an important aspect to consider when studying prey selection. Smaller crabs may not have the required skills or strength to open larger or thicker hard-shelled prey, and may, therefore, exhibit a higher degree of size selection than larger crabs which can choose from a wider range of prey types and sizes (Lee & Seed, 1992; Whetstone & Eversole, 1981). Moreover, differences in the local shore distribution between crabs of different size can have an important influence on their foraging behaviour (Rangeley & Thomas, 1987).

Selective foraging behaviour has been studied with both unlimited and restricted diets (Elner & Hughes, 1978), and results indicate that patterns of selection often occur when preferred prey are constantly available. Nevertheless, these patterns are likely to disappear when the preferred items have been depleted, suggesting that selective behaviour is flexible and partly determined by prey availability at the time of the foraging bout (Barbeau & Scheibling, 1994a; Hughes & Seed, 1981). In this way, the degree of selection can vary according to the proportions in which crabs encounter their preferred items (Hughes & Elner, 1979), as well as with hunger levels and possible interference from other predators (Kaiser *et al.*, 1990; Seed, 1993). Learning skills in the feeding behaviour of crabs have been frequently suggested (Cunningham & Hughes, 1984; Kaiser *et al.*, 1993; Micheli, 1995), and immediate previous experience with a certain type of prey can also modify dietary preference (Jubb *et al.*, 1983).

The shore crab, *Carcinus maenas*, and the edible crab, *Cancer pagurus*, are both abundantly distributed in the North Atlantic (Williams, 1984), and are particularly common around the British Isles (Ingle, 1980). *C. maenas* is a tidally migrating species, mainly distributed along the intertidal zone, although some shore crabs, especially large individuals and females, move offshore during the winter months (Chapter 2; see also Edwards, 1958; Hunter & Naylor, 1993; Naylor, 1958). *C. pagurus*, by contrast, is abundant in the subtidal zone, with only the smaller, juvenile crabs occurring between the tidal marks (Chapter 2; see also Edwards, 1979; Hall *et al.*, 1993; Lawton, 1983). Numerous works have provided evidence of the way predation by these two important and abundant decapod crustaceans can potentially influence the abundance and distribution of commercially important bivalves, that are part of their natural diet; such bivalves include mussels (e.g. Elner, 1978); oysters (e.g. Dare *et al.*, 1983); and cockles (e.g. Sanchez-Salazar *et al.*, 1987b).

Most studies on the selective feeding behaviour of crabs have focused on size selection within a certain species of prey (e.g. Barbeau & Scheibling, 1994b; Lawton & Hughes, 1985; Rheinallt, 1986; Lin, 1991; Seed, 1982), and few studies have examined prey selection when two or more species of different shell shape are presented (e.g. Boulding, 1984; Creswell & McLay, 1990). Considering the importance of selective feeding in the foraging behaviour of these two decapods, it is the purpose of this chapter to determine and describe the patterns of prey size and species selection by a wide size range of *C. maenas* and juvenile *C. pagurus* when feeding on a size range of four bivalve species with contrasting shell morphology: the mussel, *Mytilus edulis*, the flat oyster, *Ostrea edulis*, the Pacific oyster, *Crassostrea gigas*, and the cockle *Cerastoderma edule* (Plate 1, A-D). Because selective feeding can be strongly influenced by the relative abundance of different types of prey, laboratory experiments presenting prey species in varying proportions have been carried out. Differences in size selective predation between and within crab species are also examined; though a more detailed discussion regarding the basis of prey size and species selection is presented in Chapter 6.

5.2. Materials and Methods

Carcinus maenas and *Cancer pagurus* were collected by hand from the intertidal zone in the Menai Strait (Figure 2.1). To avoid bias that may result from the crabs previous experience with certain species of prey, only crabs collected at Treborth (A) were used in feeding experiments, since at this site the experimental prey species are either poorly represented or absent. Collections were made at approximately low water on several occasions between November 1994 and June 1997. *C. maenas* ranged in size between 15-70 mm in carapace width (CW), whilst *C. pagurus* ranged between 20-40 mm CW. Crabs were kept individually in plastic aquaria (30 x 20 cm for crabs < 40 mm CW; and 40 x 30 cm for crabs > 40 mm CW) filled to a depth of 10 cm with running sea water. Water temperature in the aquaria was maintained between 12-17°C, and photoperiod was kept constant at approximately 14 h light : 10 h of darkness using 40 W fluorescent lights. All crabs were starved for 48 h prior to experiments in order to standardise hunger levels. Only male crabs in the late inter-moult stage were used in order to avoid potential bias due to differences in morphology and behaviour associated with sex and moult stage (Kaiser *et al.*, 1990). Prey items were collected and kept as described in Chapter 4.

5.2.1. Experiments with single prey species.

In order to determine whether size selection occurred with each of the four prey species, crabs were individually presented with a size range of *Mytilus edulis*, *Ostrea edulis*, *Crassostrea gigas* and *Cerastoderma edule*, and their preferences in each case were recorded. Shore crabs were classified into four size categories: small (S): 15-25 mm; small-medium (SM): 25-35 mm; medium (M): 40-55 mm; and large (L): 55-70 mm CW. Three juvenile crabs (i.e. crabs that were < 35 mm CW; Chapter 3; see also Hartnoll, 1978; Lee & Seed, 1992) and two adult crabs (i.e. > 40 mm CW) from each size category were offered five prey items in each of several size classes of the four experimental prey species. Mussels ranged from 2-40 mm in shell length (SL: maximum dimension of the shell; Figure 4.1); oysters ranged from 3-40 mm SL; cockles ranged from 2-40 mm SL, and the number and size of categories in which they were classified varied between experiments depending on crab size (Appendix B2). Prey items were scattered randomly over the floor of the aquaria. In experiments with oysters and cockles, only two crabs in each of the four largest size categories were used, since the prey sizes that the smallest crabs were able to open were difficult to obtain in the required numbers. Any prey item consumed during 12 h feeding periods was recorded, and replaced by another one of similar size in order to maintain constant prey availability. When ingestion rates were especially high, feeding bouts were reduced to periods of 6 h, and prey were monitored every hour. Experiments were run continuously until a consistent feeding pattern emerged, and each experiment never lasted for more than 10 days.

Similar size selection experiments were carried out with edible crabs feeding on mussels ranging from 2-30 mm SL. Three crabs in each of two slightly different size classes (small (S): 20-30 mm; and small-medium (SM): 30-40 mm CW), were offered five mussels in each of the size classes shown in Appendix B2. Oysters and cockles ranging from 2-30 mm SL were offered to two crabs in each of two size classes (20-30 mm and 30-40 mm CW; Appendix B2), and their size preferences noted. Consumed prey items were monitored and replaced as described earlier. Results were analysed by comparing the prey size distributions using a chi-square test to detect whether these deviated from a random choice (Peterson & Renaud, 1989; Sokal & Rohlf, 1981).

In order to compare the biomass corresponding to the total number of items of each prey species that were consumed daily by each size category of crabs, the dry flesh weight (mg) of the items ingested in each size class of prey were estimated for shell lengths corresponding to the median values of the appropriate size class. Values of dry flesh weight were calculated using the allometric equations previously obtained over a wide size range of each prey species (Chapter 4).

Experiments to determine the effect of temperature on crab ingestion rates were only carried out with juvenile *C. maenas* and *C. pagurus* feeding on *M. edulis*. Seven to ten *C. pagurus* ranging from 10-40 mm CW and ten *C. maenas* ranging from 5-30 mm CW were individually presented with five *M. edulis* in each of the size classes shown in Appendix B2. Mussels fed to *C. pagurus* ranged from 2-30 mm SL, whilst those fed to *C. maenas* ranged from 1-14 mm SL, and were scattered randomly over the floor of the aquaria. Every crab was never presented with more than a total of 30 mussels, and consumed prey were monitored and replaced as described earlier. Experiments lasted an average of nine days, and were run at 8-11, 12-15, and 18-21 °C, covering the annual range of water temperatures in the Menai Strait (Chapter 2).

5.2.2. Experiments with paired combinations of prey species.

Once the preferred size ranges for each prey species had been established, paired combinations of a wide size range of prey species were offered to two *C. maenas* in each of four size categories (S, SM, M and L as above), and to two *C. pagurus* in each of two size categories (S and SM as above). The prey species combinations were *M. edulis-O. edulis*, *M. edulis-C. gigas*, *O. edulis-C. gigas*, and *M. edulis-C. edule*, and each crab was offered 5 items in each size class of prey. The size classes of prey used for these experiments were based on those preferred by crabs in the experiments where prey species were offered individually; these are summarised in Appendix B3. Care was taken so that the relative proportions of prey were equal in each trial, and only recently collected crabs were used so that any possible bias from previous feeding experience was eliminated. Consumption of prey items was monitored every 12 h, and eaten prey were replaced with others of similar size in order to maintain constant prey availability. Experiments were run continuously for 7-10 days. The biomass corresponding to the total number of items of each prey species that were consumed daily by each size category of crab was estimated as described earlier.

5.2.3. Experiments with equal and altered proportions of paired species combinations.

In order to obtain a more detailed description of the way crabs select their prey, crabs similar in size to those used previously were offered equal numbers of the preferred size range of prey species in each paired combination. The size classes of prey offered to crabs in these experiments (Appendix B4) were established on the basis of those selected in the single prey species experiments, although results of the paired species combination experiments were also taken into account. In those cases where crabs did not exhibit any apparent preference for a particular size range of prey (e.g. oysters), the size range used was comparable to that for the preferred size ranges of mussels. Each time a prey item was taken by a crab it was immediately replaced by another of similar size, and the precise order in which items were taken recorded. Once a crab encountered a prey item and recognised it as potential food, the behavioural components were categorised as: a) **prey touched and rejected** i.e. the crab touched a prey item with its pereiopods or chelipeds, and rejected it in less than 10 seconds; b) **manipulated and abandoned** i.e. the prey was manipulated, but attempts to open it were unsuccessful and the prey was finally abandoned; c) **opened** i.e. the prey was successfully opened. The behavioural components described above reflect a decreasing degree of crab preference, since crabs might be expected to have a higher preference for an item they had previously opened, than for one that had been manipulated and abandoned, and this in turn might be preferred over a prey item that has been touched but immediately rejected (see Jubb *et al.*, 1983). Because crab satiation, amongst other factors, can strongly influence the behavioural sequence adopted by an individual crab, each trial was run for 1 h, the average period of time for crabs to become satiated during preliminary observations. Experiments were repeated on a daily basis until a constant behavioural pattern emerged (usually 4-5 consecutive days). Because the relative abundance of the two types of prey presented was equal, the probability of crabs encountering each prey species was expected to be the same. The total number of times that each crab encountered each prey species was then tested for goodness-of-fit to the expected values (assuming an equal probability of encounter). Significant differences in the total number of prey of each species that were successfully opened by each individual crab was tested using the same procedure.

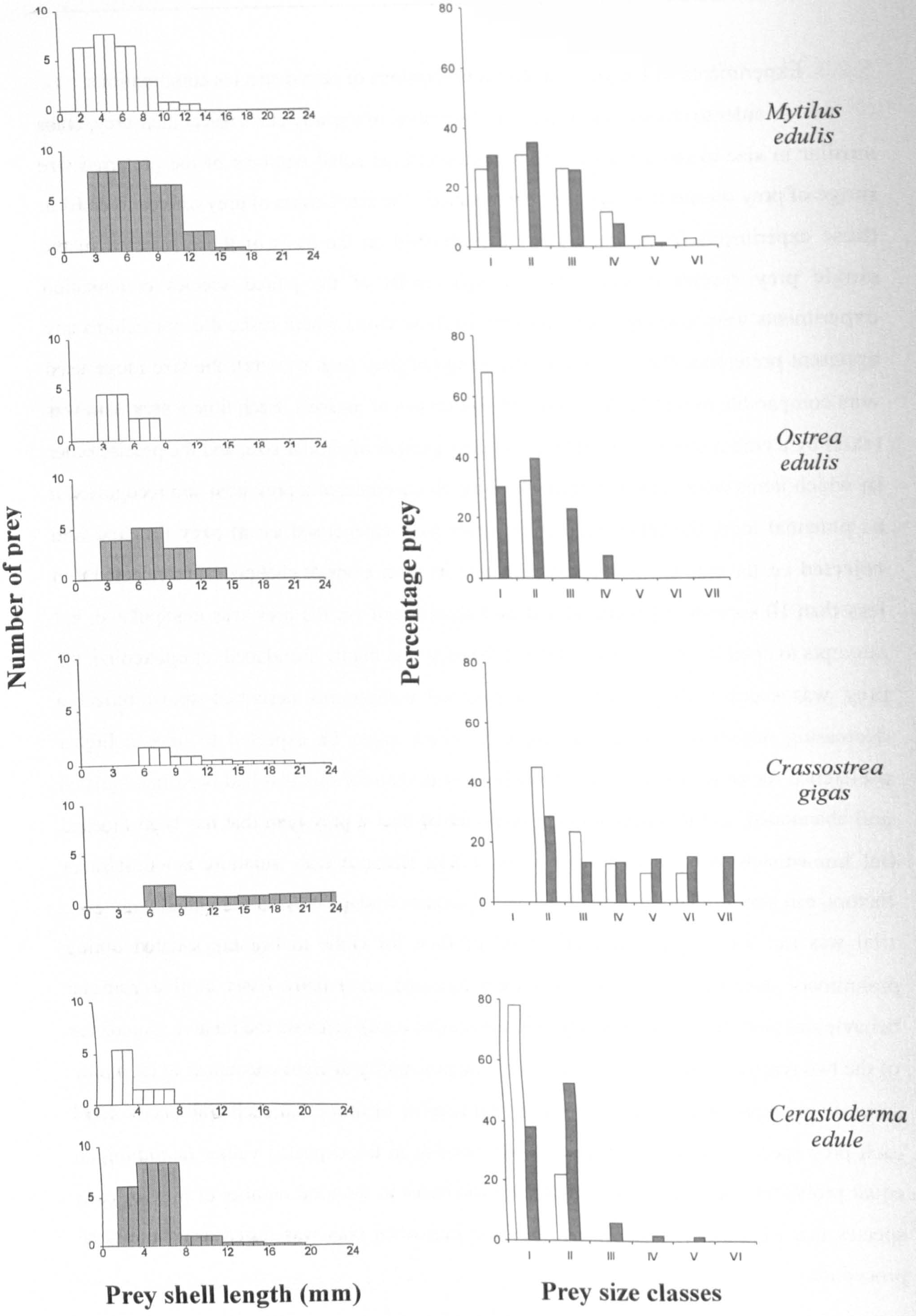

Figure 5.1. Number and percentage of prey of various size classes (mm in shell length) of *Mytilus edulis* , *Ostrea edulis* , *Crassostrea gigas* and *Cerastoderma edule* that were consumed by *Carcinus maenas* of 15-25 mm (open columns) and 25-35 mm CW (shaded columns) during the single prey species experiments. Values are mean consumption rates· crab^{-1}· day^{-1}. The size classes of prey (I, II, III, etc) offered to each size category of crab are those presented in Appendix B2.

In order to establish whether crab preference for a certain prey species was determined by the relative abundance in which it was presented i.e. whether crabs were actively selecting or passively responding to the rate in which each prey species was encountered, each individual crab was offered unequal numbers of prey items in the *M. edulis-O. edulis* and *M. edulis-C. edule* combinations. Here, however, the proportions of presented prey were altered so that the prey species that had been preferentially selected in the previous experiments was now at a lower relative abundance of 1:2 and 1:4 with respect to the less preferred species. Care was taken so that the total number of prey in each presentation was similar to that in experiments where equal numbers of prey were offered, and prey species were presented in numbers of 3:6 and 3:12, respectively. Results were recorded in a similar way as for the previous experiments, and compared accordingly. The total number of times that crabs in each size category encountered each prey species, and the total number of prey successfully opened were then tested for goodness-of-fit to the expected values (probability of encounter of 1:2 and 1:4).

5.3. Results

5.3.1. Experiments with single prey species.

The mean number of prey in each size class and species that were consumed by juvenile *Carcinus maenas* (15-35 mm CW) are shown in Figure 5.1. Small (15-25 mm CW) and small-medium (25-35 mm CW) *C. maenas* preferred mussels of 2-8 mm and 3-12 mm in shell length (SL), respectively. Small crabs preferred cockles of the smallest size class offered (2-4 mm SL), while small-medium crabs consumed more cockles of 4-8 mm SL, but also included a considerable number of the smallest cockles offered (2-4 mm SL). Very few cockles > 8 mm SL were consumed by either size categories of juvenile shore crabs. When *Ostrea edulis* was offered, small crabs preferred oysters of 3-9 mm SL, but never consumed flat oysters > 9 mm SL. Similarly, small-medium crabs preferred oysters of 3-12 mm SL, and never included flat oysters > 15 mm SL in their diet. By contrast, when *Crassostrea gigas* was offered, both small and small-medium crabs consumed Pacific oysters of all size classes, although they preferred oysters from the smaller size classes offered (6-12 and 6-9 mm SL, respectively).

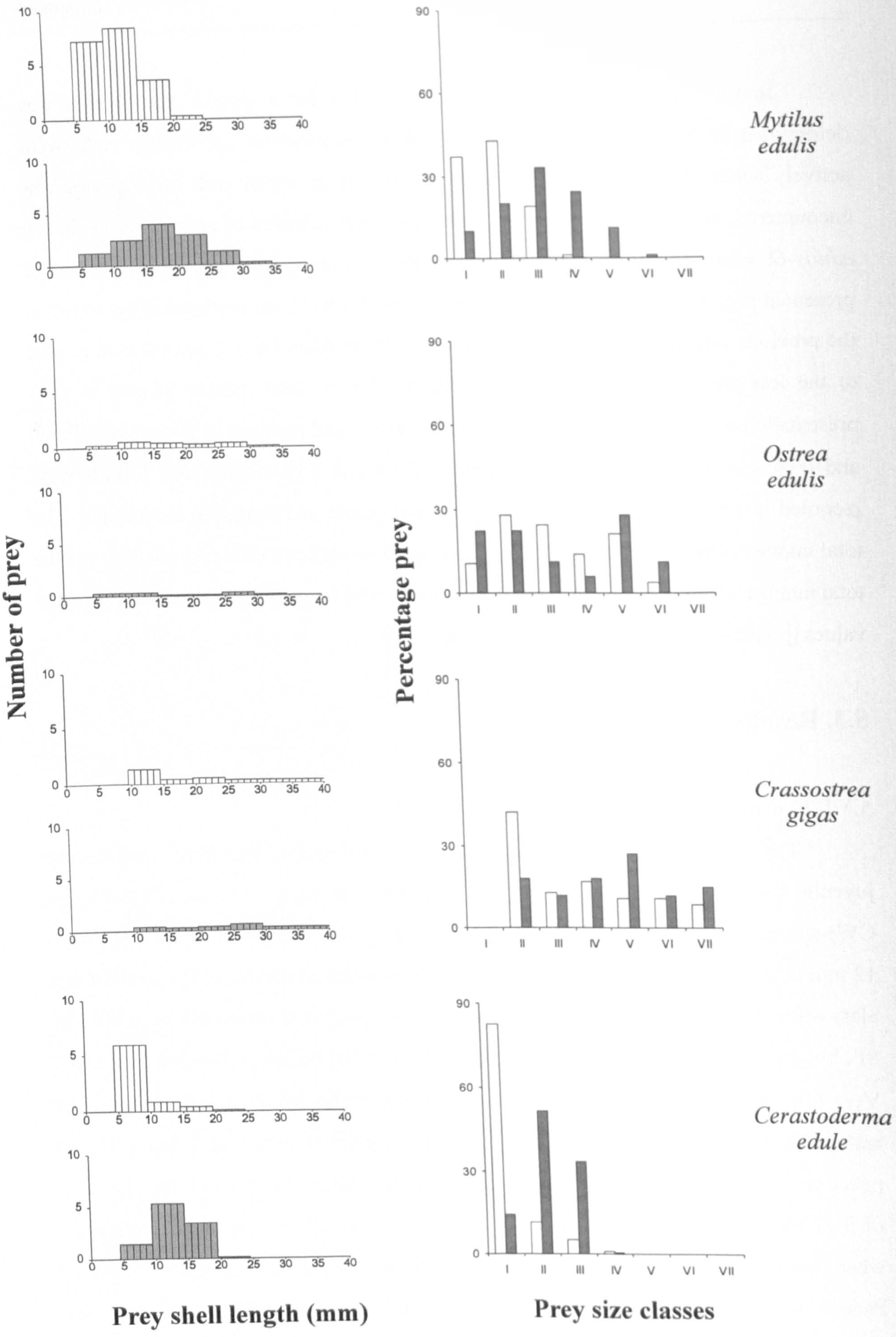

Figure 5.2. Number and percentage of prey of various size classes (mm in shell length) of *Mytilus edulis* , *Ostrea edulis* , *Crassostrea gigas* and *Cerastoderma edule* that were consumed by *Carcinus maenas* of 40-55 mm (open columns) and 55-70 mm CW (shaded columns) during the single prey species experiments. Values are mean consumption rates· crab^{-1}· day^{-1}. The size classes of prey (I, II, III, etc) offered to each size category of crab are those presented in Appendix B2.

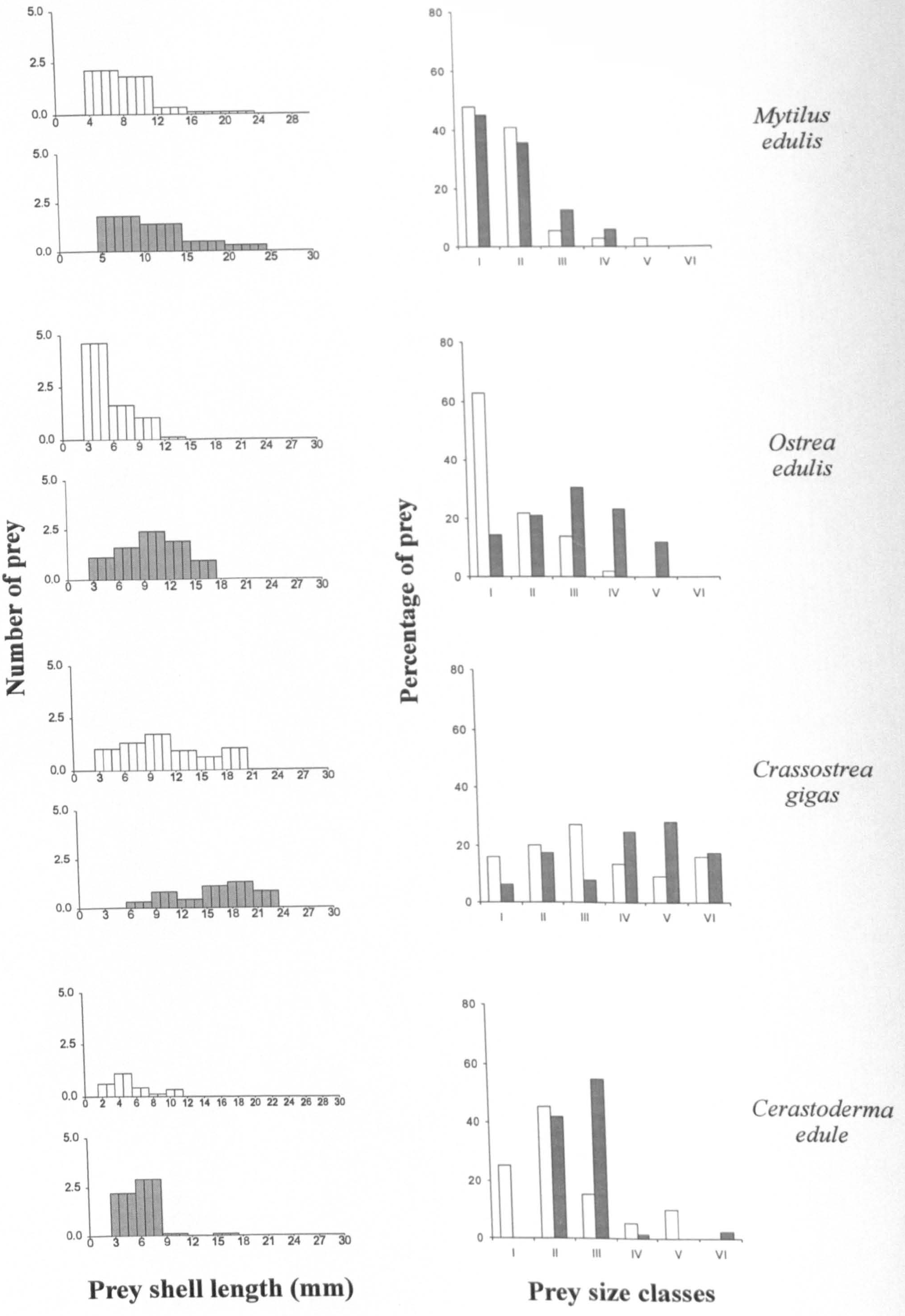

Figure 5.3. Number and percentage of prey of various size classes (mm in shell length) of *Mytilus edulis* , *Ostrea edulis* , *Crassostrea gigas* and *Cerastoderma edule* that were consumed by *Cancer pagurus* of 20-30 mm (open columns) and 30-40 mm CW (shaded columns) during the single prey species experiments. Values are mean consumption rates· crab^{-1}· day^{-1}. The size classes of prey (I, II, III, etc) offered to each size category of crab are those presented in Appendix B2.

Table 5.1. Chi-square tests on the total number of *Mytilus edulis*, *Ostrea edulis*, *Crassostrea gigas* and *Cerastoderma edule* consumed by different size categories of *Carcinus maenas* and *Cancer pagurus* in single prey species experiments. The size classes of prey offered to crabs are presented in Appendix B2. The preferred (i.e. consumed in > 20 %) size ranges of prey (mm SL) are shown in parenthesis when tests proved statistical significance. s = significant at * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$, ns = no significant departure from an expected uniform distribution.

	M. edulis		*O. edulis*		*C. gigas*		*C. edule*	
C. maenas								
15-25 mm	s ***	(2-8)	s ***	(3-9)	s ***	(6-12)	s ***	(2-4)
25-35 mm	s ***	(3-12)	s ***	(3-12)	s *	(6-9)	s ***	(2-8)
40-55 mm	s ***	(5-15)	ns	-	s ***	(5-15)	s ***	(5-10)
55-70 mm	s ***	(15-25)	ns	-	ns	-	s ***	(10-15)
C. pagurus								
20-30 mm	s ***	(4-12)	s ***	(3-9)	ns	-	s **	(2-6)
30-40 mm	s ***	(5-15)	s *	(6-15)	s *	(15-21)	s ***	(3-9)

Table 5.2. Ingested biomass (mg) corresponding to the total number of prey items (in parenthesis) in all size classes of *Mytilus edulis*, *Ostrea edulis*, *Crassostrea gigas*, and *Cerastoderma edule* consumed daily by *Carcinus maenas* and *Cancer pagurus* of various size categories during single prey species experiments. Biomass was estimated on the basis of the dry flesh weight of an individual prey item of a shell length equivalent to the median value of its size class (Chapter 4). Values are mean consumption rates • crab $^{-1}$ • day $^{-1}$.

	M. edulis		*O. edulis*		*C. gigas*		*C. edule*	
C. maenas								
15-25 mm	46.8	(24.5)	1.1	(6.6)	4.7	(3.6)	3.8	(6.9)
25-35 mm	102.7	(25.8)	6.7	(13.1)	21.2	(6.8)	44.6	(16.1)
40-55 mm	211.2	(19.4)	11.8	(1.8)	34.5	(3.0)	60.4	(7.1)
55-70 mm	417.6	(12.0)	9.2	(1.1)	37.2	(2.1)	252.5	(10.1)
C. pagurus								
20-30 mm	26.3	(4.4)	2.1	(7.3)	10.5	(6.4)	6.8	(2.5)
30-40 mm	45.1	(4.0)	9.6	(8.0)	19.2	(4.6)	19.2	(5.3)

A similar pattern emerged from the experiments with adult *C. maenas* (40-70 mm CW; Figure 5.2). Medium shore crabs (40-55 mm CW) preferred mussels of the two smallest size classes (5-15 mm SL), and cockles of the smallest size class offered (5-10 mm SL). Large crabs (55-70 mm CW) preferred slightly larger mussels (15-25 mm SL) and cockles (10-20 mm SL) than medium crabs. Neither medium nor large crabs included cockles > 20 mm, and 25 mm SL, respectively in their diets. When feeding on oysters, adult shore crabs generally showed no preference for any particular size class of either oyster species, the only exception being medium *C. maenas* that consumed *C. gigas* of 10-15 mm SL in significantly higher numbers, but included Pacific oysters of all size classes offered in their diet.

Results of the single species size selection experiments with *Cancer pagurus* are shown in Figure 5.3. Small (20-30 mm CW) and small-medium (30-40 mm CW) edible crabs preferred mussels of 4-12 mm and 5-15 mm SL, respectively. Small crabs preferred cockles of 2-6 mm SL, whilst small-medium crabs preferred cockles of 3-9 mm SL. When *O. edulis* were offered, small edible crabs preferred flat oysters of 3-9 mm SL, and did not consume flat oysters > 15 mm SL. Small-medium crabs, however, preferred flat oysters of 6-15 mm SL, although they included all size classes of flat oysters in their diet. When *C. gigas* were offered, small edible crabs showed no preference towards any size class of oyster offered, while small-medium crabs consumed more *C. gigas* of 15-18 and 18-21 mm SL. Both size classes of crabs, however, included all sizes of Pacific oysters in their diet.

Table 5.1 shows the outcome of the chi-square analysis on these data. The size classes of each prey species that were preferred by each size category of crab are included in parenthesis. All crabs feeding on *Mytilus edulis* and *Cerastoderma edule* showed a significant preference for certain size classes of prey. When feeding on *O. edulis*, juvenile *C. maenas* (15-35 mm CW) and both size categories of *C. pagurus* (20-40 mm CW) showed evidence of size-selective predation. However, adult *C. maenas* (40-70 mm CW) consumed flat oysters of all size classes indiscriminately. When feeding on *C. gigas*, shore crabs from 15-55 mm CW and edible crabs from 30-40 mm CW showed evidence of size-selective predation, whereas *C. maenas* and *C. pagurus* of 55-70 and 20-30 mm CW, respectively consumed all size classes of Pacific oysters in more or less equal numbers.

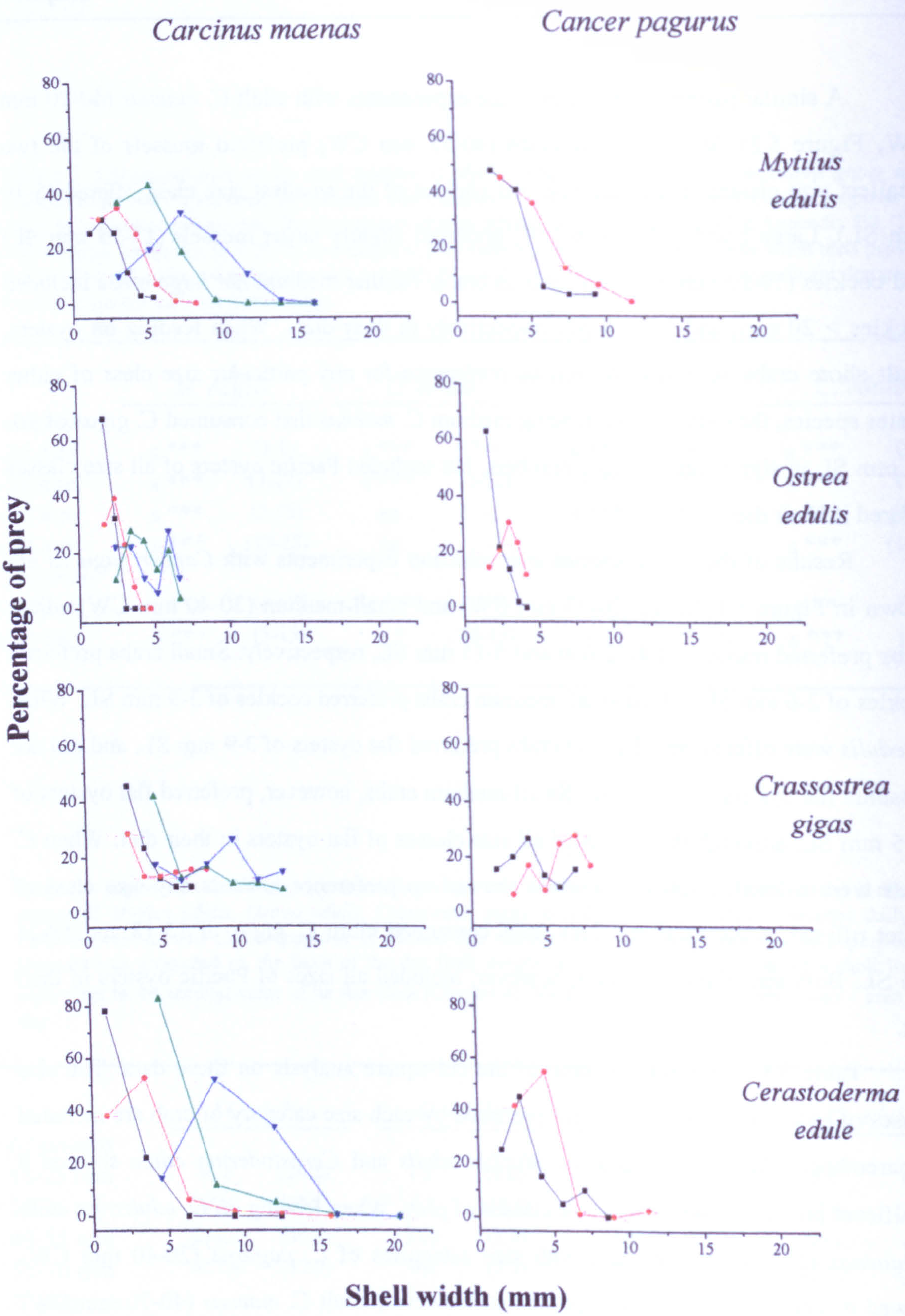

Figure 5.4. Percentage of prey in each of various size classes (mm of shell width) of the total number of *Mytilus edulis*, *Ostrea edulis*, *Crassostrea gigas*, and *Cerastoderma edule* consumed by *Carcinus maenas* of 15-25 (—▪—), 25-35 (—•—), 40-55 (—▲—), and 55-70 (—▼—) mm CW, and *Cancer pagurus* of 20-30 (—▪—) and 30-40 (—•—) mm CW during the single prey species experiments. Shell width was estimated according to equations given in Chapter 4. The size classes of prey offered to each size category of crab are presented in Appendix B2.

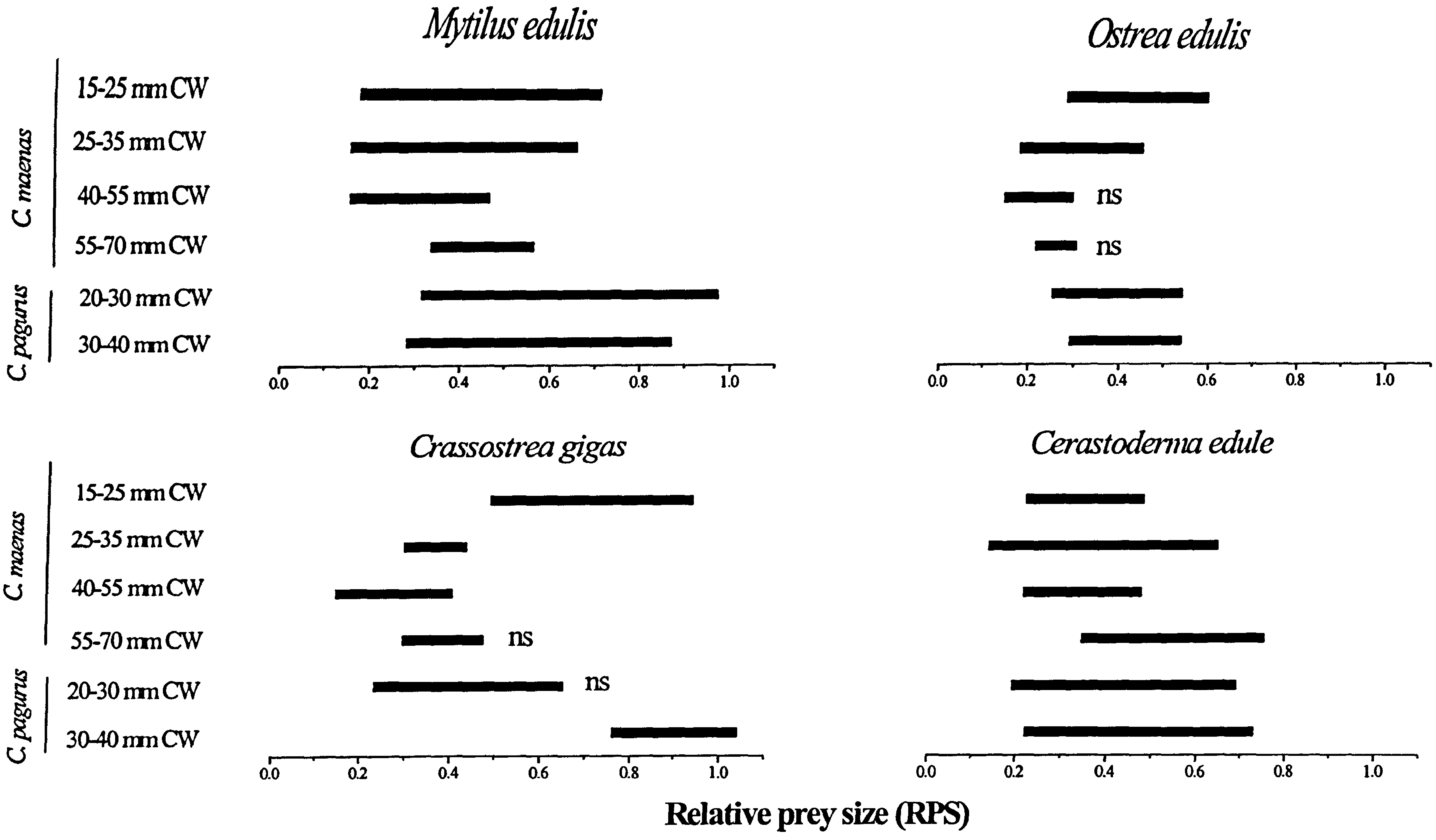

Figure 5.5. Relative prey size (RPS) of *Mytilus edulis, Ostrea edulis, Crassostrea gigas*, and *Cerastoderma edule* that were preferred (i.e. consumed in > 20%; see text) by several size categories of *Carcinus maenas* and *Cancer pagurus* during the single prey species experiments. RPS was calculated as the median value of shell width in each size class of prey divided by the height of the master or right chela in *C. maenas* and *C. pagurus*, respectively; ns denotes those size categories of crabs in which significant size selective feeding could not be detected.

Figure 5.4 shows the relationships between the percentages of consumed prey and the median value of shell width (the minimum linear dimension of the shell) in each size class of bivalve offered. The shell width of prey in each species that were most frequently consumed by crabs generally increased as crabs increased in size. The degree of crab selectivity (i.e. size distribution pattern of prey selection) and the maximum shell width of preferred prey varied from one prey species to another. While the percentage of mussels consumed by all crabs decreased slowly as mussels increased in shell width, the percentage of consumed cockles decreased steeply as cockles increased in shell width. Similarly, while crabs generally preferred small rather than large *O. edulis*, they included a wider size range of *C. gigas* in their diet, resulting in a relatively more uniform distribution in the latter than in the former oyster species.

Further comparisons of the size ranges of prey preferred by different size categories and species of crabs were made using a measure of shell size relative to each size category of crab, more specifically, the corresponding size of their chelae. A relative measure of prey size (RPS) was obtained by dividing the median value of shell width within each of the size classes of each prey species offered, by an estimate of the chelal height of the crabs in each size category. The height of the master chela in *C. maenas* and the right chela in *C. pagurus* were estimated using the logarithmically transformed regression equations between carapace width and chelal height described in Chapter 3. Since the number of size classes in which prey were offered to crabs was never less than five, in the event of chi-square tests on prey size distributions being significant, the preferred size classes of prey would be those consumed in at least > 20 % of the total number of prey consumed by each size category of crab. The RPS of each of the prey species that were consumed in > 20 % by crabs in each size category are plotted in Figure 5.5. Results analysed in this way showed that crabs generally preferred prey with a RPS less than or equal to 1, i.e. smaller or equal to the height of their largest chelae. They also showed that prey items with a high RPS were more often included as the preferred items in the diets of smaller rather than larger crabs. When feeding on a wide size range of *M. edulis*, juvenile *C. maenas* preferred mussels of a RPS of 0.15-0.70; whereas *C. pagurus* of comparable body size preferred mussels of a RPS of 0.28-0.97; adult *C. maenas*, with larger master chelae, preferred mussels with a lower RPS of 0.15-0.56 (Figure 5.5). These results indicate that edible crabs selected mussels that were slightly larger, relative to the size of their chelae, than those selected by shore crabs of similar and even larger carapace width.

In experiments with *O. edulis*, juvenile *C. maenas* and *C. pagurus* of comparable carapace width preferred flat oysters of a similar RPS of 0.17-0.58 (Figure 5.5). The *O. edulis* preferred by adult *C. maenas* were all within the range of 0.14-0.30, and *O. edulis* of a RPS > 0.6 were very rarely opened by any crab. By contrast, when *C. gigas* were offered, *C. maenas* of 25-70 mm CW preferred *C. gigas* of a RPS of 0.14-0.47, while small shore crabs (15-25 mm CW) preferred relatively larger Pacific oysters (0.48-0.93). This surprising result might be explained by the fact that stock limitations did not allow for juvenile *C. maenas* to be offered *C. gigas* < 6 mm SL (Appendix B2). This experimental condition probably forced shore crabs of 15-25 mm CW to consume larger oysters than might have been expected if the smallest *C. gigas* had been available to them. *C. pagurus* 20-30 mm and 30-40 mm CW preferred *C. gigas* of a RPS of 0.23-0.65 and 0.76-1.04, respectively.

When feeding on *C. edule*, adult *C. maenas* preferred cockles of a RPS (0.21-0.75), whereas juvenile *C. maenas* preferred cockles of a slightly lower RPS (0.13-0.64) than *C. pagurus* of comparable carapace width (0.19-0.73; Figure 5.5).

The total numbers of each prey species that were consumed daily by each size category of crab and the corresponding biomass (mg) are shown in Table 5.2. All size classes of *C. maenas* and *C. pagurus* consumed more mussel flesh than any of the other bivalves offered, although differences were generally greater between mussels and oysters than between mussels and cockles. Whilst all size categories of *C. maenas* also consumed more *M. edulis* than any other bivalve, both size categories of *C. pagurus* consumed relatively similar numbers of all prey species. There was a general trend towards higher biomass consumption as crabs increased in size, but the numbers of prey consumed generally decreased as crabs increased in carapace width. *C. pagurus* generally consumed less biomass and numbers of all prey species than *C. maenas* of comparable carapace width.

Results from experiments where crab ingestion rates at different temperatures were examined showed that ingestion rates increased with increasing water temperature for all

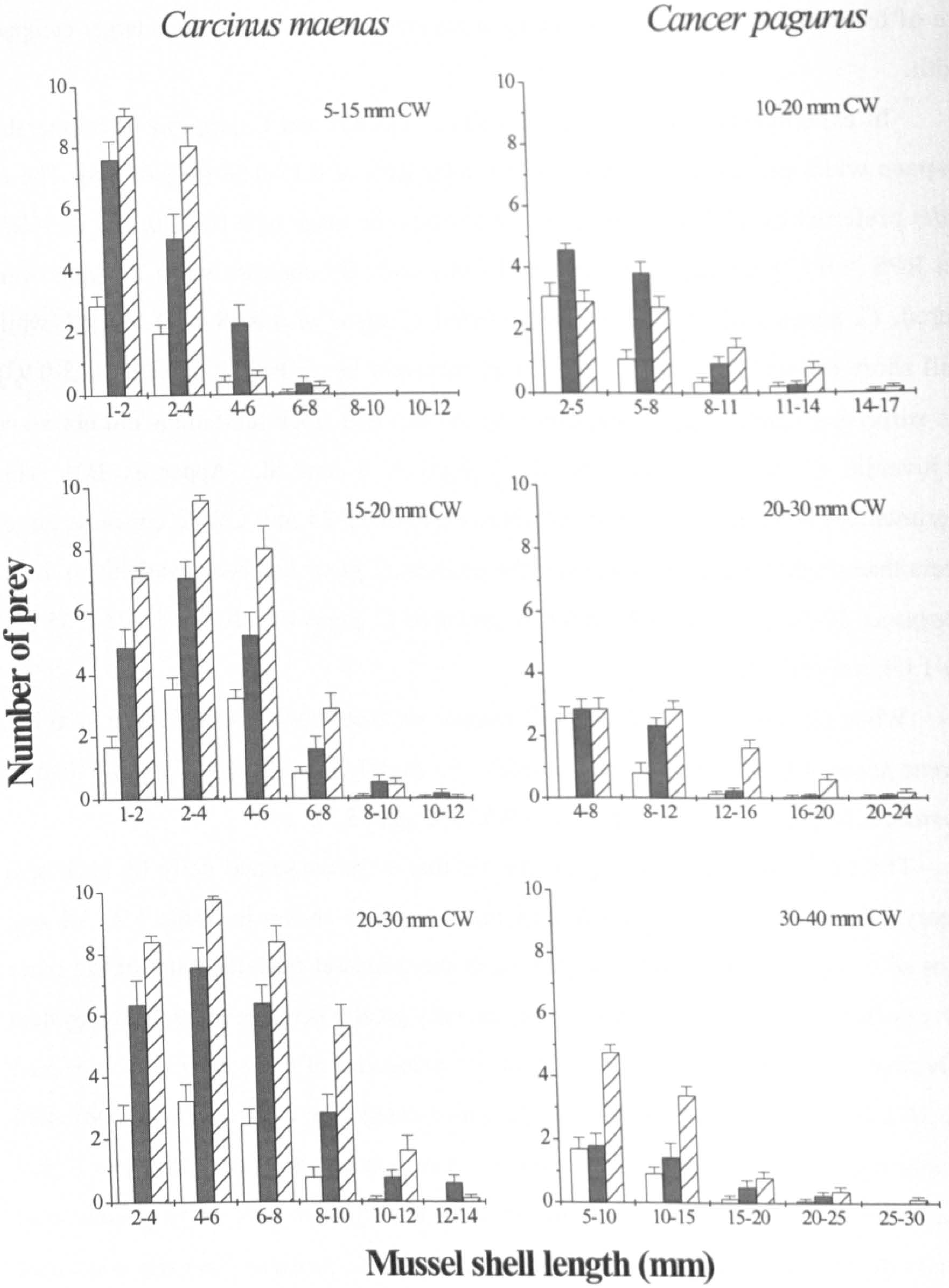

Figure 5.6. Number of *Mytilus edulis* of various size classes (mm in shell length) consumed by juvenile *Carcinus maenas* and *Cancer pagurus* of several size categories at different water temperatures; ☐ 8-11 °C, ■ 12-15 °C, ▨ 18-21 °C. Values are mean consumption rates per crab over a period of 9 days (± se). The size classes of mussels offered to each size category of crab are presented in Appendix B2.

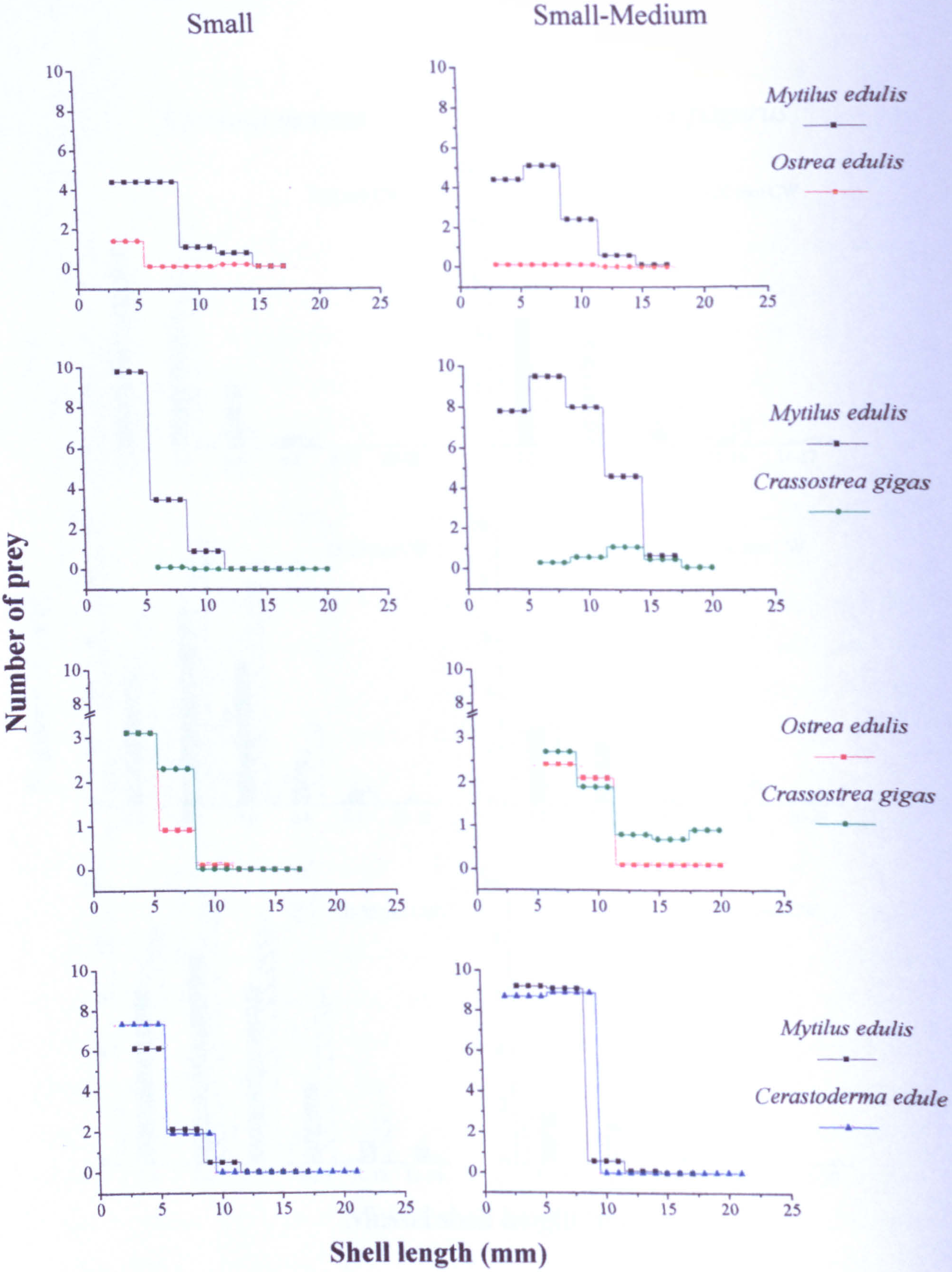

Figure 5.7. Number of prey of various size classes of *Mytilus edulis*, *Ostrea edulis*, *Crassostrea gigas* and *Cerastoderma edule* that were consumed by small (15-25 mm CW) and small medium (25-35 mm CW) *Carcinus maenas* during experiments where prey species were offered in paired combinations. Values are mean consumption rates crab $^{-1}$ day $^{-1}$. The size classes of prey offered to each size category of crab are presented in Appendix B3.

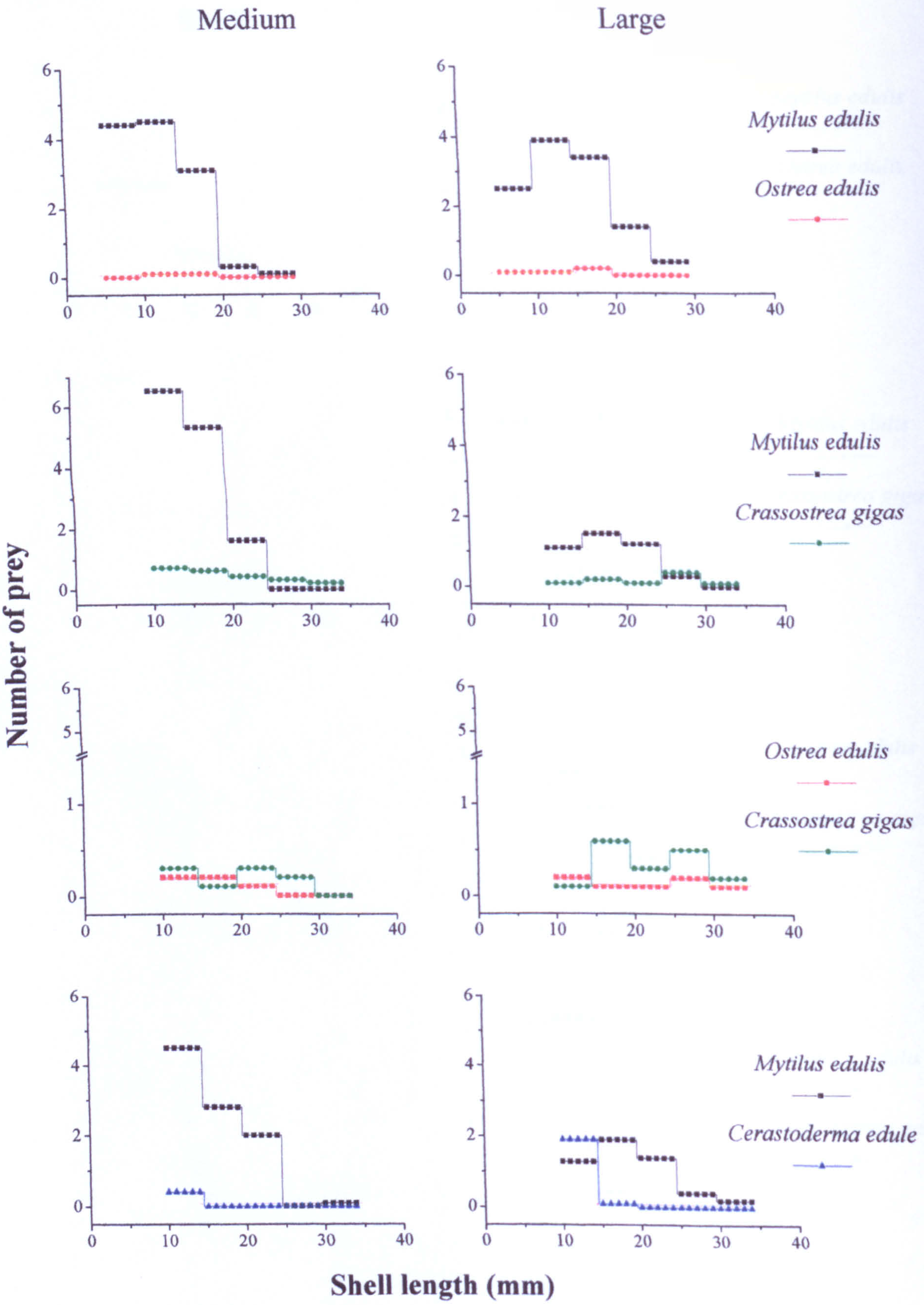

Figure 5.8. Number of prey of various size classes of *Mytilus edulis, Ostrea edulis*, *Crassostrea gigas* and *Cerastoderma edule* that were consumed by medium (40-55 mm CW) and large (55-70 mm CW) *Carcinus maenas* during experiments where crabs were offered prey species in paired combinations. Values are mean consumption rates crab $^{-1}$ day $^{-1}$. The size classes of prey offered to each size category of crab are presented in Appendix B3.

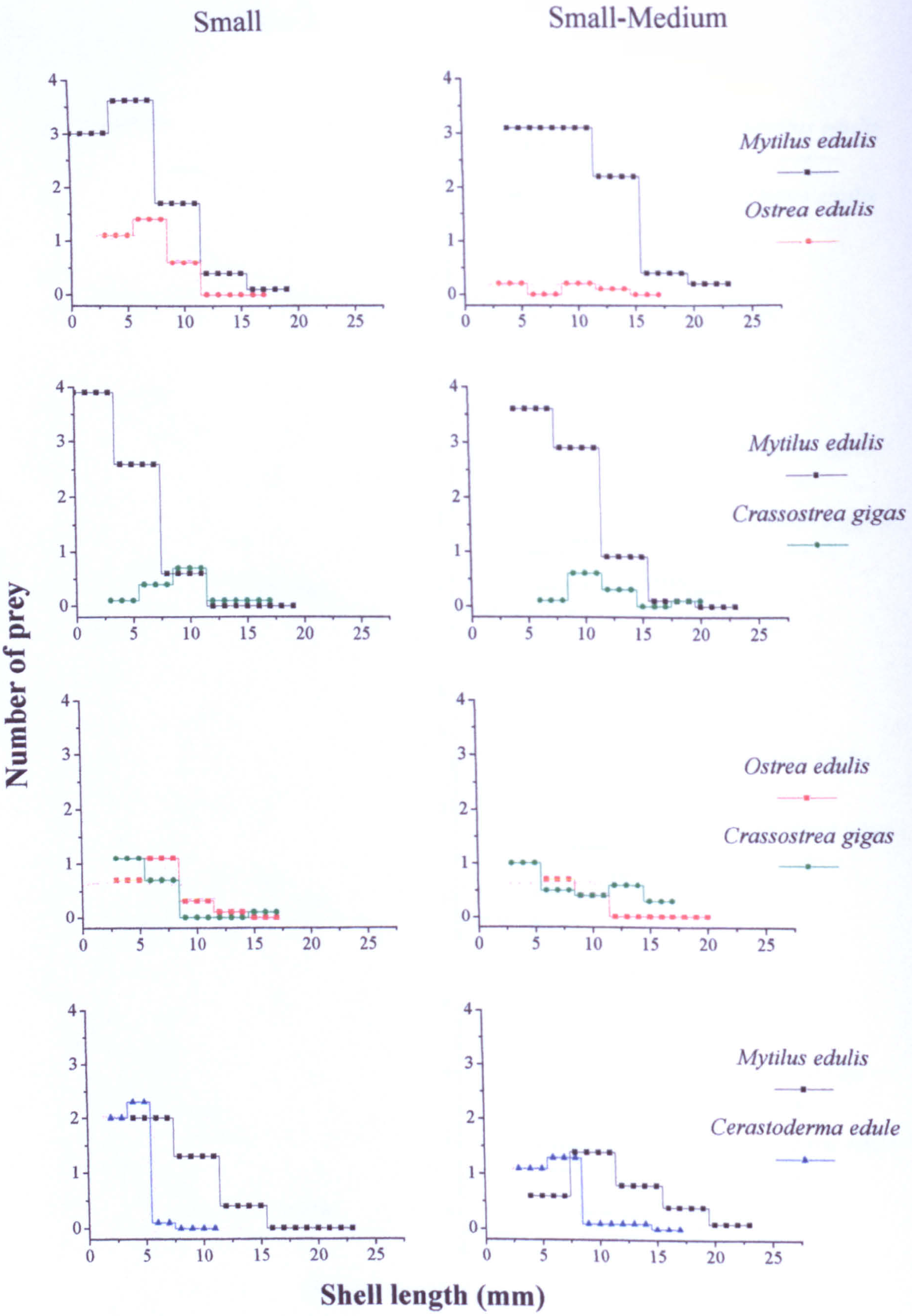

Figure 5.9. Number of prey of various size classes of *Mytilus edulis, Ostrea edulis, Crassostrea gigas* and *Cerastoderma edule* that were consumed by small (20-30 mm CW) and small-medium (30-40 mm CW) *Cancer pagurus* during experiments where prey species were offered in paired combinations. Values are mean consumption rates crab $^{-1}$ day $^{-1}$. The size classes of prey offered to each size category of crab are presented in Appendix B3.

Table 5.3. Ingested biomass (mg) corresponding to the total number of prey items (in parenthesis) in all size classes of *Mytilus edulis*, (*M.e.*) *Ostrea edulis* (*O.e.*) *Crassostrea gigas* (*C.g.*) and *Cerastoderma edule* (*C.e.*) consumed daily by *Carcinus maenas* and *Cancer pagurus* of various size categories during paired species combination experiments. Biomass was estimated on the basis of the dry flesh weight of an individual prey item of a shell length equivalent to the median value of its size class (Chapter 4). Values are mean consumption rates • crab $^{-1}$ • day $^{-1}$.

	M. edulis - O. edulis				*M. edulis - C. gigas*				*O. edulis - C. gigas*				*M. edulis - C. edule*			
	M.e.		*O.e.*		*M.e.*		*C.g.*		*O.e.*		*C.g.*		*M.e.*		*C.e.*	
C. maenas																
15-25 mm	33.5	(10.8)	0.9	(1.9)	21.3	(14.2)	0.03	(0.1)	0.7	(4.2)	0.7	(5.4)	12.9	(8.7)	4.8	(9.1)
25-35 mm	40.8	(12.6)	0.2	(0.4)	155.2	(30.6)	4.2	(2.5)	3.6	(4.8)	10.5	(7.0)	36.0	(19.1)	20.3	(17.6)
40-55 mm	159.5	(12.4)	0.6	(0.2)	112.2	(13.4)	8.4	(2.1)	0.6	(0.4)	2.9	(0.9)	103.1	(9.4)	1.5	(0.4)
50-70 mm	243.8	(11.6)	0.9	(0.3)	64.6	(4.1)	6.1	(0.9)	3.3	(0.7)	9.7	(1.7)	93.2	(5.1)	10.1	(2.1)
C. pagurus																
20-30 mm	25.1	(8.9)	1.1	(3.1)	7.2	(7.0)	1.3	(1.6)	0.9	(2.3)	0.7	(2.0)	15.3	(3.6)	4.0	(4.4)
30-40 mm	73.1	(8.9)	0.4	(0.5)	36.8	(7.5)	1.7	(1.1)	0.6	(1.1)	2.5	(2.9)	33.4	(3.2)	8.9	(2.6)

size categories of crabs (Figure 5.6). Only the smallest size category of *C. pagurus* (10-20 mm CW) had a lower ingestion rate of mussels at a high (18-21 °C) than at an intermediate temperature (12-15 °C). In addition, the increment in ingestion rate was greatest between low (8-11 °C) and intermediate temperatures amongst all *C. maenas* and *C. pagurus* of 20-30 mm CW. However, *C. pagurus* of 30-40 mm CW presented the greatest increment of ingestion rate between intermediate and high temperatures. Although the size ranges of mussels that were preferred by crabs in all size categories remained the same at varying temperatures, the number of mussels consumed in each size class was affected by temperature in a different way. With increasing temperature, the number of mussels consumed in the larger size classes increased proportionately less than the number of mussels consumed in the smaller size classes (Figure 5.6).

5.3.2. Experiments with paired combinations of prey species.

When *M. edulis* were offered in combination with either *O. edulis* or *C. gigas*, both *C. maenas* and *C. pagurus* of all size categories showed a strong preference for mussels (Figures 5.7-5.9), and both the numbers and the amount of mussel flesh consumed by all crabs were larger than that of oysters in both paired combinations (Table 5.3). In these experiments, the size classes of both *M. edulis* and *C. gigas* selected by *C. maenas* and *C. pagurus* of all size categories were broadly similar to those selected in the individual species experiments (Figures 5.1-5.3). However, the largest *O. edulis* taken in the paired combinations experiments was generally of a smaller size class than the largest *O. edulis* taken in the individual species experiments. Only small *C. maenas* (15-25 mm CW) took a few larger *O. edulis* of 9-12 and 12-15 mm SL, and virtually no *C. gigas* when each oyster species was offered in combination with mussels (Figure 5.7).

When crabs were offered a choice between *O. edulis* and *C. gigas*, neither *C. maenas* nor *C. pagurus* of any size category showed any preference for either oyster species (Figures 5.7-5.9). Differences between both the numbers and the biomass of the two oyster species were small, and only noticeable in the case of medium and large shore crabs (40-70 mm CW) and small-medium edible crabs (30-40 mm CW) which consumed more *C. gigas* than *O. edulis* (Table 5.3). Compared to the individual species experiments, all shore crabs took similar size classes of both *O. edulis* and *C. gigas* when presented

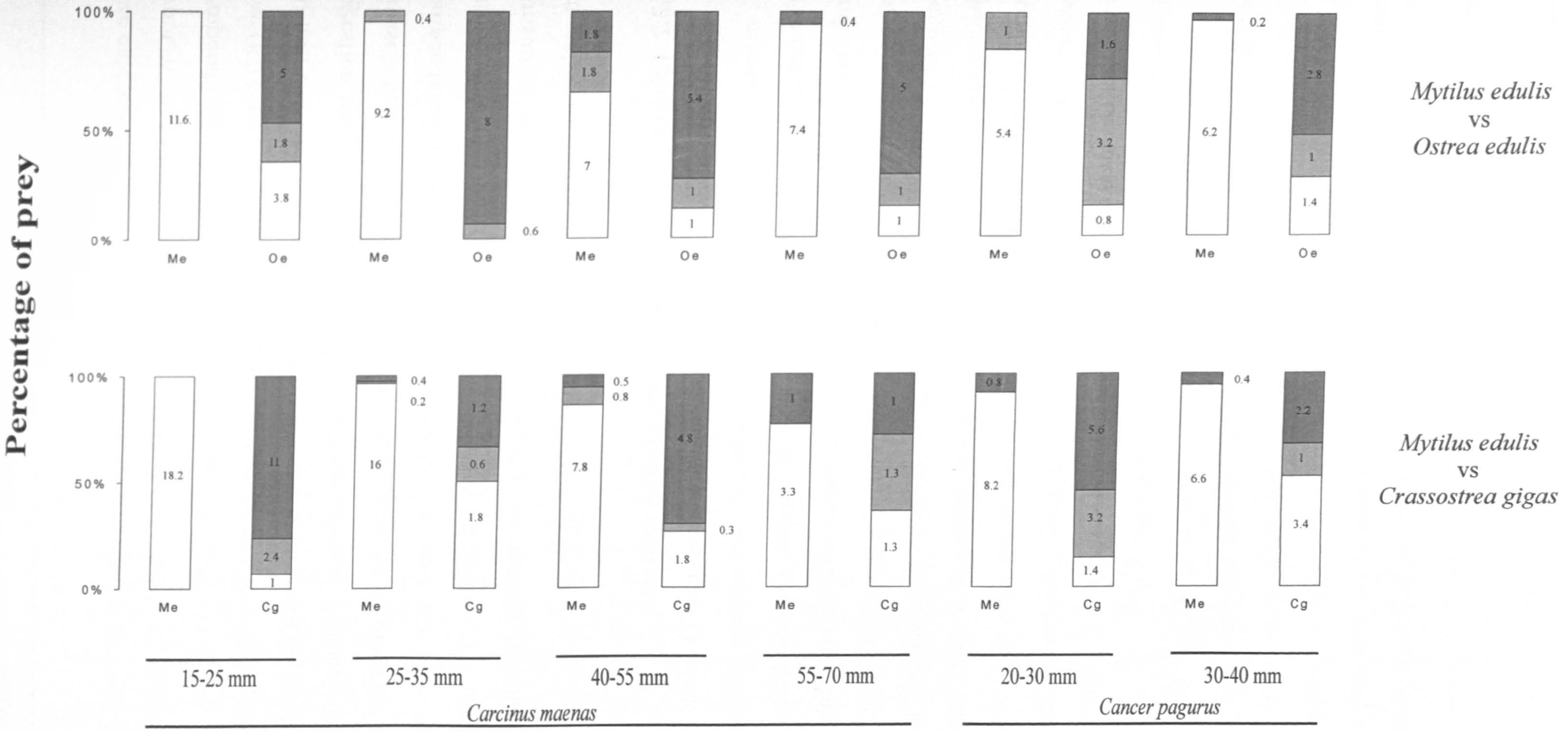

Figure 5.10. Number and percentage of *Mytilus edulis* (Me), *Ostrea edulis* (Oe), and *Crassostrea gigas* (Cg) that were successfully opened (open columns), manipulated and abandoned (light shaded columns), and touched and rejected (dark shaded columns) by several size categories of *Carcinus maenas* and *Cancer pagurus*, when crabs were offered equal numbers of the preferred size classes of each prey species in paired combinations. Values are mean consumption rates over 1 hr periods during 4-5 consecutive days. The size classes of prey offered to each size category of crab are presented in Appendix B4.

Table 5.4. Chi-square values for goodness-of-fit tests on observed encounters of individual *Carcinus maenas* and *Cancer pagurus* of various size categories when presented with paired combinations of *Mytilus edulis* (*M.e.*), *Ostrea edulis* (*O.e.*), *Crassostrea gigas* (*C.g.*) and *Cerastoderma edule* (*C.e.*) in equal proportions; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns = no significant departure from the expected ratio (H_0: 1:1).

	M.e. - O.e.	*M.e. - C.g.*	*O.e. - C.g.*	*M.e. - C.e.*
C. maenas				
15-25 mm	0.23 ns	2.22 ns	0.10 ns	1.57 ns
25-35 mm	0.28 ns	41.83 ***	0.24 ns	0.25 ns
40-55 mm	2.84 ns	1.29 ns	0.44 ns	7.48 *
55-70 mm	0.22 ns	0.29 ns	0.67 ns	0.03 ns
C. pagurus				
20-30 mm	0.27 ns	0.38 ns	0.78 ns	0.02 ns
30-40 mm	0.42 ns	0.06 ns	0.13 ns	1.07 ns

Table 5.5. Chi-square values for goodness-of-fit tests on the number of prey successfully opened by individual *Carcinus maenas* and *Cancer pagurus* of various size categories when presented with paired combinations of *Mytilus edulis* (*M.e.*), *Ostrea edulis* (*O.e.*), *Crassostrea gigas* (*C.g.*) and *Cerastoderma edule* (*C.e.*) in equal proportions; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns = no significant departure from the expected ratio (H_0: 1:1); NTA = cases in which the results did not allow for the test to be applied.

	M.e. - O.e.	*M.e. - C.g.*	*O.e. - C.g.*	*M.e. - C.e.*
C. maenas				
15-25 mm	19.75 ***	77.04 ***	0.05 ns	3.75 ns
25-35 mm	NTA	56.64 ***	0.19 ns	0.79 ns
40-55 mm	22.50 ***	15.16 ***	0.44 ns	9.28 **
55-70 mm	24.38 ***	3.56 ns	1.19 ns	0.00 ns
C. pagurus				
20-30 mm	17.03 ***	24.08 ***	0.15 ns	0.08 ns
30-40 mm	15.16 ***	5.12 *	0.24 ns	0.61 ns

individually and in combination (Figures 5.6-5.7). Small *C. pagurus* (20-30 mm CW) also took similar size ranges of both oyster species, whereas small-medium edible crabs (30-40 mm CW) consumed *C. gigas* of all the size range, and selected only the smallest *O. edulis*, thus contrasting with the wide range of sizes of the flat oyster that were consumed by edible crabs in this size category during the individual species experiments (Figure 5.9).

When given a choice between *M. edulis* and *C. edule*, small (15-25 mm CW) and small-medium (25-35 mm CW) *C. maenas* did not show any marked preference for either prey species (Figure 5.7). Whilst medium *C. maenas* (40-55 mm) clearly preferred mussels, large shore crabs (55-70 mm CW) consumed similar numbers of both prey of 10-15 mm SL, but only consumed mussels from the larger size classes (Figure 5.8). *C. pagurus* of both size categories did not show any preference for either mussels or cockles in the smaller size classes, but selected more mussels than cockles as prey increased in size (Figure 5.9). A larger amount of mussel than of cockle flesh was consumed by *C. maenas* and *C. pagurus* in all size categories (Table 5.3). However, the numbers of mussels and cockles consumed by juvenile *C. maenas* and both size categories of *C. pagurus* were similar, whereas adult *C. maenas* consumed more mussels than cockles.

5.3.3. Experiments with equal and altered proportions of paired species combinations.

In these experiments *C. maenas* and *C. pagurus* of all size categories showed the same trends of species selection they had shown in experiments where a wide size range of prey species was offered in paired combinations. When crabs were presented with equal numbers of *M. edulis* in combination with either *O. edulis* or *C. gigas*, the proportion of mussels opened by *C. maenas* and *C. pagurus* in all size categories was significantly higher than that for oysters (Figure 5.10; Table 5.4). Of all the mussels that were encountered in these experiments, very few were rejected either initially or after a period of manipulation. By contrast, any encountered *O. edulis* were only occasionally consumed, and were more frequently rejected before, rather than after, crabs had attempted to open them. Only small *C. pagurus* (20-30 mm CW) manipulated and abandoned a higher proportion of *O. edulis* than the proportion of oysters that they encountered and rejected. In the *M. edulis*-*C. gigas* combination, crabs also opened *C. gigas* less frequently than mussels, but they generally opened more *C. gigas* compared to the numbers of *O. edulis* opened in the *M. edulis*-*O.*

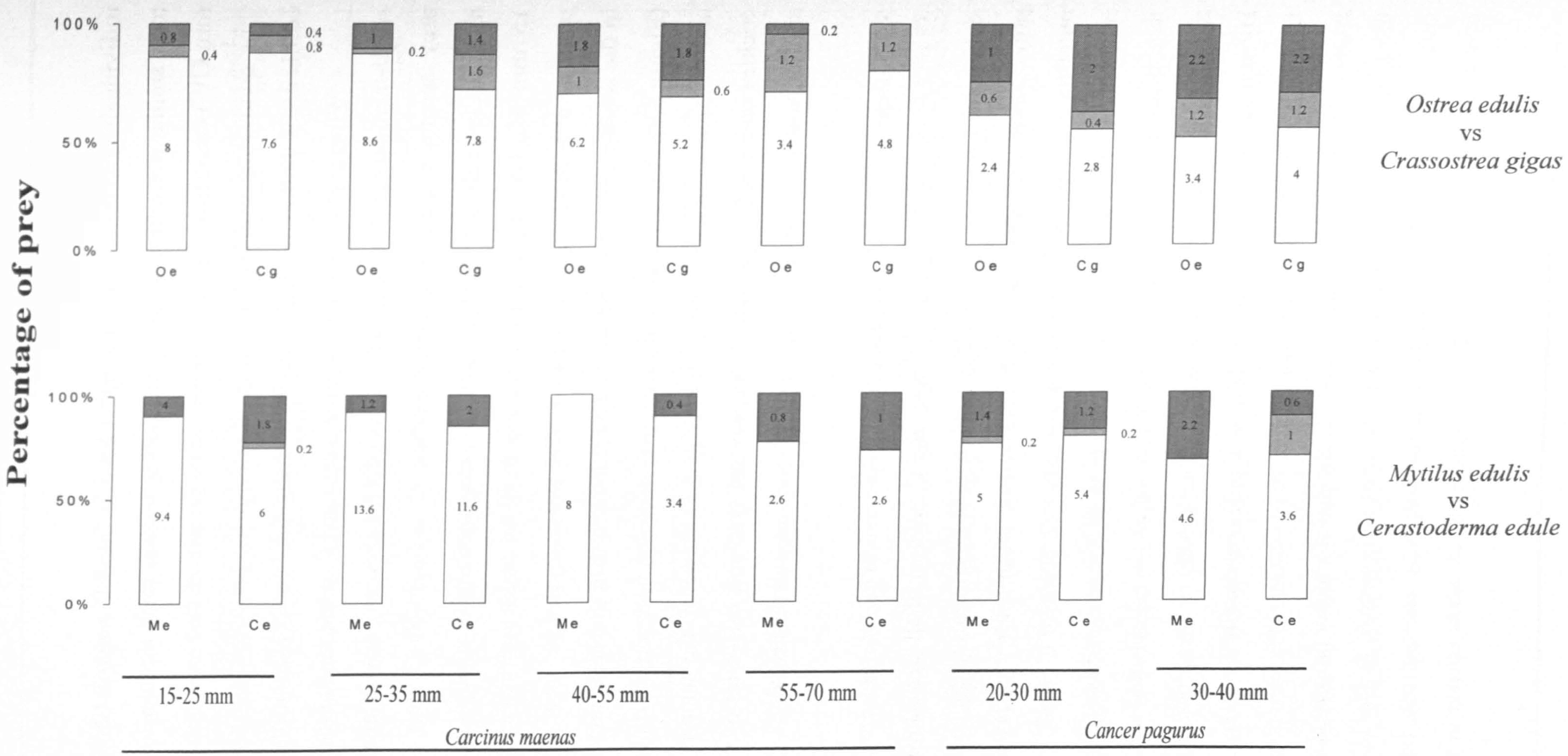

Figure 5.11. Number and percentage of *Mytilus edulis* (Me), *Ostrea edulis* (Oe) *Crassostrea gigas* (Cg), and *Cerastoderma edule* (Ce) that were successfully opened (open columns), manipulated and abandoned (light shaded columns), and touched and rejected (dark shaded columns) by several size categories of *Carcinus maenas* and *Cancer pagurus*, when crabs were offered equal numbers of the preferred size classes of each prey species in paired combinations. Values are mean consumption rates over 1 hr periods during 4-5 consecutive days. The size classes of prey offered to each size category of crab are presented in Appendix B4.

edulis combination (Figure 5.10). The proportion of *C. gigas* initially rejected was generally higher than that of the *C. gigas* abandoned after manipulation, the only exception being for large *C. maenas* (55-70 mm CW) where the reverse was true.

When crabs were given a choice between *O. edulis* and *C. gigas*, similar proportions of both oyster species were generally consumed (Figure 5.11; Table 5.4). The proportion of prey manipulated and abandoned, and touched and rejected, was similar for both oyster species. While the proportion of *O. edulis* and *C. gigas* that were opened was always higher than that of rejected prey, the proportion in which crabs initially rejected both oyster species was generally higher than the proportion in which they abandoned prey after several opening attempts. The only exception was large *C. maenas* (55-70 mm CW) that encountered and rejected very few *O. edulis*, and rejected *C. gigas* only after attempting to open them.

In the experiments where equal numbers of *M. edulis* and *C. edule* were presented, again crabs opened similar proportions of both prey species (Figure 5.11; Table 5.4). The only exception was medium *C. maenas* (40-55 mm CW) that opened all the mussels encountered, but encountered and rejected a few cockles. The numbers of opened cockles, however, was much higher compared to that of oysters opened in the mussel-oyster combinations (Figure 5.10). *C. edule* encountered in these experiments were mostly rejected without crabs attempting to open them, although small-medium *C. pagurus* (30-40 mm CW) abandoned cockles after several opening attempts in a higher proportion than that of cockles rejected initially.

The results of the goodness-of-fit tests between the expected and observed encounters of crabs in each size category are presented in Table 5.5. The observed encounters were not significantly different from those expected (equal probability of encounter) in all size categories of crabs except in two instances. Only small-medium *C. maenas* (25-35 mm CW) encountered significantly more *M. edulis* than *C. gigas* ($\chi^2 = 41.83, p < 0.001$), and medium *C. maenas* (40-55 mm CW) encountered significantly more mussels than cockles ($\chi^2 = 7.48, p < 0.05$).

Results obtained from these experiments indicated that the prey species with a higher proportion of successfully opened items was probably the preferred species, since this proportion represented the prey items handled by crabs with a highest persistence, hence, the highest attack success. The proportions of each prey species that were manipulated and

Table 5.6. Percentage and numbers (in parenthesis) of *Mytilus edulis* and *Ostrea edulis* that were accepted or rejected by *Carcinus maenas* and *Cancer pagurus* of various size categories in experiments where crabs were presented with the preferred size classes of mussels and oysters in proportions of 1:1, 1:2, and 1:4. Values are mean consumption rates over 1 h periods during 4-5 consecutive days. Mean percentage of encounter rates ± SD of all crabs with mussels and oysters are shown at the bottom of each presentation trial; * denotes prey species accepted in significantly higher numbers ($p < 0.01$), NTA = cases in which results did not allow for chi-square tests to be applied.

		1 : 1				1 : 2				1 : 4			
		M. edulis		*O. edulis*		*M. edulis*		*O. edulis*		*M. edulis*		*O. edulis*	
C. maenas													
15-25 mm	acc	75	(11.6) *	25	(3.8)	79	(10.2) *	22	(2.8)	62	(5.6) *	38	(3.4)
	rej	0	(0)	100	(6.8)	0	(0)	100	(12.4)	0	(0)	100	(16.6)
25-35 mm	acc	100	(9.2) $^{\text{NTA}}$	0	(0)	100	(6) $^{\text{NTA}}$	0	(0)	100	(5.6) $^{\text{NTA}}$	0	(0)
	rej	4	(0.4)	96	(8.6)	3	(0.4)	97	(12.8)	1	(0.2)	99	(15.8)
40-55 mm	acc	88	(7) *	13	(1)	91	(11.4) *	19	(2.6)	77	(4.6) *	23	(1.4)
	rej	36	(3.6)	64	(6.4)	4	(0.8)	96	(17.8)	4	(0.6)	96	(15.4)
55-70 mm	acc	88	(7.4) *	12	(1)	100	(2) $^{\text{NTA}}$	0	(0)	100	(1.4) $^{\text{NTA}}$	0	(0)
	rej	6	(0.4)	94	(6)	33	(3.8)	67	(7.8)	11	(0.6)	89	(4.8)
C. pagurus													
20-30 mm	acc	87	(5.4) *	13	(0.8)	79	(4.6) *	21	(1.2)	70	(3.2) *	30	(1.4)
	rej	17	(1)	83	(4.8)	2	(0.2)	98	(8.2)	2	(0.2)	98	(10.6)
30-40 mm	acc	82	(6.2) *	18	(1.4)	63	(4.4) *	37	(2.6)	82	(2.8) *	18	(0.6)
	rej	5	(0.2)	95	(3.8)	3	(0.2)	97	(5.6)	0	(0)	100	(9.8)
		54.2 ± 2.3		45.8 ± 2.3		37.2 ± 3.3		62.8 ± 3.3		24.2 ± 2.9		75.8 ± 2.9	

Table 5.7. Percentage and numbers (in parenthesis) of *Mytilus edulis* and *Cerastoderma edule* that were accepted or rejected by *Carcinus maenas* and *Cancer pagurus* of various size categories in experiments where crabs were presented with the preferred size classes of mussels and cockles in proportions of 1:1, 1:2, and 1:4. Values are mean consumption rates over 1 h periods during 4-5 consecutive days. Mean percentage of encounter rates ± SD of all crabs with mussels and cockles are shown at the bottom of each presentation trial; * denotes prey species accepted in significantly higher numbers ($p < 0.01$), ns = no significant differences.

		1 : 1				1 : 2				1 : 4			
		M. edulis		*C. edule*		*M. edulis*		*C. edule*		*M. edulis*		*C. edule*	
C. maenas													
15-25 mm	acc	61	(9.4) ns	39	(6)	34	(4.8) ns	66	(9.2)	25	(5.2) ns	75	(15.6)
	rej	33	(1)	67	(2)	0	(0)	100	(0.2)	60	(0.6)	40	(0.4)
25-35 mm	acc	54	(13.6) ns	46	(11.6)	38	(7.8) ns	62	(12.8)	19	(4.8) ns	82	(21.2)
	rej	38	(1.2)	63	(2)	43	(0.6)	57	(0.8)	63	(2.4)	37	(1.4)
40-55 mm	acc	70	(8) *	30	(3.4)	54	(8.4) *	46	(7.2)	49	(8.2) *	51	(8.6)
	rej	0	(0)	100	(0.4)	10	(0.2)	90	(1.8)	8	(0.4)	92	(4.6)
55-70 mm	acc	50	(2.6) ns	50	(2.6)	38	(4.2) ns	62	(6.8)	9	(0.6) ns	91	(6.2)
	rej	44	(0.8)	56	(1)	50	(0.8)	50	(0.8)	56	(1)	44	(0.8)
C. pagurus													
20-30 mm	acc	48	(5) ns	52	(5.4)	36	(4.4) ns	65	(8)	20	(2.8) ns	80	(11)
	rej	53	(1.6)	47	(1.4)	36	(0.8)	64	(1.4)	50	(0.2)	50	(0.2)
30-40 mm	acc	56	(4.6) ns	44	(3.6)	35	(4) ns	66	(7.6)	23	(2.4) ns	77	(8)
	rej	58	(2.2)	42	(1.6)	20	(0.2)	80	(0.8)	0	(0)	100	(0.4)
		55.2 ± 6.5		44.9 ± 6.5		38.3 ± 5.3		61.8 ± 5.3		25.4 ± 6.8		74.6 ± 6.8	

abandoned, and touched and rejected by crabs were expected to represent a decreasing preference by crabs for those prey species. However, the proportions of touched and rejected items were generally higher than those of manipulated and abandoned prey. Moreover, only occasionally did crabs reject a prey item following an attempt to open it, and were frequently successful once they had persisted minimally in their attack. This is not surprising since the size classes of prey used in these experiments were not only well within the range of prey that crabs could easily open, but were of the size classes that had been selected by crabs in previous experiments. For this reason, in the following experiments the numbers of manipulated and abandoned, and touched and rejected prey items were added and included into only one category of 'rejected' prey. The proportion of items in this new category now represented those for which crabs had the least preference, since experiments did not last long enough for crabs to reject prey because of total lack of hunger, and once an item had been rejected crabs generally continued to feed on the alternative prey species.

Results of experiments where paired combinations of *M. edulis*-*O. edulis* and of *M. edulis*-*C. edule* were offered to crabs in a ratio of 1:2 and 1:4 are presented in Tables 5.6 and 5.7. Results of the mussel-oyster combination showed that of the total number of accepted and successfully opened prey, a 60-100 % corresponded to *M. edulis* in experiments with *C. maenas* and *C. pagurus* of the different size categories. By contrast, *O. edulis* accepted by crabs was never higher than 40 %, even when the alternative mussel species became scarce (Table 5.6). In addition, as crabs decreasingly encountered mussels (mean encounter rates of $54.2 \pm 2.3 > 37.2 \pm 3.3 > 24.2 \pm 2.9 \cdot h^{-1}$), the percentage in which crabs accepted *M. edulis* remained high and approximately constant. While the percentage of rejected oysters was constantly high, the already low percentage of rejected mussels in the 1:2 ratio experiments decreased even more in the 1:4 ratio experiments, where mussels were at their lowest relative abundance.

In the mussel-cockle combination, the percentage of accepted and rejected prey varied with the rates in which crabs encountered both prey species (Table 5.7). Of the total number of accepted prey, the percentage of *M. edulis* that were successfully opened by crabs decreased as mussels became scarce. Similarly, the percentage of accepted *C. edule* increased as their relative abundance increased. These variations closely corresponded to the decrease in the mean encounter rates of mussels ($55.2 \pm 6.5 > 38.3 \pm 5.3 > 25.4 \pm 6.8 \cdot h^{-1}$)

Table 5.8. Chi-square values for goodness-of fit tests on observed encounters of individual *Carcinus maenas* and *Cancer pagurus* of various size categories when presented with paired combinations of *Mytilus edulis-Ostrea edulis* (*M.e.-O.e.*), and *Mytilus edulis-Cerastoderma edule* (*M.e.-C.e.*) in proportions of 1:2 and 1:4, mussels:oysters/cockles; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns = no significant departure from the expected ratios (H_0: 1:2; H_0: 1:4).

	M.e. - O.e.		*M.e. - C.e.*	
	1:2	1:4	1:2	1:4
C. maenas				
15-25 mm	2.68 ns	0.28 ns	0.01 ns	2.97 ns
25-35 mm	0.00 ns	3.17 ns	1.15 ns	1.61 ns
40-55 mm	1.24 ns	0.91 ns	9.60 **	25.77 ***
55-70 mm	2.63 ns	1.88 ns	1.63 ns	0.05 ns
C. pagurus				
20-30 mm	0.06 ns	0.21 ns	0.18 ns	0.06 ns
30-40 mm	0.20 ns	0.06 ns	0.00 ns	0.17 ns

in all size categories of *C. maenas* and *C. pagurus*, except medium sized shore crabs (40-55 mm CW). Although this size category of crab also accepted mussels and cockles in the same proportions as they encountered both prey species, the encounter rates of mussels and cockles did not correspond to the relative abundance in which they were offered (0.5:1 and 0.25:1 mussels : cockles in the 1:2 and 1:4 ratios, respectively). Overall, the percentage of rejected mussels generally increased as they became scarce, while the percentage of rejected cockles decreased as they became more abundant. Only small-medium *C. pagurus* (30-40 mm CW) rejected all the cockles and opened all of the mussels encountered in the 1:4 ratio experiments.

In these experiments, the probability of encountering mussels were 0.5 (1:2 ratio trials) and 0.25 (1:4 ratio trials) of the probability of encountering either oysters or cockles. The results of the goodness-of fit tests between the expected and observed encounters of crabs in each size category with each prey species are presented in Table 5.8. The number of observed encounters was not significantly different from those expected for all except one size category of crab in the mussel-cockle combination. Only medium sized *C. maenas* (40-55 mm CW) encountered mussels and cockles in numbers that were significantly different from the expected ($\chi^2 = 9.6, p < 0.01$ and $\chi^2 = 25.77, p < 0.001$, respectively). These crabs encountered mussels and cockles in statistically indistinguishable numbers in the 1:2 ratio trail ($\chi^2 = 0.05, p = 0.83$), and encountered mussels and cockles in a proportion of 1:2 in the 1:4 ratio trial ($\chi^2 = 1.85, p = 0.17$).

5.4. Discussion

5.4.1. Size-selective predation.

Although crabs are known to be opportunistic predators, feeding on a wide variety of prey types (Muntz *et al.*, 1965; Ropes, 1968), prey size selection has been frequently reported in a diversity of brachyuran crabs feeding on various species of hard-shelled molluscan prey (e.g. Arnold, 1984; Barbeau & Scheibling, 1994a; Brown & Haight, 1992; Ebling *et al.*, 1964; Hughes, 1979; Hughes & Elner, 1989; Juanes, 1992; Zipser & Vermeij, 1978). In the present study, each size category of *Carcinus maenas* and *Cancer* *pagurus* consumed a particular size range of *Mytilus edulis* and *Cerastoderma edule* in numbers higher than expected by chance (Table 5.1), suggesting that size-selective predation occurs amongst these crab-bivalve interactions. However, when feeding on *Ostrea edulis* and *Crassostrea gigas*, the degree of selectivity varied with crab size and oyster species. Juvenile *C. maenas* (15-35 mm CW) and *C. pagurus* (20-40 mm CW) showed significant size selection when feeding on *O. edulis*, whereas adult shore crabs (40-70 mm CW) consumed all size classes of this oyster species in approximately equal numbers. When feeding on *C. gigas*, only the largest *C. maenas* (55-70 mm CW) and the smallest *C. pagurus* (20-30 mm CW) showed no significant preference for any size class of the Pacific oyster.

Because the size-selective feeding behaviour of both *C. maenas* and *C. pagurus* varied markedly from one prey species to another, it seems reasonable to suggest that differences in the size distribution patterns of selection amongst prey species were mainly due to the contrasting morphological features of their shells, and the way these features influence the vulnerability of prey to predation by various size categories of crabs (Figure 5.4). Evidence for the importance of geometric shape, infrastructure and thickness of prey shells in determining crab preference has been demonstrated for several crab species (e.g. Boulding, 1984; Chilton & Bull, 1986; Creswell & McLay, 1990), including both *C. maenas* (Hughes & Elner, 1979) and *C. pagurus* (Lawton & Hughes, 1985). Furthermore, not only do the four bivalves examined in the present study have contrasting shell shapes (Plate 1, A-D), but as they increase in size, their flesh content increases at different relative rates (Chapter 4) thus affecting their profitability, and hence the foraging behaviour exhibited by crabs that feed on them. The differences in the total biomass consumed by crabs when they were offered each of the four prey species individually partly reflects the variations in flesh content amongst these bivalve prey (Table 5.2). However, differences in the numbers of prey items consumed suggest that biomass consumption amongst prey species also reflect crab feeding preferences.

Previous studies have reported that the mean number of prey consumed increases with increasing temperature, although crabs continue to prefer similar size ranges of prey (Elner, 1980; Sanchez-Salazar *et al.*, 1987a). Authors have explained this increment as the consequence of increased crab metabolic rates following high water temperatures (Klein

Breteler, 1975a; Wallace, 1973). Results in the present study confirm their findings, and suggest that an increment in metabolic rate has a greater effect on the consumption of smaller than of larger size classes of mussels, since with increasing water temperature the consumption of small mussels augmented proportionately more than that of large ones (Figure 5.6).

When *C. maenas* and *C. pagurus* were presented with a size range of *M. edulis*, the sizes classes of preferred mussels clearly increased as crabs increased in size (Figures 5.1-5.3). Results confirm the findings of previous studies on these (Dare *et al.*, 1983; Elner & Hughes, 1978; Lawton, 1983) and other brachyuran crabs (Creswell & McLay, 1990; Rheinallt, 1986), and emphasise that mussel size selection is strongly influenced by the relationship between carapace width, more specifically chelal height, and prey size (Davidson, 1986; Elner, 1980). When *C. maenas* and *C. pagurus* were presented with a size range of *C. edule*, increasingly larger crabs also preferred increasingly larger size classes of cockles (Figures 5.1-5.3). Results similar to these have previously been reported for *C. maenas* (Sanchez-Salazar *et al.*, 1987a) and for other species of *Cancer* feeding on several infaunal bivalves (Boulding, 1984; Jamieson, *et al.*, 1982; Juanes & Hartwick, 1990; Lake *et al.*, 1987; Pearson, *et al.*, 1981). In the present study, however, comparisons between size selection in mussels and cockles showed that all crabs of both species consistently selected the smallest size classes of cockles offered, contrasting with the mussel experiments, where adult shore crabs selected medium-sized mussels (Figures 5.1-5.3). In addition, the percentage of prey consumed by all crabs decreased more steeply when cockles than when mussels increased in size (Figure 5.4). The leftover shell fragments of the preferred size classes of prey indicated that crabs generally used the most efficient, least time-consuming crushing methods. Consequently, it can be suggested that the ability of crabs to crush open prey decreased more abruptly when cockles than when mussels increased in size. As the globular shaped cockles increase in length, the width of the shell increases more rapidly than the shell width of the more elongate mussels, and thus cockles have a significantly wider shell than mussels of similar shell length (Chapter 4). The presence of a higher dome in the more convex cockle shell probably reduces its vulnerability to outright crushing, forcing crabs to use more time consuming opening techniques or to abandon the cockle for a smaller one that is easier to open. Boulding and

LaBarbera (1986) reported that the domed shape of *Protothaca staminea* could result in increased force applications by *Cancer productus* to successfully open this infaunal bivalve. Shell features such as large size, increased thickness, more inflation, and the absence of gape reduced vulnerability of clams to predation by *C. productus* (Boulding, 1984), and have been suggested to influence size-related preferences of crabs (Blundon & Kennedy, 1982a; Elner, 1978; Walne & Dean, 1972) and other decapods (Griffiths & Seiderer, 1980) feeding on various bivalve prey.

While crabs of all size categories preferred cockles of a shell length slightly smaller than the preferred mussels (Figures 5.1-5.3), the preferred mussels and cockles were of a more similar shell width (Figure 5.4). These results suggest that crab preference for a particular size range of prey is more strongly related to the minimum than to the maximum linear dimension of the shell (Chapter 6). As bivalves increase in size, their increased minimum shell dimension makes them too large to fit entirely within the chela, decreasing the amount of force that can be applied (Boulding, 1984).

The difficulty of comparing the size ranges of the four bivalve species that were preferred by crabs of different size category and species, arouse a further need to establish a measure of prey size that was relevant to crab feeding behaviour. Results expressed in terms of RPS showed that the size ranges of prey preferred by crabs were all within the RPS of 0.13-1.04. The initial position of the prey within the chela during the first attack strongly influences the time taken by *Cancer productus* to crush open various species of infaunal prey (Boulding & LaBarbera, 1986). In the present study, this position was consistently observed to be with the widest, most voluminous part of the shell at the region of the chela where dactylus and propus close to form a gape (Chapter 4). If crabs selected prey that yielded in the least time to their crushing efforts, then it is reasonable to suggest that they would consistently select those prey with a shell width that is equivalent or smaller than the maximum height of their chelae. This is not surprising, since size-selective feeding is strongly related to chelal height (Elner & Raffaelli, 1980; Rheinallt, 1986; Seed & Hughes, 1997), and RPS calculated as shell width/chelal height reflects the importance of the shell shape, volume, and position of prey when handled by crabs in diverse attack strategies (see also Lawton, 1983; 1989). Thus, when crab foraging behaviour is being examined, prey size based solely on shell length is not an appropriate indicator of the morphological characteristics of the shell associated with crab preference, and the geometry and crushing resistance of prey shells should be taken into account in future studies.

The importance of shell shape and volume also became evident in experiments where crabs were presented with a wide size range of *O. edulis* and *C. gigas*. While juvenile *C. maenas* (15-35 mm CW) and small *C. pagurus* (20-30 mm CW) preferred the smallest *O. edulis* offered, and their preference decreased steeply as flat oysters increased in size, larger crabs of both species did not preferentially consume the smallest *O. edulis* (Figures 5.1-5.3). By contrast, the patterns of size selection in all crabs feeding on *C. gigas* were more uniform, since all crabs included larger Pacific oysters in broadly similar proportions (Figure 5.4). Here again, as oysters increased in size, differences in shell morphology between prey species seemed to be the most important factor influencing the ability of different size categories of crabs to open them. As *O. edulis* and *C. gigas* increase in total shell length, *O. edulis* grows significantly higher, but not wider than *C. gigas* (Chapter 4). Both the smallest *O. edulis* and *C. gigas* fit between the propus and dactylus in any position and can easily be crushed even by the smallest crabs. The total shell height of *O. edulis*, and its smaller width, might constitute a shape-related restriction that makes smaller crabs unable to accommodate the flat oyster shell into the widest aperture of the chelae, or firmly grasp it in a horizontal position for crushing. Larger crabs, however, were able to feed on *O. edulis* of a wider size range probably because even the largest flat oyster offered had a shell height that could be held within the widest chelal gape. *C. gigas* of comparable shell length, however, has a more elongate shape that allows a firm grasp within the chelae which facilitates umbone crushing. The shape-related restriction imposed by the shell dimensions in *O. edulis* is probably more similar for the small than for the large crabs of both species, since inter-specific differences between chelal size (and gape) increase as *C. maenas* and *C. pagurus* increase in carapace width (Chapter 3; see also Lawton, 1983; Warner & Jones 1976). However, the lack of a similar restriction in *C. gigas*, may account for the wider and larger range of sizes that are vulnerable to *C. maenas* and *C. pagurus* of all size categories.

The size distribution patterns of selection of oysters in these experiments are in accordance with those previously reported for *C. maenas* and *C. pagurus* feeding on *C.*

gigas and another flat oyster *Tiostrea* (= *Ostrea*) *lutaria* (Richardson *et al.*, 1993), although the size ranges of oysters offered by these authors were larger than the ones used in the present study. Similarly, *C. maenas* of several size categories have been reported to successfully open *C. gigas* of up to 50-60 mm SL (Dare *et al.*, 1983). While Richardson *et al.* (1993) suggested that the strong reluctance of *C. maenas* and *C. pagurus* to feed on the flat oyster could be related to characteristics in the shape of its shell, Dare *et al.* (1983) explained their own results in terms of the presence of thin 'window' areas in the valves of *C. gigas*, which made these oysters more vulnerable. The lack of size selection by crabs feeding on other bivalve species has previously been explained in terms of the shell constituting an ineffective barrier to predation (Boulding, 1984; Yamada *et al.*, 1993). *Cancer productus*, for example, showed no size selection when feeding on *Protothaca staminea* of different size classes (Boulding & Hay, 1984). Moreover, the oysters used in the present study were cultivated in trays, where, according to Yamada *et al.* (1993), shells are much thinner than in sea bottom-reared oysters. This condition helps to explain the lack of a size selective feeding on *C. gigas* whose vulnerable shell might not constitute an effective barrier to crab crushing.

Comparisons between the selective feeding behaviour of *C. maenas* and *C. pagurus* of similar carapace width based on a relative measure of prey shell width (RPS), showed that the range of size classes of *M. edulis* preferred (consumed in > 20 %) by both size categories of *C. pagurus* (0.28-0.97) is higher than that preferred by *C. maenas* of comparable (0.17-0.70), and even larger carapace width (0.15-0.56). If it is assumed that crabs used any of the efficient crushing methods to open the selected size classes of prey, then it can be suggested that *C. pagurus* can readily crush larger mussels, relative to the size of their chelae, than *C. maenas* of similar or greater chelal height. Previous studies have related differences in prey size selection by different species of crabs to their contrasting chelal morphology and general feeding behaviour (Lake *et al.*, 1987; Rheinallt & Hughes, 1985). Elner and Lavoi (1983) reported that mud crabs, *Neopane sayi* had predation rates on attached spat similar to that of rock crabs *Cancer irroratus*, twice their size. Bisker and Castagna (1987) showed that mud crabs *Panopeus herbstii* had higher predation rates on oyster spat of *Crassostrea virginica* than blue crabs, *Callinectes sapidus*, of similar carapace width. The authors compared their findings with those reported for *Panopeus herbstii* (Whetstone & Eversole, 1981) and concluded that mud crabs could cause higher mortality to both oyster spat and juvenile clams, *Mercenaria mercenaria*, which are more than twice the size of those affected by blue crabs. They explained their results in terms of the presence of a large molariform tooth in the claw of *P. herbstii* which gives it a distinct mechanical advantage when crushing bivalve shells. Although such a structure is absent from the chelae in *C. pagurus*, occlusive geometry and general morphology in this species, suggest that edible crabs possess powerful monomorphic claws that operated at a significantly higher mechanical advantage than the master chelae of shore crabs (Chapter 3), and might help to explain why *C. pagurus* selects mussels of a shell width that can be equivalent to the height of its monomorphic chelae.

In the present study, *C. maenas* showed a consistent pattern of mussel size selection, where intermediate size classes of mussels were generally consumed in the highest percentage, while mussels in the smallest and largest size classes offered were consumed in a slightly lower percentage (Figure 5.4). This resulted in bell-shaped patterns of mussel size selection in all size categories of *C. maenas*, which were particularly evident amongst adult shore crabs. Results similar to these have been previously reported for adult *C. maenas* feeding on *M. edulis* (Elner & Hughes, 1978; Jubb *et al.*, 1983;), as well as for other portunids e.g. *Necora puber* (Rheinallt, 1986), *Ovalipes catharus* (Davidson, 1986). *C. pagurus*, however, always consumed the smallest mussels offered in the highest percentage, resulting in a monotonically decreasing pattern (Figure 5.4). Since *C. pagurus* were not offered mussels < 4 mm SL, it cannot be established whether edible crabs would have consumed such mussels in a lower percentage than the smallest size class available. Nevertheless, the monotonically decreasing pattern of mussel selection exhibited by *C. pagurus* in the present study is similar to that reported by Lawton (1983), and is not uncommon amongst brachyuran crabs feeding on mussels or other molluscan prey. While the numbers of *Pecten maximus* (Lake *et al.*, 1986) and *Nucella lapillus* (Lawton & Hughes, 1985) taken by *C. pagurus* decreased monotonically as scallops and snails increased in size, authors studying other *Cancer* species have reported that crabs consistently preferred the smallest size classes of *Prothotaca staminea* (e.g. Juanes & Hartwick, 1990; Pearson *et al.*, 1981), *Mya arenaria* and *Saxidomus giganteus*, (Boulding, 1984). Similarly, several studies of the swimming crab, *Callinectes sapidus*, feeding on the marsh mussel, *Geukensia demissa* (Bertness & Grosholz, 1985; Hughes & Seed, 1981; Seed, 1982), have shown that crabs consistently selected the smallest size class of mussels offered. The findings of these authors have been related to specific behavioural strategies which minimise foraging time (Hughes & Seed, 1981), minimise claw damage (Juanes, 1992; Juanes & Hartwick, 1990), or have been considered to be the result of a passive mechanism that improves their energetic reward when foraging on prey that differ in relative abundance and predictability (Eggleston *et al.*, 1992; Lawton & Hughes, 1985; Micheli, 1995; Hughes & Elner, 1979).

Differences in the order in which several size classes of *M. edulis* were taken by *C. maenas* and *C. pagurus*, therefore, testify to the importance of specific crab characteristics, such as chelal strength and morphology, and crab behaviour, in prey size selection. Nevertheless, these differences varied with the prey species that was offered to crabs, indicating that inter-specific differences in crab foraging behaviour are also influenced by the diverse degrees of vulnerability amongst bivalve prey. When crabs were offered *C. edule* and *O. edulis* individually, the patterns of size selection did not differ markedly between crab species (Figure 5.4). In addition, *C. pagurus* preferred cockles of a RPS only slightly greater than those preferred by *C. maenas* of similar carapace width, whereas the RPS of *O. edulis* preferred by both crab species was very similar (Figure 5.5). While the relatively inflated shell of *C. edule* might constitute a highly effective barrier to even the most powerful chelae in *C. pagurus*, the reluctance of the smallest crabs of both species to feed on large size classes of *O. edulis* probably reflects the equal difficulties of these crabs to manipulate the flat oyster's relatively wider shell (Chapter 4). When feeding on *C. gigas*, however, the patterns of size selection of *C. maenas* and *C. pagurus* of comparable body size, differed considerably (Figure 5.4). In addition, the RPS of Pacific oysters preferred by both size categories of *C. pagurus* (20-40 mm CW) was substantially larger than that preferred by small-medium *C. maenas* (25-35 mm CW), suggesting that large *C. gigas* are more vulnerable to crushing by *C. pagurus* than *C. maenas*. Previous authors comparing the results of several studies reported that while the rate of successful attacks by *C. maenas* decreased monotonically as marine snails (Hughes & Elner, 1979) and periwinkles (Elner & Raffaelli, 1980) increased in size, shore crabs consistently selected mussels of intermediate size classes (Elner & Hughes, 1978). These authors concluded that inter-specific variations in the vulnerability of gastropods and mussels, together with differences between their spatial distribution, made profitability of gastropods more unpredictable than that of mussels. If variations in prey vulnerability can influence the degree in which crabs predict prey value, then it is reasonable to suggest that they can determine, at least in part, the foraging tactic that is most appropriate for each prey species. In this context, results from the present work constitute further evidence of the complex relationship between crab chelae and prey shell, and its importance in determining feeding habits and prey preferences.

The amount of dry flesh tissue of all four prey species consumed by crabs increased with increasing carapace width (Table 5.2). These results are in accordance with findings from previous works (Bisker & Castagna, 1987; Chilton & Bull, 1986; Creswell & McLay, 1990; Dare *et al.*, 1983; Whetstone & Eversole, 1981), and partly reflect the larger size classes of prey that were consumed by crabs as their chelae increased in strength and crushing power. Nevertheless, the marked increase in consumed biomass observed amongst larger crabs constitutes evidence to support that ingestion rate increases with crab size as a result of an increment in their metabolic needs.

In the present study, small crabs generally consumed more prey items of each species than large crabs (Table 5.2). Although the absolute size of prey preferred by small crabs was smaller than that preferred by large crabs, small crabs generally preferred prey items with a greater RPS than large crabs (Figure 5.5), suggesting that juvenile crabs frequently included prey items that were larger, relative to chelal size, than adults with larger and stronger claws. A possible explanation of this is that prey resistance to crushing by crabs not only depends on the width or length of the shell, but can also be influenced by the thickness and deposition of carbonated calcium of its layers (Boulding, 1984). Differences in growth rate amongst bivalves can influence the thickness of the shell (Seed, 1968; Seed & Brown, 1978), as well as, shell weight and inflation (Newell & Hidu, 1982). The fast-growing bivalve spat are not only smaller in size, but also possess a proportionately thinner and weaker shell than adult bivalves, making them particularly vulnerable to predation (Yamada *et al.*, 1993). Consequently, prey items of a small shell width will have less resistance to crushing than larger items of a similar RPS. In addition, the volume of flesh contained in the shell of all four bivalves increased as the cube of its length (Chapter 4). If large crabs increase energy intake by consuming relatively few large prey, whilst small crabs do so by increasing the number of small prey consumed (Chilton & Bull, 1986), small crabs, feeding on small prey, probably included more items near the upper limit of their preferred size range to increase the amount of flesh consumed.

5.4.2. Species-selective predation.

When crabs were offered a wide size range of oysters and mussels simultaneously, crabs in all size categories consistently selected *M. edulis* (Figures 5.7-5.9). In addition, both the numbers and mussel biomass consumed in these experiments were much larger than that of oysters (Table 5.3). While the differences between the biomass of mussels and oysters consumed might reflect the higher dry tissue weight of *M. edulis* when compared to either *O. edulis* or *C. gigas* of similar shell length (Chapter 4), the difference in numbers of prey consumed indicate that all crabs clearly preferred mussels over either oyster species. Indeed, previous authors have shown that *C. maenas* of 25-75 mm CW consumed *M. edulis* at more than twice the rate in which they consumed *C. gigas* (Dare *et al.*, 1983), and that *Cancer novaezelandiae* also preferred *M. edulis* when offered a choice of mussels and gastropods (Creswell & McLay, 1990). Further evidence of crab preference for *M. edulis* over both *O. edulis* and *C. gigas* was observed in experiments where crabs were given a choice of equal numbers of the preferred size classes of mussels and oysters. Although crabs generally encountered mussels and oysters in similar numbers (Table 5.4), the proportion of mussels successfully opened by all crabs was significantly higher than that of oysters, which in turn were more frequently rejected before, rather that after, an attempt by crabs to open them (Figure 5.10; Table 5.5). Moreover, when *M. edulis* was encountered by crabs in 1/2 and 1/4 of the numbers in which *O. edulis* was encountered (Table 5.8), the high percentage of accepted mussels (60-100 % of the total accepted prey) and the low percentage of accepted oysters (< 40 %) remained broadly the same (Table 5.6). These results suggest that preference for mussels, and the lack of preference for oysters, are independent of the relative abundance in which either prey species are found. The fact that the percentage of rejected mussels slightly decreased from the 1:2 to the 1:4 ratio experiments, indicates that even as mussels became scarce, crabs accepted and successfully opened them in an increasing proportion (Table 5.6).

Previous studies have related crab preference to the selection of prey with a higher value or profitability, expressed as the net energy intake per unit of handling time (Creswell & McLay, 1990; Elner & Hughes, 1978, Elner & Raffaelli, 1980). However, authors have noted that selection of optimum prey could result from a greater chance of encountering items with a larger surface area and/or reduced handling times due to a lower predatory resistance (Barbeau & Scheibling, 1994a), in which case, prey selection should be considered a consequence of passive choice. Passive or mechanistic prey selection usually results from physical properties and behaviour of predator and prey (Hughes, 1980) that determine the probability of encountering and opening alternative prey types. Body size, speed of movement and density of predator and prey can influence the probability of encountering, recognising.and predicting valuable prey (Lawton, 1989; Lawton & Hughes, 1985;), whereas contrasting morphologies in bivalve shells and the mechanical properties involved in crab attack can affect prey vulnerability (Boulding, 1984; Brown & Haight, 1992), hence the probability of opening encountered prey (Sih & Moore, 1990).

Barbeau and Scheibling (1994a) indicated that active selection could be recognised by comparing prey size-specific consumption rates in single and multiple choice experiments. In the present study, active and passive components of crab selection for prey species could not be analysed in this way, since variations in the experimental design from single and paired combination experiments did not allow for direct comparisons between consumption rate data to be made. However, the preference for *M. edulis* exhibited by crabs was very consistent throughout experiments where both prey types were encountered in varying and contrasting proportions (Table 5.6). This indicates that selection of mussels, whether a result of relatively higher mechanical difficulties in handling oysters than mussels (passive) or of differences in profitability between prey species (active), reflects a markedly strong preference of *C. maenas* and *C. pagurus* for *M. edulis.*

Contrasting results were obtained when crabs were offered a choice between a wide size range of *O. edulis* and *C. gigas*. *C. maenas* and *C. pagurus* did not exhibit any marked preference for either oyster species (Figures 5.7-5.9), and crabs generally consumed similar numbers of both *O. edulis* and *C. gigas* (Table 5.3). Similar results were obtained when crabs were offered equal numbers of the preferred size classes of *O. edulis* and *C. gigas*, since in experiments with all crabs the proportion of opened, manipulated and abandoned, and touched and rejected prey items were similar for both species (Figure 5.11). In a study of *C. maenas* and *C. pagurus* feeding on *C. gigas* and the New Zealand oyster, *Tiostrea* (= *Ostrea*) *lutaria*, Richardson *et al.* (1993) found that when each oyster species was presented individually, crabs consumed very few *T. lutaria*, but fed extensively on *C. gigas*. When these oysters were presented simultaneously, however, crabs selected *C. gigas*, whereas no *T. lutaria* were consumed by either crab species. Differences between the results reported by Richardson *et al.* (1993) and those of the present study might be due to the fact that these authors used much larger *C. gigas* (40-70 mm SL) than the ones used in the present study (3-35 mm SL). Small *O. edulis* and *C. gigas* of comparable shell length can have similar amounts of dry tissue weight (Chapter 4). Amongst large oysters, however, the relatively voluminous shell of *C. gigas* can hold considerably more flesh than the flat *O. edulis* of similar shell length (Chapter 4). The larger *C. gigas* offered to crabs in the study by Richardson *et al.* (1993) would render more biomass per prey item than the smaller *C. gigas* offered to crabs in the present study. Therefore, *C. maenas* used in the present study probably needed to include *O. edulis* in their diet in order to increase biomass consumption. The slightly higher biomass consumption of *C. gigas* than of *O. edulis* (Table 5.3) further supports this idea, since it probably reflects differences in flesh weight between the two oyster species, particularly amongst larger crabs where these differences are greater.

When given a choice between *M. edulis* and *C. edule*, juvenile *C. maenas* (15-35 mm CW) showed no preference for either species (Figure 5.7). Although they consumed a higher amount of mussel than cockle flesh (Table 5.3), the numbers of *M. edulis* and *C. edule* consumed by juvenile shore crabs were broadly similar, suggesting that differences in total consumed biomass were probably due to differences in the amount of flesh contained in mussel and cockle shells. However, when adult *C. maenas* (40-70 mm) were offered a choice, these crabs tended to select mussels over cockles, particularly amongst the larger size classes of prey (Figure 5.8). Here, not only the amount of mussel flesh, but also the number of mussels consumed by adult shore crabs was higher than that of cockles (Table 5.3), suggesting that larger, adult *C. maenas* have a stronger preference for mussels than do juvenile shore crabs. Because the size range of mussels and cockles selected by adult *C. maenas* were larger than those selected by juvenile crabs (Figures 5.7-5.8), these results indicate that feeding preferences of crabs regarding prey species can be influenced by the size ranges of each prey that are easily opened by different size categories of crabs.

Rangeley and Thomas (1987) related differences in the proportions of gastropods and barnacles between the diets of juvenile and adult *C. maenas* to variations in the size range of prey that crabs of different size could successfully attack. Juvenile *C. maenas* feed on a narrow size range of prey, reduced by the lack of chelal strength, dexterity and time to open prey over a certain size limit. A feeding strategy which includes a wider variety of prey species of a smaller size range might allow these crabs to ingest a sufficient amount of biomass to meet the energy requirements for their rapid growth. By contrast, large crabs were always able to open barnacles of any size, but had many unsuccessful attacks on gastropods. In the present study, the size ranges of mussels and cockles selected by juvenile shore crabs were probably similar in both flesh content and vulnerability, thus, small crabs consumed these prey items in equivalent numbers. As prey increased in size, however, the more tumid, globular shell of cockles made them less vulnerable to attack from larger crabs than the more elongate mussel shells (Chapter 4). Although both large mussels and cockles have similar dry tissue weight, adult *C. maenas* were able to open a wider size range of mussels and satisfy their hunger, and did not need to include as many large, more resistant cockles in their diet.

A previous study comparing the vulnerability of different infaunal bivalves to crushing by *Cancer productus* found that amongst larger prey sizes, differences in vulnerability between shell morphology could outweigh differences in size (Boulding, 1984). Consequently, amongst smaller prey sizes, differences in size might be more important in determining vulnerability and crab selection than the morphological variations in the shells of different prey species. From these findings, it appears that juvenile shore crabs are limited in their choice in terms of prey size, and are thus forced to be less selective regarding prey species. Conversely, adult *C. maenas* do not have such a constriction in prey size selection, and can afford to be more selective in terms of prey species.

Small (20-30 mm CW) and small-medium (30-40 mm CW) *C. pagurus* showed no preference for either *M. edulis* or *C. edule* in the smaller sizes of prey, but selected more mussels than cockles as prey size increased (Figure 5.9). Another cancrid, *Cancer* *novaezelandiae* of 105-115 mm CW showed a similar pattern when given a choice of small (10-15), medium (28-35) and large (40-45 mm SL) mussels, *M. edulis* and cockles, *Austrovenus stutchburyi* (Creswell & McLay, 1990). When given a choice of small prey items, crabs preferred cockles; no species preference was evident for medium prey, whilst crabs preferred large mussels over large cockles. Present results, however, also showed that both size categories of *C. pagurus* selectively fed on mussels and cockles in a pattern that was more similar to that exhibited by larger, adult shore crabs than to that of juvenile shore crabs of comparable carapace width. If differences in chelal size and strength make smaller *C. maenas* less species-selective in their feeding behaviour than larger crabs, then inter-specific differences in chelal morphology and occlusive geometry amongst *C. maenas* and *C. pagurus* of similar body size are expected to have an effect on the degree of prey selectivity in these crab species. Previous studies comparing the crushing abilities of different brachyuran crabs have suggested that crabs possessing stronger and larger chelae are able to exploit a wider size range of hard-bodied prey (Lee & Seed, 1992). These findings, together with variations in the general behaviour of different species of crabs (e.g. aggression, use of shelter, local distribution on the shore, etc.) might help to explain some of the differences between the feeding behaviour exhibited by *C. maenas* and *C. pagurus* throughout the present experiments.

Further evidence of the lack of any marked preference of crabs to consume either mussels or cockles was provided by the results of feeding experiments where crabs were offered equal (1:1) and unequal numbers (1:2 and 1:4) of the preferred size classes of *M. edulis* and *C. edule*. In the 1:1 ratio experiments, the proportions of both prey species that were successfully opened, manipulated and abandoned, and touched and rejected by crabs in all size categories were broadly similar (Figure 5.10; Table 5.5). In addition, when crabs were offered mussels and cockles in the ratios of 1:2 and 1:4, the proportions of accepted and rejected *M. edulis* and *C. edule* were generally in accordance with the proportions in which both prey species were encountered by crabs (Table 5.7). However, while crabs in all except one size category encountered mussels and cockles in numbers similar to the proportions in which both prey species were offered (Tables 5.4 and 5.8), medium *C. maenas* (40-55 mm CW) encountered mussels twice as often (67 %) as they encountered cockles (32 %) in the 1:1 ratio trial; medium shore crabs encountered mussels (49 %) and cockles (51 %) in approximately equal number in the 1:2 ratio trial, but encountered mussels in much less frequency (39 %) than they encountered cockles (61 %) in the 1:4 ratio experiments. Because the size classes used in these experiments were those mostly preferred by crabs in previous experiments (Appendix B4), these results suggest that the size range of *M. edulis* and *C. edule* that were preferred by all but medium *C. maenas* were of similar volume, whereas the size range of cockles preferred by medium shore crabs (5-10 mm SL) was approximately half that of the preferred size class of mussels (10-15 mm SL).

Active selection can be considered an important component of predation when a predator selects a prey type more often than expected when given a choice of prey types than when not given a choice (see also Liszka & Underwood, 1990). The present findings indicate that crabs selected cockles and mussels as expected by their relative abundance, and more specifically, by the frequency in which various size categories of crabs encountered the preferred size ranges of prey. Evidence of active selection may be found in a predator's decision on whether to attack an encountered prey or continue searching, or whether to reject or persist with a prey that is being manipulated (Jubb *et al.*, 1983). Since the proportions of touched and rejected, manipulated and abandoned, and successfully opened mussels were not markedly different than those of cockles in the 1:1 ratio experiments, it seems reasonable to suggest that the active component of selection in this particular prey combination is not important in determining crab preference. The observed differences in the foraging behaviour of both *C. maenas* and *C. pagurus* when feeding on a combination of mussels and oysters and a combination of mussels and cockles further supports the view that the relative importance of active and passive selection in explaining prey choice may differ with each predator-prey system (Abele *et al.*, 1981).

5.5. Summary

1. When crabs were offered a wide size range of *Mytilus edulis* and *Cerastoderma edule* presented individually, the sizes of preferred prey clearly increased as crabs increased in size, confirming that both mussel and cockle size selection were strongly influenced by the relationship between carapace width, more specifically chelal height, and prey size. The percentage of prey consumed by crabs, however, decreased more steeply when cockles than

when mussels increased in size. When feeding on a wide size range of *Ostrea edulis*, small crabs of both species preferred the smallest flat oyster offered, and their preference decreased steeply as flat oysters increased in size. Large crabs, however, did not exhibit size selective feeding on *O. edulis*. By contrast, the patterns of size selection in *Crassostrea gigas* were more uniform, since crabs in all size categories included Pacific oysters of all the size range offered in broadly similar percentages.

2. Whilst the mean daily consumption of *M. edulis* increased with increasing temperature, juvenile *Carcinus maenas* and *Cancer pagurus* continued to prefer similar size ranges of prey. These results confirm that consumption rates are partly a consequence of crab metabolic rates associated with water temperatures, and suggest that increments in metabolic rate have a greater effect on the consumption of smaller than of larger size classes of mussels.

3. Crab preference for a particular size range of prey was more strongly related with the minimum than with the maximum shell dimension. Thus, when crab foraging behaviour is examined, prey size based solely on shell length is not an appropriate indicator of the morphological characteristics of the shell associated with crab preference. Shell features such as shape, variations in the thickness at different regions of the shell, or the presence of gape can influence the vulnerability of bivalve prey to crab attack, and should be taken into account in future studies.

4. *C. pagurus* readily crushed larger mussels relative to the size of the chelae than *C. maenas* of similar or even greater chelal height. This is related to the fact that *C. pagurus* possesses powerful monomorphic chelae that operate at a higher mechanical advantage than the master chela of *C. maenas*. However, differences in prey size selection between crab species varied with the prey species offered. While the relatively inflated shell of *C. edule* constituted a highly effective barrier to even the most powerful chelae in *C. pagurus*, the reluctance of the smallest crabs of both species to feed on large size classes of *O. edulis* reflected the equal difficulties of these crabs to manipulate the flat oyster's relatively wide shell. The relative prey size (RPS) of *C. gigas* preferred by *C. pagurus* was substantially larger than

that preferred by *C. maenas* of comparable size, suggesting that large Pacific oysters are more vulnerable to predation by *C. pagurus* than by *C. maenas*.

5. The total biomass of all four prey species consumed daily by *C. maenas* and *C. pagurus* increased with increasing carapace width, indicating that ingestion rates increase with crab size as a result of an increment in their metabolic needs. Large crabs increase energy intake by consuming relatively few large prey, whilst small crabs do so by increasing the number of small prey consumed. Juvenile crabs frequently included prey items that were larger relative to chelal size, than adults with larger and stronger claws. This can be explained by differences in growth amongst bivalves that result in bivalve spat to have proportionately thinner and weaker shells than adult bivalves. Consequently, small prey items will have less resistance to crushing than larger items of similar RPS.

6. When crabs were offered a wide size range of oysters and mussels simultaneously, crabs in all size categories consistently selected *M. edulis*. Moreover, when mussels became scarce relative to oysters, crabs consumed them in an increasing proportion. These results reflect the strong preference of both *C. maenas* and *C. pagurus* for *M. edulis*. When offered a choice between both a wide size range and equal numbers of the preferred size ranges of *O. edulis* and *C. gigas*, crabs did not exhibit a marked preference for either oyster species. When given a choice between *M. edulis* and *C. edule*, juvenile *C. maenas* showed no preference for either species. However, when adult *C. maenas* were offered a choice, these crabs tended to select mussels over cockles, particularly amongst the larger size classes of prey. This indicates that feeding preferences of crabs regarding prey species can be influenced by the size ranges of each prey that are readily opened by different size categories of crabs. The size ranges of mussels and cockles selected by juvenile shore crabs were similar in both flesh content and vulnerability, thus, small crabs consumed them in equivalent numbers. As prey increased in size, however, the more tumid, globular shell of cockles probably made them less vulnerable to attack from larger crabs than the elongate mussel shells. Adult *C. maenas* were able to open a wider size range of mussels and did not need to include as many large, more resistant cockles in their diet.

7. Crabs selected cockles and mussels as expected by their relative abundance, and more specifically, by the frequency in which various size categories of crabs encountered the preferred size ranges of prey. Thus, the active component of selection in this particular prey combination is not important in determining crab preference. In the mussel-oyster combinations, by contrast, crab preference for mussels, and the lack of preference for oysters, were independent of the relative abundance in which either prey species were encountered. Results, therefore, did not allow to establish whether the reluctance of crabs to feed on oysters is the result of the relatively higher mechanical difficulties in handling oysters than mussels (passive) or of differences in profitability between prey species (active).

8. From results in the present study, it appears that juvenile shore crabs are limited in their choice in terms of prey size, thus, forced to be less selective regarding prey species. Conversely, adult *C. maenas* do not have such a constriction in prey size selection, and can afford to be more species-selective. Since differences in chelal size and strength make smaller *C. maenas* less species-selective in their feeding behaviour than larger crabs, then inter-specific differences in chelal morphology and occlusive geometry amongst *C. maenas* and *C. pagurus* of similar body size are expected to have an effect on the degree of prey selectivity in these crab species.

9. Taking into account not only the size classes of each prey species that were selected by crabs, but also the numbers and biomass of each bivalve that were consumed in both single and paired species experiments, the results of the present chapter suggest that *C. maenas* and *C. pagurus* exhibited an increasing preference for the four bivalve prey through the sequence: - *O. edulis* < *C. gigas* < *C. edule* < *M. edulis*. Both the patterns of prey size- and species-selective feeding observed in the course of this study were mainly determined by the contrasting morphological features of the bivalve shells, and the way these features influence the vulnerability of prey to predation by various size categories of crabs.

Chapter 6

Basis for Selective Foraging Behaviour

6.1. Introduction

Behavioural and mechanical aspects of predation by crabs that forage extensively on bivalve populations has been a recurrent topic in recent research (Blundon & Kennedy, 1982a; Hill, 1979; Seed, 1990). Several species of brachyuran crabs are known to select certain species as well as certain size ranges of prey (Arnold, 1984; Creswell & McLay, 1990; Hughes & Elner, 1989). This selective foraging not only influences the abundance and distribution of the prey, but can also be an important factor structuring prey populations of high economical value (Gee *et al.*, 1985; Richardson *et al.*, 1993; Sanchez-Salazar *et al.*, 1987b). Information concerning the basis of selective foraging behaviour can extend our understanding of predator-prey interactions, and can be of valuable use in the successful application of natural resource management and culture strategies (Castagna & Kreuter, 1977; Dare *et al.*, 1983).

Numerous works have been dedicated to an understanding of the basis of crab selective foraging behaviour, and various aspects of the predator-prey interaction have also been considered (e.g. Burrows & Hughes, 1990; Elner & Jamieson, 1979; Palmer, 1981; Rheinallt, 1982). Many authors have related their findings to the Optimum Foraging Theorem, whereby a predator chooses its diet to maximise net energy intake per unit of handling time (Estabrook & Dunham, 1976; Hughes, 1980; McNair, 1982; Pyke, 1984). Given a choice of different sizes and species of prey, a crab should select that with the highest dietary value (Pyke *et al.*, 1977). However, minimisation of handling times (Sanchez-Salazar *et al.*, 1987a; Hughes & Seed, 1981) and the risk of claw damage associated with attacks on larger, more resistant prey (Juanes & Hartwick 1990) have been suggested as causal factors in several crab-mollusc predatory relationships.

Because handling times, and hence prey values, have a complex variation related to morphological characteristics of the crab chelae and prey shell, foraging tactics can vary when feeding on species of prey with contrasting shell morphology (Creswell & McLay, 1990; Elner & Raffaelli, 1980). Moreover, certain differences in the foraging strategies between crab species can also be related to differences in the patterns of prey dispersion that crabs encounter in their natural habitats (Elner & Lavoie, 1983; Seed, 1980; 1982). Thus, comparisons between the foraging behaviour of different species feeding on several species of bivalves can reveal enlightening results regarding the basis for their selective feeding (Hughes & Seed, 1995). Whereas numerous works have addressed the dietary and energetic consequences of selective feeding (Hughes, 1990), few have identified the cues that make such foraging behaviour possible (e.g. Croy & Hughes, 1991a).

Both *Carcinus maenas* and *Cancer pagurus* have been considered important pests on commercial beds of the Pacific oyster, *Crassostrea gigas* and the mussel, *Mytilus edulis* in North Wales (Dare *et al.*, 1983; Richardson *et al*, 1993). In addition, studies have reported that selective predation by shore crabs can be a strong influence on the distribution of natural populations of the edible cockle, *Cerastoderma edule* in the Menai Strait (Sanchez-Salazar *et al.*, 1987b), and several species of cancrid crabs are known to feed extensively on other infaunal bivalves, such as *Protothaca staminea, Saxidomus giganeus*, and *Mya arenaria* (Boulding, 1984; Boulding & Hay, 1984; Pearson *et al.*, 1981).

The aim of this chapter is to investigate the basis for the selective foraging behaviour of *C. maenas* and *C. pagurus* when feeding on four bivalve species with contrasting morphologies and from different habitats. Comparisons will be made between the foraging strategies of crabs feeding on the mussel, *Mytilus edulis*; the flat oyster, *Ostrea edulis*; the Pacific oyster, *Crassostrea gigas*; and the cockle, *Cerastoderma edule.* Considerations will also be given to the differences between the foraging strategies of juvenile and adult shore crabs. The stimuli involved in the crabs selective response to prey types, and the relative importance at various decisive moments during the foraging bout will also be briefly considered.

6.2. Materials and Methods

All crabs and bivalves used for these experiments were collected and maintained as described previously in Chapters 4 & 5.

6.2.1. Handling times and profitability.

Male *Carcinus maenas* of 10-70 mm of carapace width (CW) were fed individual *Mytilus edulis* ranging from 2-35 mm in shell length (SL), *Ostrea edulis* from 6-30 mm

SL, *Crassostrea gigas* from 6-35 mm SL, and *Cerastoderma edule* from 2-20 mm shell length (SL). Male *Cancer pagurus* of 20-40 mm CW were fed individual mussels ranging from 2-15 mm SL, oysters of 3-25 mm SL, and cockles of 2-20 mm SL. In each trial the following events were recorded with a stopwatch: i) **breaking time (Tb)**, the time from the first physical contact with the prey item, through the period of manipulation to the point where the shell was finally opened and the flesh exposed; ii) **eating time** (Te), the period from when the prey was opened to the point were the meal was completed and the empty shell abandoned; iii) and **handling time (Th**: sum of **Tb** and **Te**). If the crab abandoned the prey item, **abandoning time (Ta)**, i.e. the period from the first physical contact between crab and prey to the point when the unopened prey item was definitely rejected was noted and the prey replaced with another one of smaller size. In cases where crabs were reluctant to eat, they were starved for 1-3 days until hunger levels recovered. Water temperature throughout the trials ranged from 12-18°C.

Least squares regressions on previously log-transformed handling times showed that data best fitted the exponential model. Thus, handling time curves were predicted for each individual crab based on the equation

$$Th = a\,e^{b\,SL}$$

where a and b are the parameters of the exponential relationship between Th (sec) and shell length (mm SL). Prey profitability values were estimated as dry flesh weight per unit of observed handling time ($mg \cdot sec^{-1}$) and plotted against shell length. Dry flesh weights were estimated using the equations previously obtained for each prey species (Chapter 4). Profitability curves were then obtained by dividing the estimated dry flesh weight of a prey item of known shell length by the handling time predicted by the exponential model.

Because handling times have a complex interaction between shell strength and chelal power, profitability curves must be obtained empirically for each predator-prey combination, and these can rarely be resolved analytically (e.g. Elner & Hughes, 1978; Hughes, 1980). For this reason, statistical comparisons between breaking times and profitability values were performed on the basis of the size ranges of prey that were consumed in > 20 % of the total number of prey opened during experiments where crabs were offered an unlimited supply of each individual prey species (Chapter 5). Species profitability values for each size category of crab were log-transformed before analysis of variance was applied. For each size category of crab, log-transformed breaking times of the size ranges of preferred prey recorded during handling time experiments were compared using the same procedure (ANOVA and Scheffe's Method were applied on parametric data sets, and Kruskal-Wallis and Dunn's Method on non-parametric data sets; Appendix C2).

6.2.2. Chemical and mechanical stimuli.

Two experiments were designed to examine whether preference for a certain prey species was influenced by the odour/flavour of its flesh. First, five individually maintained *C. maenas* (50-60 mm CW) were presented with 10 agar cylinders (9 x 10 mm), 5 with mussel odour/flavour and 5 with oyster odour/flavour. Agar gels were made using a filtrate of 10 g of either mussel or oyster flesh homogenised in 100 ml of seawater, and poured to a depth of 10 mm into petri dishes. When set, the cylinders were cut with a cork borer of 9 mm in diameter and stored at -10 °C. The number of cylinders that were attacked was monitored every 10 min during a period of 1 h. Differences between the number of each type of cylinders destroyed within 10, 30 and 60 min were tested for goodness-of-fit to equal expected numbers.

The second experiment presented individually maintained *C. maenas* of 50-60 mm CW with models made of mussel and oyster shells (15-20 mm SL) filled with either mussel or oyster gel. Intact bivalves were briefly submerged into boiling water in order to extract the flesh and thoroughly clean the shells. Empty shells were then dried, and a hole was drilled through the valves so that they could be closed together using fuse wire. Five individually maintained crabs were then offered 5 mussel shells + mussel gel and 5 mussel shell + oyster gel; another five crabs were offered 5 oyster shells + mussel gel and 5 oyster shells + oyster gel. Every time a crab opened a model another one of the same type was introduced in the aquarium to maintain constant model availability. The time elapsed from the moment a crab touched each model, until it is definitely abandoned was recorded with a stopwatch, and was defined as **persistence time (Tp)** in order to distinguish it from **abandoning time** recorded for live prey. The number of models that were accepted and rejected within 1 h was recorded. The total number of times that each crab encountered each model type (i.e. models with similar shells, but different gel) was then tested for goodness-of-fit to the expected values (assuming an equal probability of encounter). Significant differences in the total number of models that were accepted by each individual crab were tested using the same procedure. Comparisons of persistence time between models of similar shell types, but different gel contents were examined using 2-sample *t*-tests on previously log-transformed data.

6.2.3. Prey shell.

In order to assess the importance of shell characteristics on crab feeding preferences, experiments were carried out by presenting medium (M: 40-55 mm CW) and large (L: 55-70 mm CW) *C. maenas* with inedible models of comparable size to that of the preferred live prey. Models of zero profitability were constructed by filling empty shells of the preferred size range of each prey species with epoxy resin (Appendix B4), so that the weight of the model was not significantly different to that of comparable live prey. Because crabs showed no preference for any particular size range of *O. edulis* and *C. gigas*, the size range of oysters used was equivalent to that of the preferred size ranges of mussels. The prey combinations offered were: *M. edulis-O. edulis* (M-O), *M. edulis-C. gigas* (M-C), *O. edulis-C. gigas* (O-C), and *M. edulis-C. edule* (M-E). Trials consisted of presenting an individual crab with equal numbers of paired combinations of model prey species. Sometimes crabs were able to break the models and tear off shell fragments. When this happened, a new model of the same type was introduced into the aquarium so that proportions of intact models were kept constant. The order in which models were taken and the behavioural responses to each prey type were recorded in a similar way to those described in experiments using live prey (Chapter 5). Because crabs did not obtain any food from their opening attempts, only those models that had been touched and immediately rejected were subsequently classified as 'rejected' (**a**), while 'accepted' prey included both items that had been manipulated and abandoned (**b**), as well as 'opened' models (**c**). The total number of times that crabs in each size category encountered each model species were then tested for goodness-of-fit to the expected values assuming equal

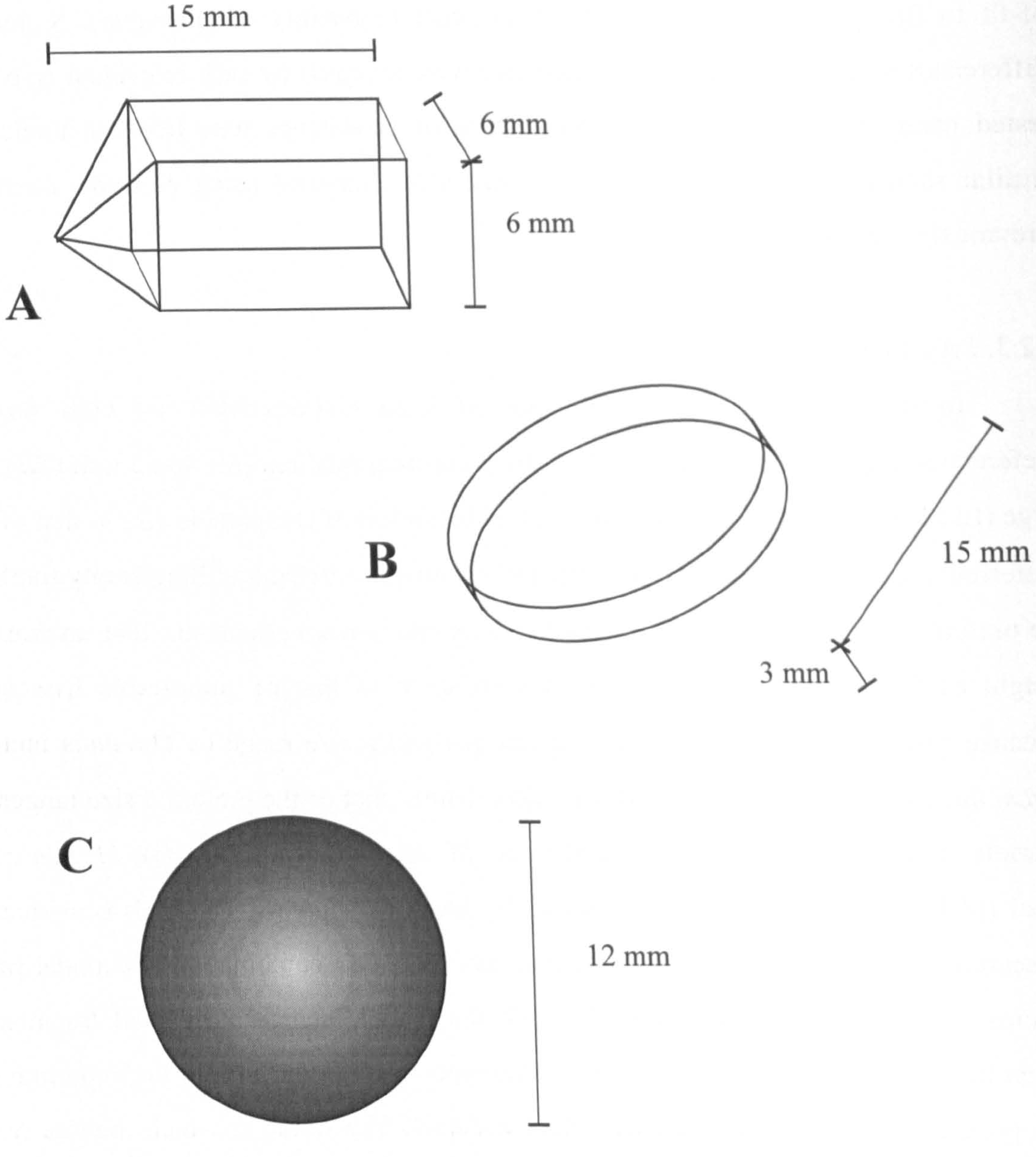

Figure 6.1. Epoxy resin models of contrasting geometric shapes, but approximately similar volume that were offered to *Carcinus maenas* (50-60 mm CW) to examine the importance of shell shape in crab foraging behaviour: **A**) wedged rectangle (420 mm^3); **B**) flat disc (530 mm^3); **C**) sphere (904 mm^3).

probability of encounter. Significant differences in the total number of prey of each species that were accepted by each individual crab were tested using the same procedure.

In order to compare persistence time of inedible models in each paired combination, four *C. maenas* (50-60 mm CW), each maintained separately, were presented with a sequence of six models of the same type. As soon as a crab finished manipulating one model in the sequence it was presented with the next. On day 1, two crabs were presented with six models of a certain type, whilst two crabs were presented with six models of another. On day 2 the treatment was reversed so that each individual crab was presented with a paired combination of model prey (M-O, M-C, O-C, and M-E). Persistence time with each model was recorded with a stopwatch and data were logarithmically transformed before analysis of variance (balanced design with 'model in sequence' and 'model type' as fixed factors, and 'crab' as a random factor) was performed.

The importance of shell shape in determining crab persistence was examined by presenting *C. maenas* of 50-60 mm CW with epoxy resin models of three contrasting geometric shapes of similar volumes : a "cockle" (sphere: 904 mm ^{3}), a "mussel" (wedged rectangle: 420 mm ^{3}) and an "oyster" (flat disc: 530 mm ^{3}; Figure 6.1). The resin models had similar maximum lengths (sphere: 12 mm, rectangle and disc: 15 mm) but differed in maximum height (sphere: 12 mm; rectangle: 6 mm; disc: 15 mm) and width (sphere: 12 mm; rectangle: 6 mm; disc: 3 mm). On each day, 6 individually maintained crabs received a sequence of 5 models of one of the three model types and their persistence times were recorded. Over a three day period, each crab had experienced each of the different model types. After each trial, crabs were fed on mussel flesh for 1 h before being starved until the next day. The order in which each crab experienced the different model types was random. Data were logarithmically transformed before differences in persistence time were examined using analysis of variance (balanced design with 'model in sequence' and 'model type' as fixed factors and 'crab' as a random factor).

6.2.4. Learning experiments.

To test whether crabs can improve their handling efficiency, and whether the acquisition of handling skills influences prey species selection, the following experiment was designed. Three naive *C. maenas* of 60-65 mm CW were fed with their preferred size

Table 6.1. Equation parameters for the exponential relationships between handling time (Th sec) and shell length (SL mm) for *Carcinus maenas* and *Cancer pagurus* of several size categories feeding on a size range of *Mytilus edulis*, *Ostrea edulis*, *Crassostrea gigas*, and *Cerastoderma edule*; a and b were estimated as: ln Th = ln a + b SL; r^2 is the coefficient of determination.

	Mytilus edulis				*Ostrea edulis*			
	a	b	r^2	n	a	b	r^2	n
Carcinus maenas								
15-25 mm CW	2.36	0.45	0.95	30	-	-	-	-
25-35 mm CW	2.97	0.34	0.96	35	3.74	0.13	0.49	15
40-55 mm CW	2.93	0.24	0.87	50	1.94	0.21	0.74	26
55-70 mm CW	2.41	0.21	0.80	33	3.28	0.14	0.56	15
Cancer pagurus								
20-30 mm CW	3.80	0.25	0.85	31	1.88	0.40	0.93	17
30-40 mm CW	3.67	0.18	0.61	34	2.92	0.21	0.96	26

	Crassostrea gigas				*Cerastoderma edule*			
	a	b	r^2	n	a	b	r^2	n
Carcinus maenas								
15-25 mm CW	-	-	-	-	2.76	0.58	0.86	26
25-35 mm CW	2.94	0.27	0.73	19	3.00	0.33	0.85	27
40-55 mm CW	2.99	0.18	0.81	26	3.27	0.19	0.69	23
55-70 mm CW	3.18	0.14	0.90	21	2.21	0.24	0.68	24
Cancer pagurus								
20-30 mm CW	2.98	0.26	0.93	23	3.82	0.35	0.94	23
30-40 mm CW	3.60	0.18	0.84	22	3.84	0.21	0.93	27

range of *M. edulis* (15-20 mm SL), whilst another three similar sized crabs were fed on the preferred size range of *C. edule* (10-15 mm SL). Individual breaking times were recorded during a 1 h period for four consecutive days. Crabs were then allowed unlimited access to these prey types for a period of 5 consecutive days. A total of twenty prey items of similar size were offered to the crabs over this period, and those which were consumed within 12 h periods were noted and replaced. After five days of continuous feeding, these crabs were again offered a size range of their respective prey species, and breaking times were recorded. If crabs had learned to handle a particular prey species, then breaking times were expected to improve. Data were logarithmically transformed and 2- sample *t*-tests performed.

To determine the effect of conditioning on further selective feeding behaviour, each crab was then offered 20 mussels and 20 cockles of comparable size ranges. Crabs were monitored every 12 h during five consecutive days and any item consumed was noted and replaced with another one of the same prey species. If learning has a positive influence on crab preference, then crabs might be expected to select the prey type to which they had been previously exposed. Results were analysed by means of a chi-square test of association. Similar trials were carried out for shore crabs feeding on *M. edulis* and *C. gigas*.

6.3. Results

6.3.1. Handling time and profitability.

The time taken by each size category of crab to handle individual prey items of all species increased exponentially with prey size, and the estimated parameters for these relationships are summarised in Table 6.1. The strong reluctance of small *Carcinus maenas* (15-25 mm CW) to feed on *Ostrea edulis* and *Crassostrea gigas* did not allow for handling curves to be obtained, since the data points obtained were not significantly correlated to oyster shell length ($r = 0.49$ and $r = 0.31$, respectively, both $p > 0.05$,); for similar reasons, meaningful handling time data could not be obtained for *Cancer pagurus* of both size categories (20-30 and 30-40 mm) feeding on *Mytilus edulis* > 13 mm SL.

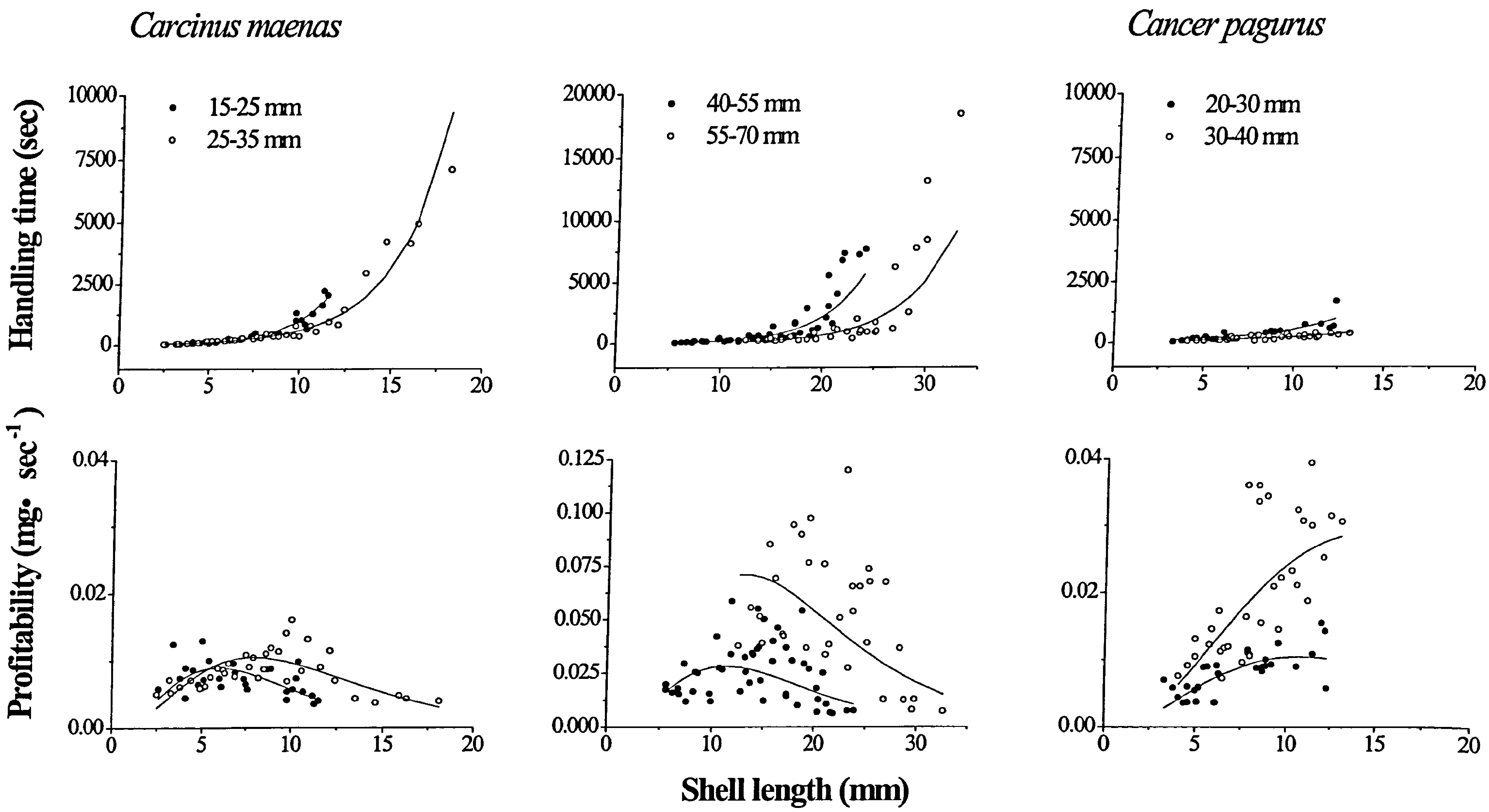

Figure 6.2. Handling time and profitability for a size range of *Mytilus edulis* that were consumed by *Carcinus maenas* and *Cancer pagurus* of several size categories. Solid lines represent predicted values based on the parameters of the exponential equations in Table 6.1, and on the dry flesh weight - shell length relationships of prey described in Chapter 4.

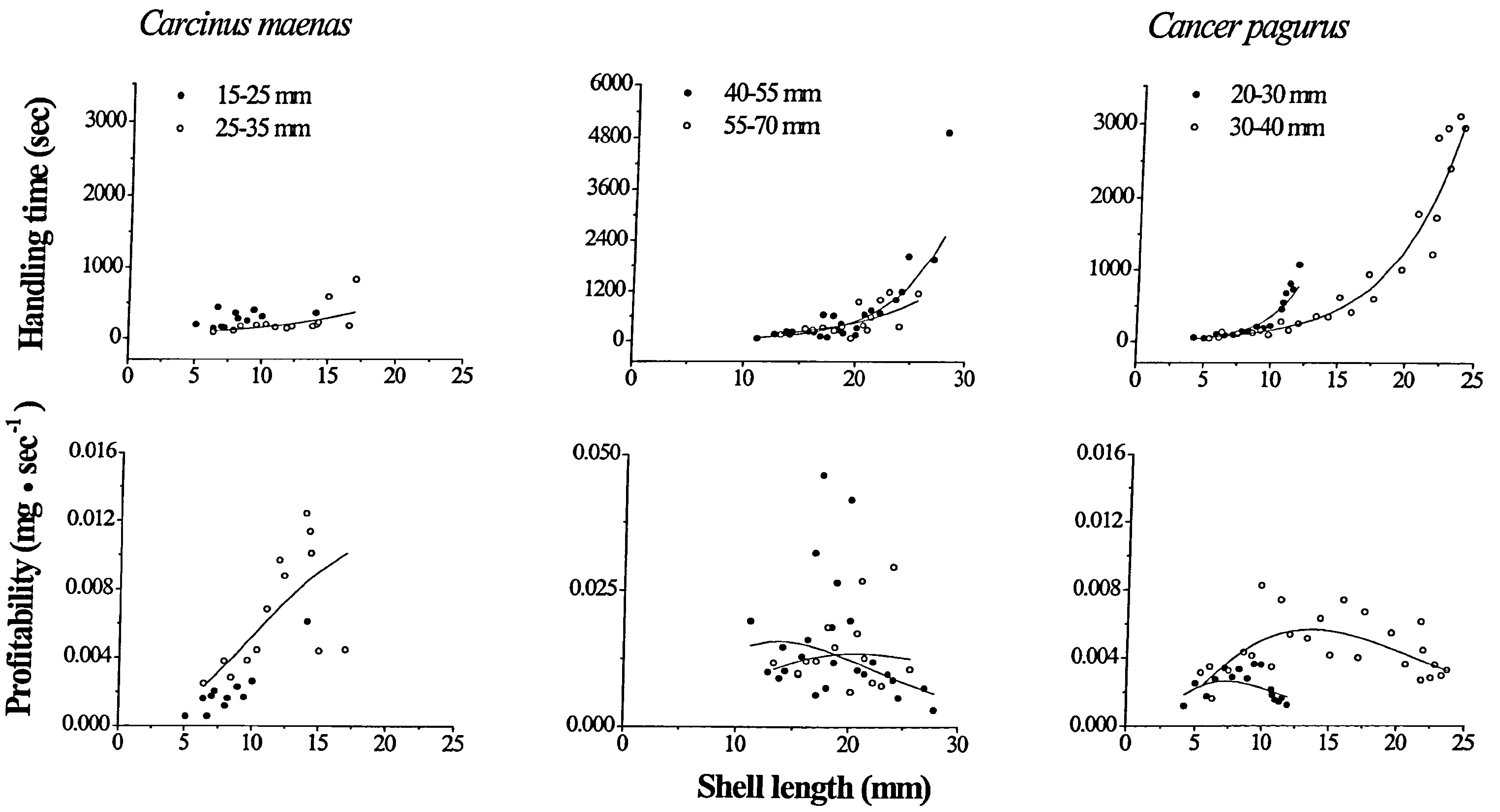

Figure 6.3. Handling time and profitability for a size range of *Ostrea edulis* that were consumed by *Carcinus maenas* and *Cancer pagurus* of several size categories. Solid lines represent predicted values based on the parameters of the exponential equations in Table 6.1, and on the dry flesh weight - shell length relationships of prey described in Chapter 4. Note the broad peaks of profitability for *C. maenas* 40-70 mm CW.

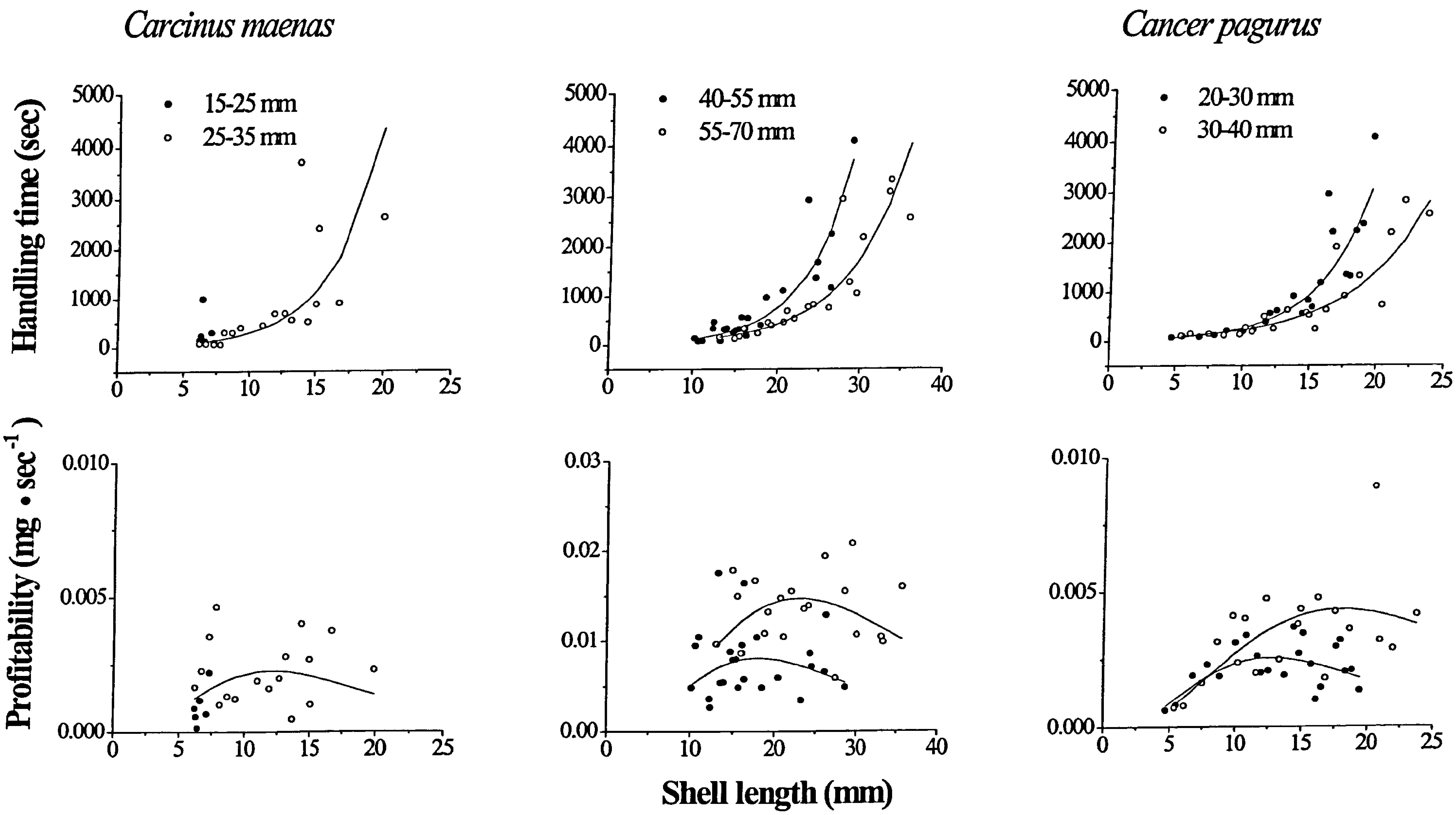

Figure 6.4. Handling time and profitability for a size range of *Crassostrea gigas* that were consumed by *Carcinus maenas* and *Cancer pagurus* of several size categories. Solid lines represent predicted values based on the parameters of the exponential equations in Table 6.1, and on the dry flesh weight - shell length relationships of prey described in Chapter 4. Note the broad peaks of profitability for all size categories of crabs.

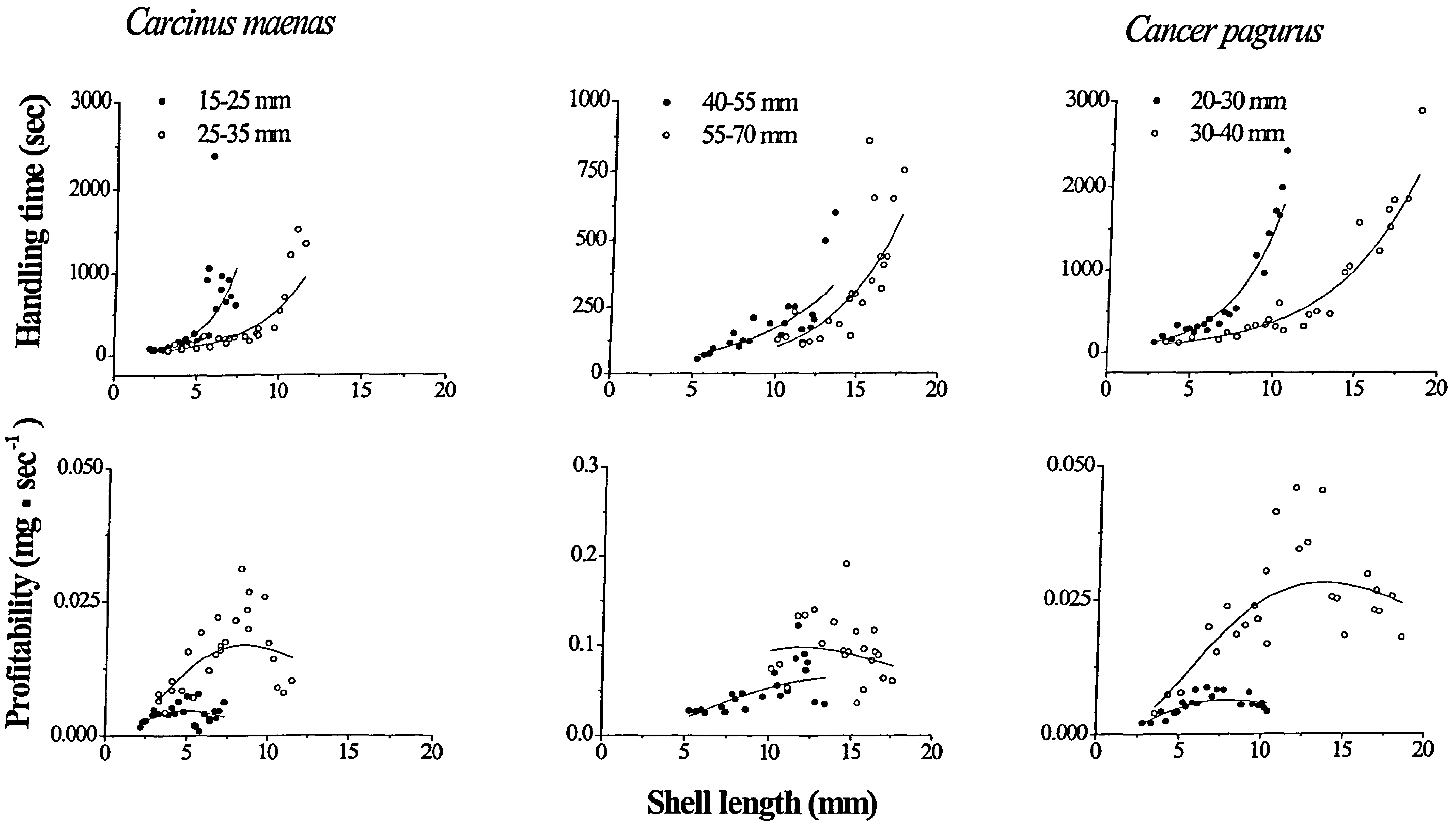

Figure 6.5. Handling time and profitability for a size range of *Cerastoderma edule* that were consumed by *Carcinus maenas* and *Cancer pagurus* of several size categories. Solid lines represent predicted values based on the parameters of the exponenetial equations in Table 6.1, and on the dry flesh weight - shell length relationships of prey described in Chapter 4.

Handling time and profitability curves for each size category of crab feeding on each prey species are shown in Figures 6.2-6.5. From the handling time data it is clear that larger crabs require progressively less time to handle prey of any particular shell length, and consequently they have access to progressively larger prey items of any species. Comparisons between crab species showed that handling times for *M. edulis* and *Cerastoderma edule* amongst small *C. maenas* and *C. pagurus* (15-25 and 20-30 mm CW, respectively) were similar, whereas small-medium *C. pagurus* (30-40 mm CW) successfully handled both mussels and cockles more quickly than did small-medium (25-35 mm CW) *C. maenas* (Figures 6.2 & 6.5). Both size categories of juvenile *C. maenas* and *C. pagurus* showed similar handling times when feeding on *O. edulis* and *C. gigas* of equivalent shell length, but edible crabs were able to open larger oysters than shore crabs of comparable carapace width (Figures 6.3-6.4).

Results show a considerable scatter within the handling time data for each prey species, and this becomes more extreme when data are transformed to profitability values, particularly amongst crabs feeding on *O. edulis* and *C. gigas* (Figures 6.3-6.4). Nonetheless, profitability plots suggest that larger crabs are consistently capable of obtaining higher profitability than smaller crabs, regardless of the size and species of prey offered. There also appears to be an optimum size of prey, below and above which prey profitability decreases, and this optimal size seems to increase as a function of crab size. In some cases, however, the size range at which profitability is maximised is quite wide and peaks are relatively broad (e.g. Figures 6.3-6.4). Comparisons of profitability curves between different species of crabs showed that *M. edulis*, *C. edule* and *C. gigas* were more profitable to *C. pagurus* than to *C. maenas* of comparable carapace width when these crabs consumed similar size classes of these prey. These differences were more pronounced amongst small-medium (25-35 and 30-40 mm CW) than amongst small (15-25 and 20-30 mm CW) crabs of both species. However, profitability values overall were similar for both crab species when feeding on *O. edulis*.

The relationships between mean profitability values of the preferred size ranges of each prey species and relative prey size (RPS = shell width/chelal height) are shown in Figures 6.6-6.8. Results of the analysis of variance showed that profitability values of *M. edulis* and *C. edule* were similar for *C. maenas* 25-70 mm CW and for *C. pagurus* 30-40

Table 6.2. Results of analysis of variance on log-transformed profitability of the size ranges of *Mytilus edulis* (M), *Ostrea edulis* (O), *Crassostrea gigas* (C), and *Cerastoderma edule* (E) that were preferred by *Carcinus maenas* and *Cancer pagurus* of several size categories during single prey species experiments; *** $p < 0.001$.

	Overall F value	Summary of selected pairwise comparisons [1]			
Carcinus maenas					
15-25 mm CW	48.19 ***	M>O	M>C	O=C	M>E
25-35 mm CW	34.17 ***	M>O	M>C	O=C	M=E
40-55 mm CW	30.98 ***	M>O	M>C	O=C	M=E
55-70 mm CW	69.00 ***	M>O	M>C	O=C	M=E
Cancer pagurus					
20-30 mm CW	33.75 ***	M>O	M>C	O=C	M>E
30-40 mm CW	29.47 ***	M>O	M>C	O=C	M=E

[1] Statistical values for all of the six pairwise comparisons in each test can be found in Appendix C1.

Table 6.3. Results of analysis of variance on log-transformed breaking times that *Carcinus maenas* and *Cancer pagurus* of several size categories spent on the size ranges of *Mytilus edulis* (M), *Ostrea edulis* (O), *Crassostrea gigas* (C), and *Cerastoderma edule* (E) that were selected by crabs during single prey species experiments; ** $p < 0.01$; *** $p < 0.001$; ns = no significant differences.

	Overall F value [2]	Summary of selected pairwise comparisons [1]			
Carcinus maenas					
15-25 mm CW	6.08 **	M=O	M=C	O=C	M=E
25-35 mm CW	14.67 **	M=O	M=C	O=C	M>E
40-55 mm CW	16.92 ***	M=O	M=C	O=C	M>E
55-70 mm CW	4.30 **	M=O	M=C	O=C	M=E
Cancer pagurus					
20-30 mm CW	2.44 ns	M=O	M=C	O=C	M=E
30-40 mm CW	8.84 ***	M=O	M<C	O=C	M=E

[1] Statistical values for all of the six pairwise comparisons in each test can be found in Appendix C2.

[2] Values for *C. maenas* 25-35 mm CW and *C. pagurus* 20-30 mm CW correspond to values of H in the Kruskal-Wallis tests applied in these cases (see Appendix C2).

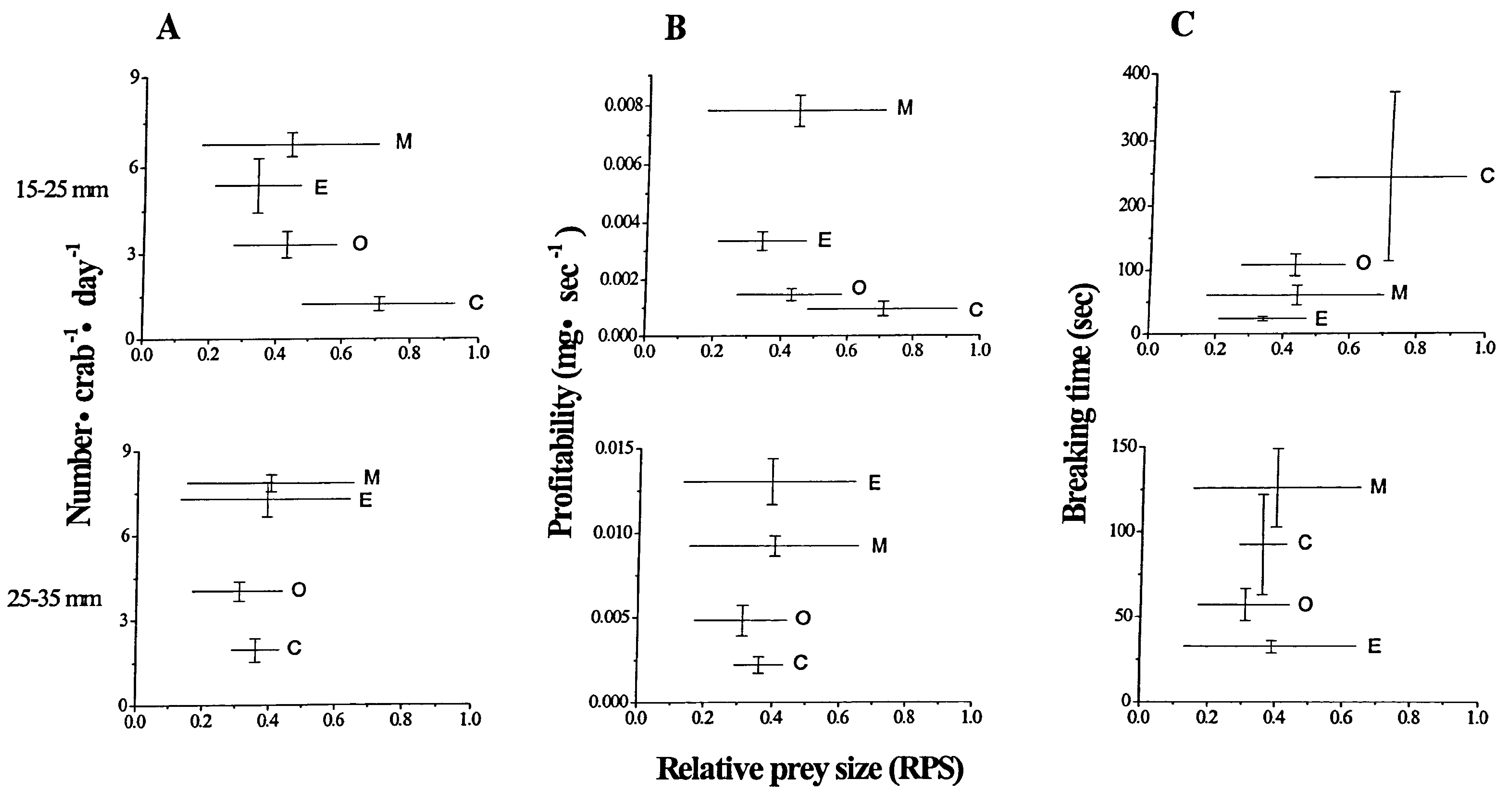

Figure 6.6. Mean (± se) number (A), profitability (B), and breaking times (C) for the preferred size range (RPS = shell depth/chelal height) of *Mytilus edulis* (*M*), *Ostrea edulis* (*O*), *Crassostrea gigas* (*C*), and *Cerastoderma edule* (*E*) that were consumed by two size categories of juvenile (15-25 mm (upper) and 25-35 mm (lower) CW) *Carcinus maenas* during the single prey species experiments described in Chapter 5.

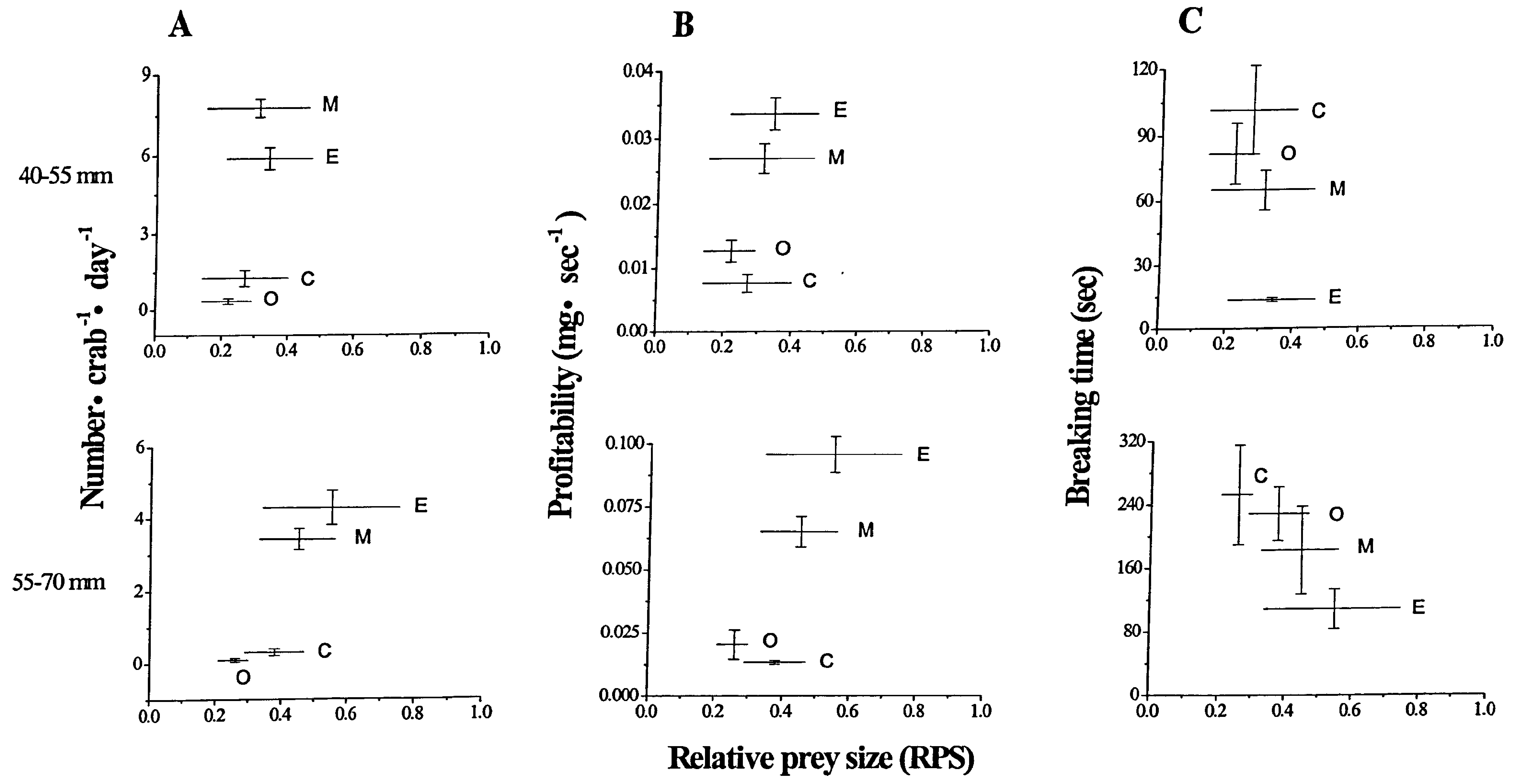

Figure 6.7. Mean (± se) number (A), profitability (B), and breaking times (C) for the preferred size range (RPS = shell depth/chelal height) of *Mytilus edulis* (*M*), *Ostrea edulis* (*O*), *Crassostrea gigas* (*C*), and *Cerastoderma edule* (*E*) that were consumed by two size categories of adult (40-55 mm (upper) and 55-70 mm (lower) CW) *Carcinus maenas* during the single prey species experiments described in Chapter 5.

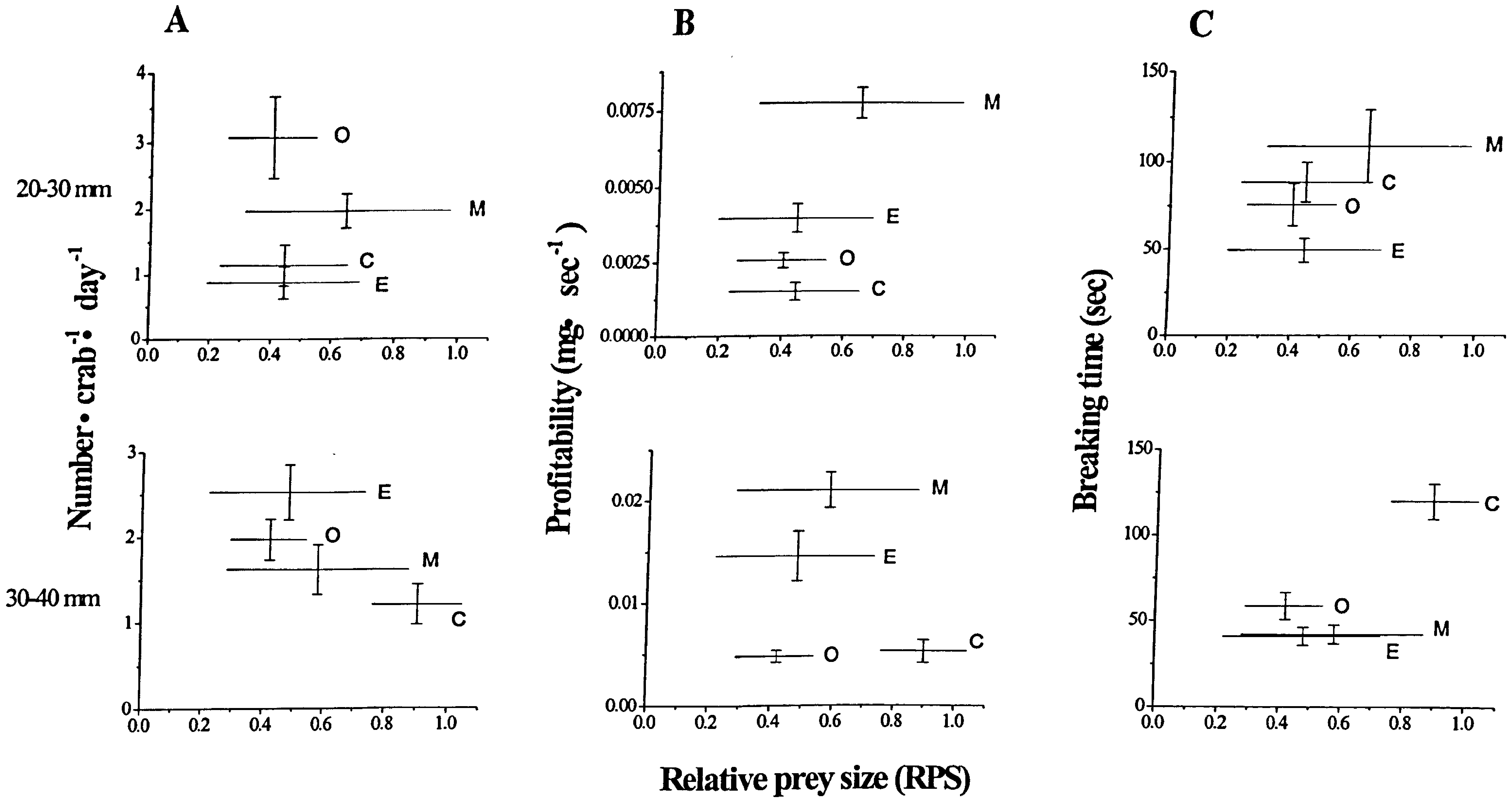

Figure 6.8. Mean (± se) number (A), profitability (B), and breaking times (C) for the preferred size range (RPS = shell depth/chelal height) of *Mytilus edulis* (*M*), *Ostrea edulis* (*O*), *Crassostrea gigas* (*C*), and *Cerastoderma edule* (*E*) that were consumed by two size categories of juvenile (20-30 mm (upper) and 30-40 mm (lower) CW) *Cancer pagurus* during the single prey species experiments described in Chapter 5.

mm CW (Table 6.2). For these size categories of crabs, profitability values for *M. edulis* were significantly higher than those of both *O. edulis* and *C. gigas* (Table 6.2). However, for both small *C. maenas* (15-25 mm CW) and small *C. pagurus* (20-30 mm CW), mean profitability values of mussels were significantly higher than both those of cockles and oysters (Table 6.2). No significant differences were detected between the profitability values of the preferred size classes of *O. edulis* and *C. gigas* for any size category of crab (Table 6.2).

Comparisons between breaking times of the preferred size range of each prey species showed that, overall, crabs took increasingly more time to open prey in the following order: *C. edule* → *M. edulis* → *O. edulis* → *C. gigas* (Figures 6.6-6.8). However, statistical analysis of pairwise comparisons did not reveal significant differences between breaking times throughout the size categories and species of crabs examined (Table 6.3), suggesting that crabs took approximately similar times to open all four bivalve prey. The only exceptions were for small-medium (25-35 mm CW) and medium *C. maenas* (40-55 mm CW), where breaking times for *M. edulis* were significantly greater than for *C. edule*, and for small-medium *C. pagurus* (30-40 mm CW) where breaking times for *C. gigas* were significantly greater than for *M. edulis* (Table 6.3). It should be noted, however, that *C. edule* was always opened in the shortest time, and that significant differences were never found between the breaking times of the two oyster species.

To establish whether crabs selected prey species on the basis of their ranked profitability, the mean number of prey of the size ranges that were consumed preferentially by crabs in experiments with single prey species are shown (Figures 6.6-6.8). Results indicate that for *C. maenas* 25-70 mm CW and *C. pagurus* 30-40 mm CW, the ranking order of prey profitability generally paralleled the order in which prey species were consumed during single prey species experiments, suggesting that prey value can influence species selection amongst these size categories of crabs. *C. maenas* of 15-25 mm CW and *C. pagurus* of 20-30 mm CW also selected mussels and oysters as expected by the rankings of their profitability. These size categories of crabs, however, obtained a significantly higher profitability feeding on the preferred size classes of *M. edulis* than on *C. edule*, but consumed mussels and cockles in similar rates, suggesting that other factors might be involved in prey species selection by these smaller crabs.

Table 6.4. Number of models accepted and rejected by five *Carcinus maenas* (50-60 mm CW; I-V) presented with mussel-shell models and another five *C. maenas* (VI-X) presented with oyster-shell models over a 1 h period. Models were constructed by filling shells of *Mytilus edulis* and *Ostrea edulis* with two different types of gel.

	Mussel shell					Oyster shell			
	Oyster gel		Mussel gel			Oyster gel		Mussel gel	
	acc	rej	acc	rej		acc	rej	acc	rej
I	3	0	1	1	VI	3	3	3	4
II	2	2	2	2	VII	2	4	2	5
III	1	1	0	1	VIII	5	2	2	9
IV	1	1	3	0	IX	3	1	2	8
V	4	1	3	0	X	1	2	3	0
Total	11	5	9	4	Total	14	12	12	26

Table 6.5. Chi-square values for goodness-of-fit tests on encounter rates of individual *Carcinus maenas* of two size categories presented with equal proportions of epoxy resin models of *Mytilus edulis* (*M.e.*), *Ostrea edulis* (*O.e.*), *Crassostrea gigas* (*C.g.*) and *Cerastoderma edule* (*C.e.*). Chi-square values for goodness-of-fit tests on the number of models of each prey species that were accepted by crabs are also presented; * $p < 0.05$; ns = no significant departure from expected ratio (H_0: 1:1).

C. maenas	*M.e. - O.e.*	*M.e. - C.g.*	*O.e. - C.g.*	*M.e. - C.e.*
Encounter rates:				
40-55 mm	0.69 ns	0.04 ns	0.43 ns	4.46 *
55-70 mm	0.03 ns	1.49 ns	1.96 ns	0.07 ns
Accepted prey:				
40-55 mm	7.00 **	0.11 ns	2.46 ns	0.93 ns
55-70 mm	18.75 ***	0.03 ns	9.38 **	0.67 ns

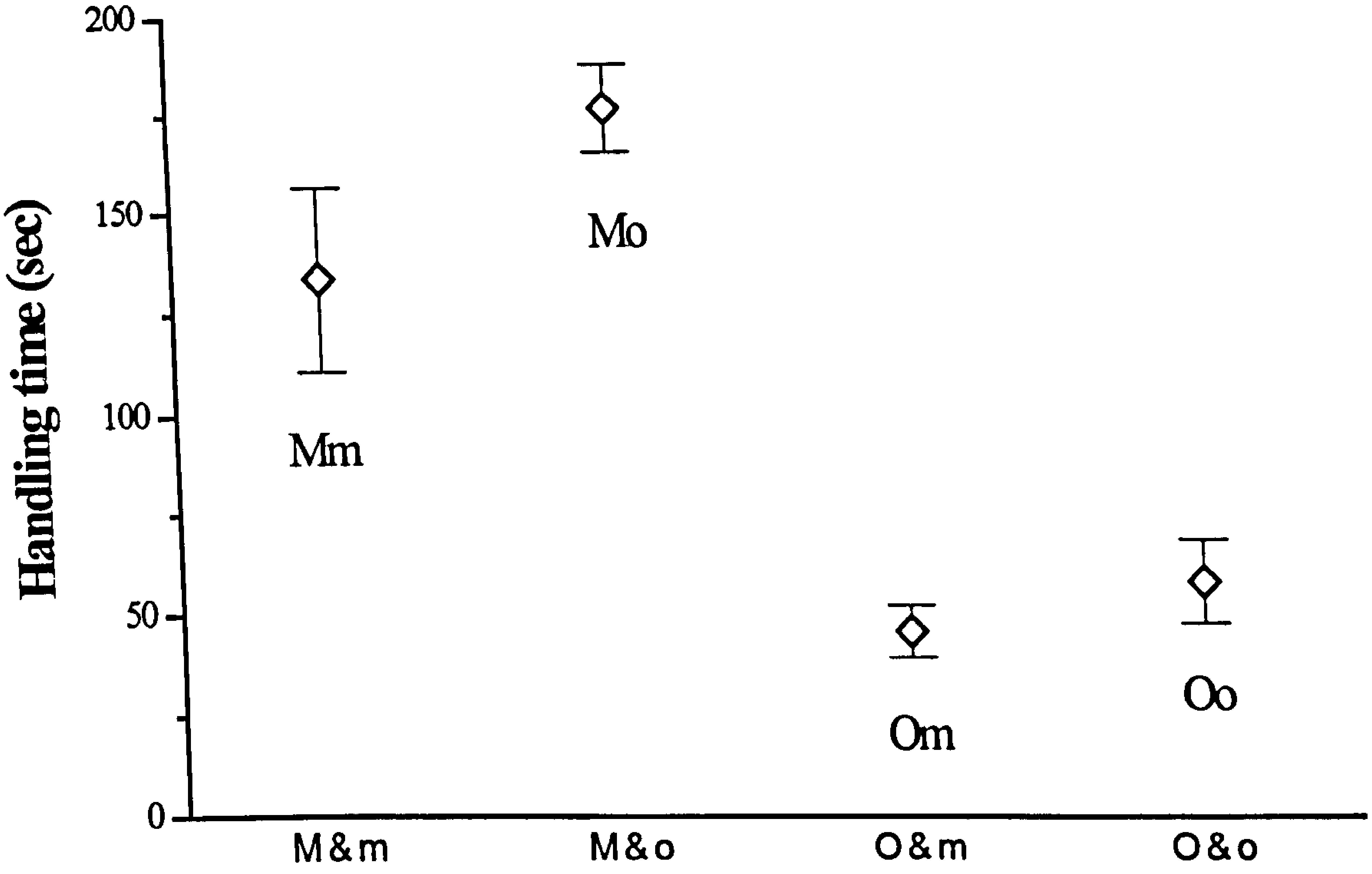

Figure 6.9. Mean handling times (sec ± se) taken by *Carcinus maenas* (50-60 mm CW) to open shells of either *Mytilus edulis* (M) or *Ostrea edulis* (O) filled with gels of either mussel (m) or oyster (o) flesh.

6.3.2. Chemical and mechanical stimuli.

When *C. maenas* (50-60 mm CW) were offered a choice between mussel and oyster agar cylinders, these were readily attacked whenever they were encountered. At the end of the experiment crabs had attacked 14 agar mussels and 13 agar oysters, and no significant differences in the number of mussel and oyster agar cylinders attacked after 10 min, 30 min and 1 h were detected (χ^2 values ranged from 0.08-0.89, all at $p > 0.05$).

Results of the experiments where *C. maenas* (50-60 mm CW) were offered mussel and oyster shells filled with either mussel or oyster gel are shown in Table 6.4. When crabs were presented with mussel shells filled with either mussel or oyster gel, they encountered both model types in similar proportions ($\chi^2 = 0.31$; $p = 0.58$). Crabs also accepted similar numbers of mussel shells filled with either type of gel ($\chi^2 = 0.20$; $p = 0.66$). When oyster shells filled with either mussel or oyster gel were offered, the encounter rates for both model types were again similar ($\chi^2 = 2.25$; $p = 0.13$), and crabs again accepted similar numbers of oyster shells filled with either type of gel ($\chi^2 = 0.15$; $p = 0.70$). Since crabs showed no apparent preference for one type of gel or another, results from experiments with different type of gel, but similar type of shell were combined. Comparisons of results between experiments with mussel shells and those with oyster shells showed that although crabs encountered significantly more oyster shells than mussel shells ($\chi^2 = 16.46$; $p < 0.001$), they accepted mussels and oysters in similar proportions ($\chi^2 = 1.13$; $p = 0.78$). Crabs, however, rejected a significantly higher proportion of oyster shells than mussel shells ($\chi^2 = 26.28$; $p < 0.001$), suggesting that in experiments with oyster shells, crabs rejected most of the models encountered.

The mean persistence times of *C. maenas* with each model type are shown in Figure 6.9. Crabs persisted a similar amount of time on mussel shells filled with either mussel gel (133.9 ± 21.5) or oyster gel (176.5 ± 10.8; $t = -1.84$; $p = 0.09$). They also persisted a similar amount of time handling oyster shells filled with either mussel gel (45.9 ± 6.5) or oyster gel (58.4 ± 10.2; $t = -1.01$; $p = 0.32$). Since persistence times with different gel types were in each case similar, results for similar types of shell were combined. Persistence times for mussel shells were significantly longer than for oyster shells regardless of the type of gel with which they had been filled ($t = 7.79$, $p < 0.001$). In

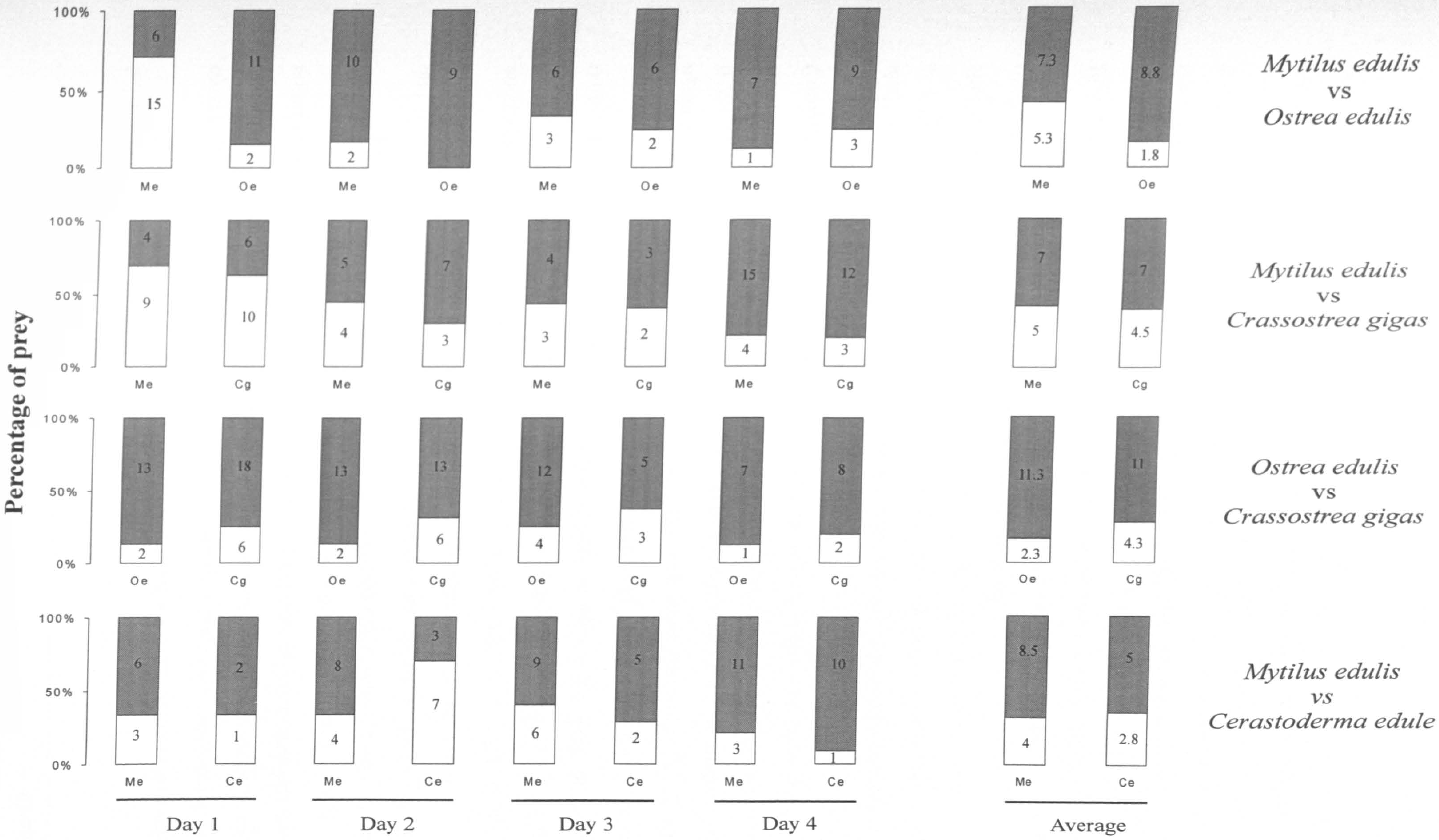

Figure 6.10. Number and percentage of inedible models of *Mytilus edulis* (Me), *Ostrea edulis* (Oe), *Crassostrea gigas* (Cg), and *Cerastoderma edule* (Ce) that were accepted (open columns) or rejected (shaded columns) by medium *Carcinus maenas* (40-55 mm CW) over a period of four consecutive days when crabs were presented with equal numbers of the preferred size classes of each model type in paired combinations. Mean values of the four days are shown separately.

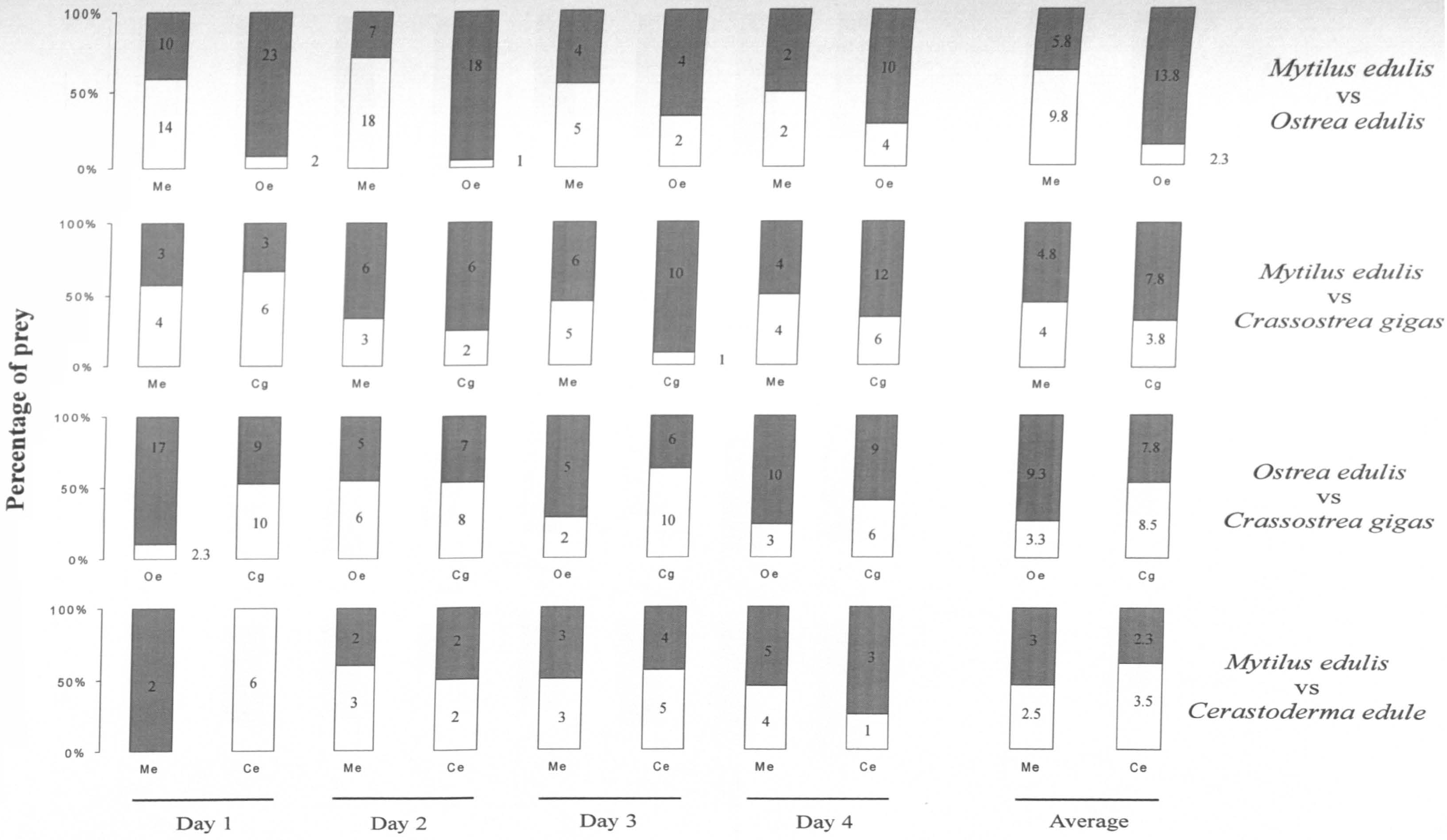

Figure 6.11. Number and percentage of inedible models of *Mytilus edulis* (Me), *Ostrea edulis* (Oe), *Crassostrea gigas* (Cg), and *Cerastoderma edule* (Ce) that were opened (open columns) or rejected (shaded columns) by large *Carcinus maenas* (55-70 mm CW) over a period of 4 consecutive days when crabs were presented with equal numbers of the preferred size ranges of each model type in paired combinations (Appendix B4). Mean values of the four days are shown separately.

summary, the results of these experiments indicate that crabs showed no preference for either mussel or oyster gel, but clearly preferred mussel shells.

6.3.3. Prey shell.

In the acceptance-rejection sequences of paired combinations of epoxy resin models of M-O, M-C, and O-C, both medium and large *C. maenas* encountered mussel and oyster models in approximately equal numbers, suggesting that encounters with mussels and oysters were directly proportional to their relative abundance (1:1; Table 6.5). In the M-E combination, however, whilst large crabs also encountered mussel and cockle models in the expected similar proportions, medium crabs encountered mussel models twice as often as they encountered cockle models ($\chi^2 = 0.89$; $p = 0.34$), even though the two model types were presented in equal proportions.

The numbers and proportions of each model type that were either accepted or rejected by medium (40-55 mm CW) and large (55-70 mm CW) *C. maenas* are shown in Figures 6.10-6.11. Differences between the numbers of rejected and accepted model types in each pair combination of prey species could only be detected at the beginning of the experimental trials (days 1-2), because towards the end of the trials (day 3 and 4), both size categories of crabs generally rejected more than they accepted prey items amongst all model types. This suggests that crabs learn that they do not obtain any reward by attempting to open the 'zero profitable' epoxy resin models. Chi-square goodness-of-fit tests on the total numbers of accepted models of each prey species, however, showed that both medium and large crabs accepted significantly more *M. edulis* than *O. edulis* models in the M-O combination (Table 6.5). However, when offered models of *M. edulis* and *C. gigas*, neither medium nor large crabs showed any significant trend to accept or reject either model type (Table 6.5). Large *C. maenas* accepted significantly more *C. gigas* than *O. edulis* models in the O-C combination, whereas medium *C. maenas* accepted *C. gigas* and *O. edulis* models in similar numbers (Table 6.5). In the M-E combination, medium crabs accepted and rejected *M. edulis* and *C. edule* models in similar proportions. However, the numbers of accepted and rejected mussels were higher than for cockles, indicating that medium crabs encountered more mussels than cockles (Figure 6.10; Table 6.5). Large crabs accepted all the cockles and rejected all the mussels encountered on the

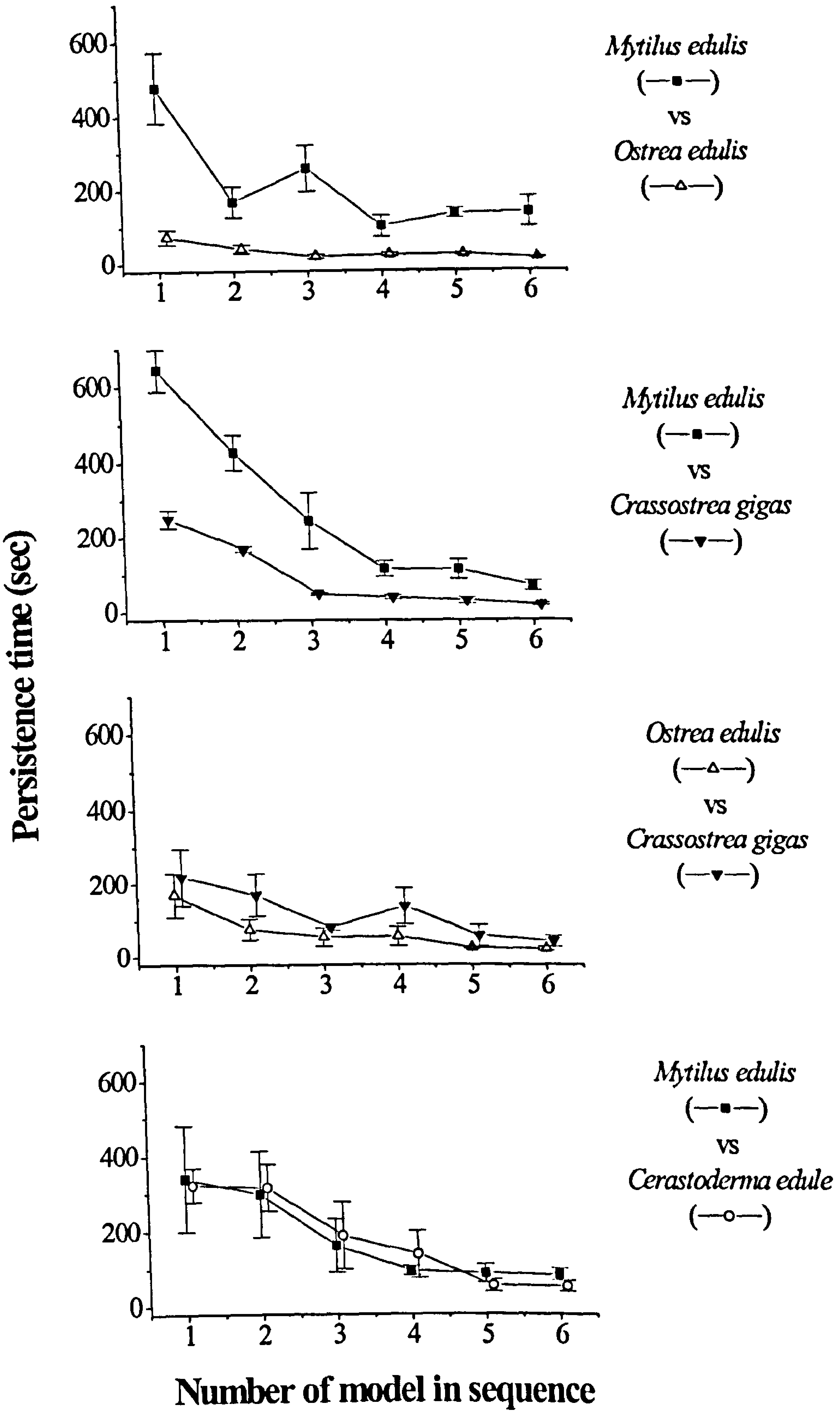

Figure 6.12. Mean persistence times (sec ± se) for inedible models of *Mytilus edulis*, *Ostrea edulis*, *Crassostrea gigas*, and *Cerastoderma edule* sequentially presented to *Carcinus maenas* of 50-60 mm CW. Models were of the size ranges preferred by crabs during experiments using single species of live prey.

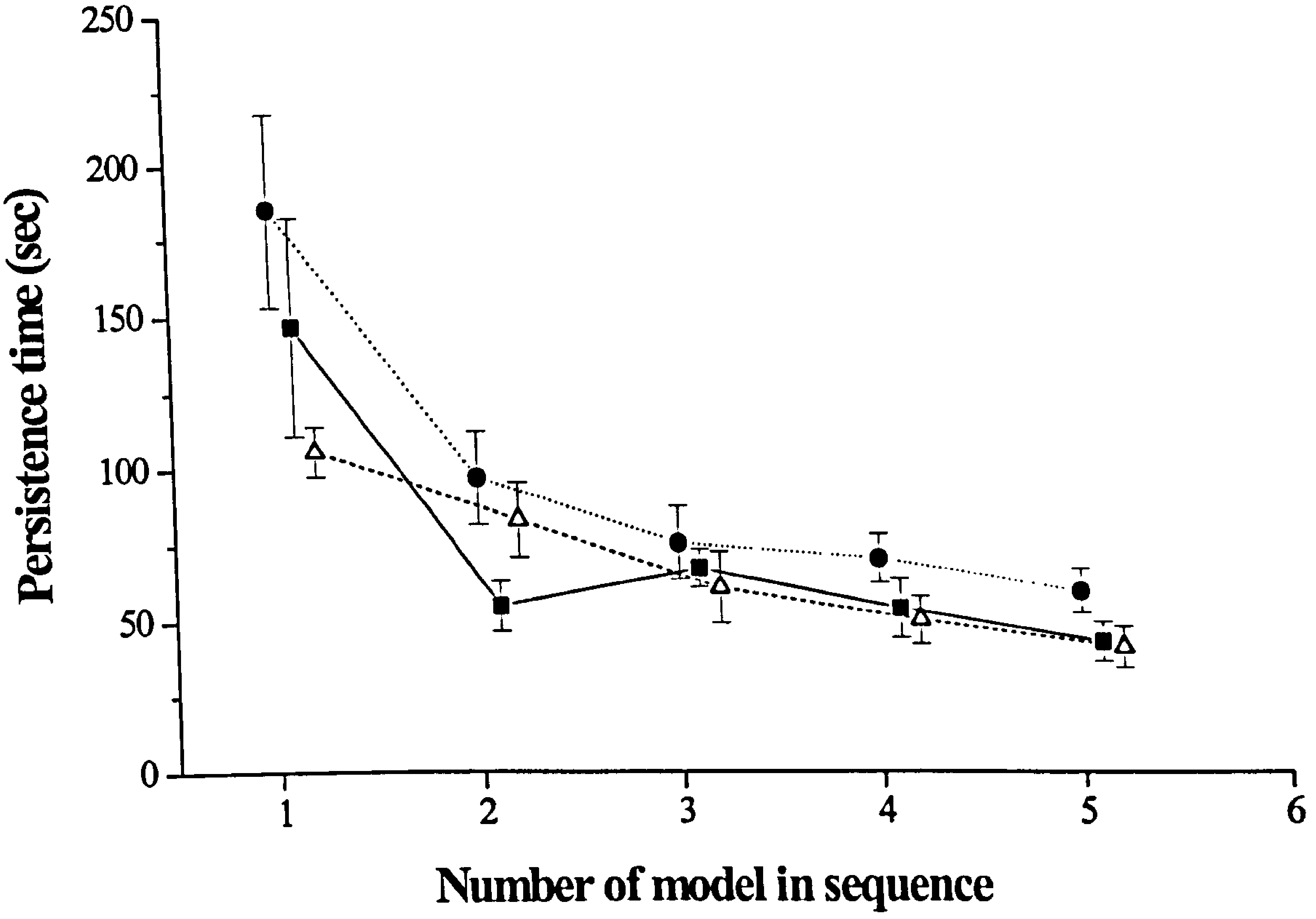

Figure 6.13. Mean persistence time (sec ± se) for inedible models of three contrasting geometric shapes that were sequentially presented to *Carcinus maenas* of 50-60 mm CW; —■— wedged rectangle, ---△--- flat disc, ·····●····· sphere.

Table 6.6. Results of ANOVA for the sequential presentation of epoxy resin models of four prey species in four combinations to four *Carcinus maenas* of 50-60 mm CW. ANOVA: Persistence time = sequence • model type (fixed factors); crab (random factor).

Mytilus edulis - Ostrea edulis

Source	*df*	SS	MS	*F*	*p*
Sequence	5	1.94387	0.38877	6.78	< 0.001
Model type	1	7.55544	7.55544	131.76	< 0.001
Sequence • Model type	5	0.38005	0.07601	1.33	0.278
Crab	3	0.32239	0.10746	1.87	0.153
Error	33	1.89235	0.05734		
Total	47	12.09411			

Mytilus edulis - Crassostrea gigas

Source	*df*	SS	MS	*F*	*p*
Sequence	5	6.79175	1.35	47.16	< 0.001
Model type	1	3.01310	3.01310	104.6	< 0.001
Sequence • Model type	5	0.08968	0.01794	0.62	0.683
Crab	3	0.31961	0.10654	3.70	0.021
Error	33	0.95057	0.02881		
Total	47	11.16471			

Ostrea edulis - Crassostrea gigas

Source	*df*	SS	MS	*F*	*p*
Sequence	5	3.23497	0.64699	13.23	< 0.001
Model type	1	0.90604	0.90604	18.53	< 0.001
Sequence • Model type	5	0.19873	0.03975	0.81	0.549
Crab	3	2.84772	0.94924	19.41	< 0.001
Error	33	1.61388	0.04891		
Total	47	8.80136			

Mytilus edulis - Cerastoderma edule

Source	*df*	SS	MS	*F*	*p*
Sequence	5	3.1709	0.6342	6.31	< 0.001
Model type	1	0.0004	0.0004	0.00	0.951
Sequence • Model type	5	0.2725	0.0545	0.54	0.743
Crab	3	0.9271	0.3090	3.07	0.041
Error	33	3.3184	0.1006		
Total	47	7.6893			

Table 6.7. Results of ANOVA for the sequential presentation of epoxy resin models of three geometric shapes offered to six individual *Carcinus maenas* (50-60 mm CW). ANOVA: Persistence time = sequence • model type (fixed factors); crab (random factor).

Source	*df*	SS	MS	*F*	*p*
Sequence	4	2.36971	0.59243	20.46	<0.001
Model type	2	0.42326	0.21163	7.31	0.001
Sequence • Model type	8	0.17461	0.02183	0.75	0.644
Crab	5	0.28896	0.05779	2.00	0.090
Error	70	2.02658	0.02895		
Total	89	5.28312			

first day of the trial, but the numbers of accepted and rejected prey items of both model types were very similar from the second day onwards, and differences between the total number of models accepted were statistically indistinguishable (Figure 6.11; Table 6.5). Overall, *M. edulis* and *C. edule* models were accepted most frequently, followed by *C. gigas*, and *O. edulis*, the latter being the models most frequently rejected.

The mean persistence times of *C. maenas* (50-60 mm CW) with each model type in each prey combination are plotted in Figure 6.12. Analysis of variance of all prey combinations (Table 6.6) showed that crabs persisted for a significantly shorter time through the sequence of the first to the last model presented (M-O: $F = 6.78$; $p < 0.001$; M-C: $F = 47.16$; $p < 0.001$; O-C: $F = 13.23$; $p < 0.001$; M-E: $F = 6.31$; $p < 0.001$). Crabs persisted significantly longer on the first model of *M. edulis* presented than on either the *O. edulis* or *C. gigas* models in the M-O and M-C combinations ($F = 131.76$; $p < 0.001$; $F = 104.60$; $p < 0.001$, respectively), and persisted significantly longer with the first *C. gigas* than on the first *O. edulis* in the O-C combination ($F = 18.53$; $p < 0.001$). However, crabs did not differ in their persistence time on the first models of either type in the M-E combination ($F < 0.01$; $p = 0.95$). The lack of a significant contribution of the interaction between the model in sequence and model type to the overall variance of the data for all prey combinations (Table 6.6) indicates that the decrease in persistence time throughout the sequence of presentation was similar regardless of the type of prey handled by crabs. Analysis of variance also showed significant differences in the persistence time between individual crabs in the M-C ($F = 3.70$; $p < 0.05$), the O-C ($F = 19.41$; $p < 0.001$), and the M-E ($F = 3.07$; $p < 0.05$) combinations. However, no significant differences were detected between the crabs in the M-O combination ($F = 1.87$; $p = 0.15$).

When *C. maenas* (50-60 mm CW) were presented with epoxy resin models of three contrasting geometric shape, persistence time decreased significantly through the sequence of models regardless of their shape (Figure 6.13; $F = 20.46$; $p < 0.001$; Table 6.7). Although the decrease in persistence time was similar for all three geometric shapes ($F = 0.75$; $p = 0.64$), crabs persisted a significantly longer time with the first sphere and wedged rectangle than with first flat disc ($F = 7.31$; $p < 0.001$). No significant differences in persistence time between individual crabs were detected ($F = 2.00$; $p = 0.09$).

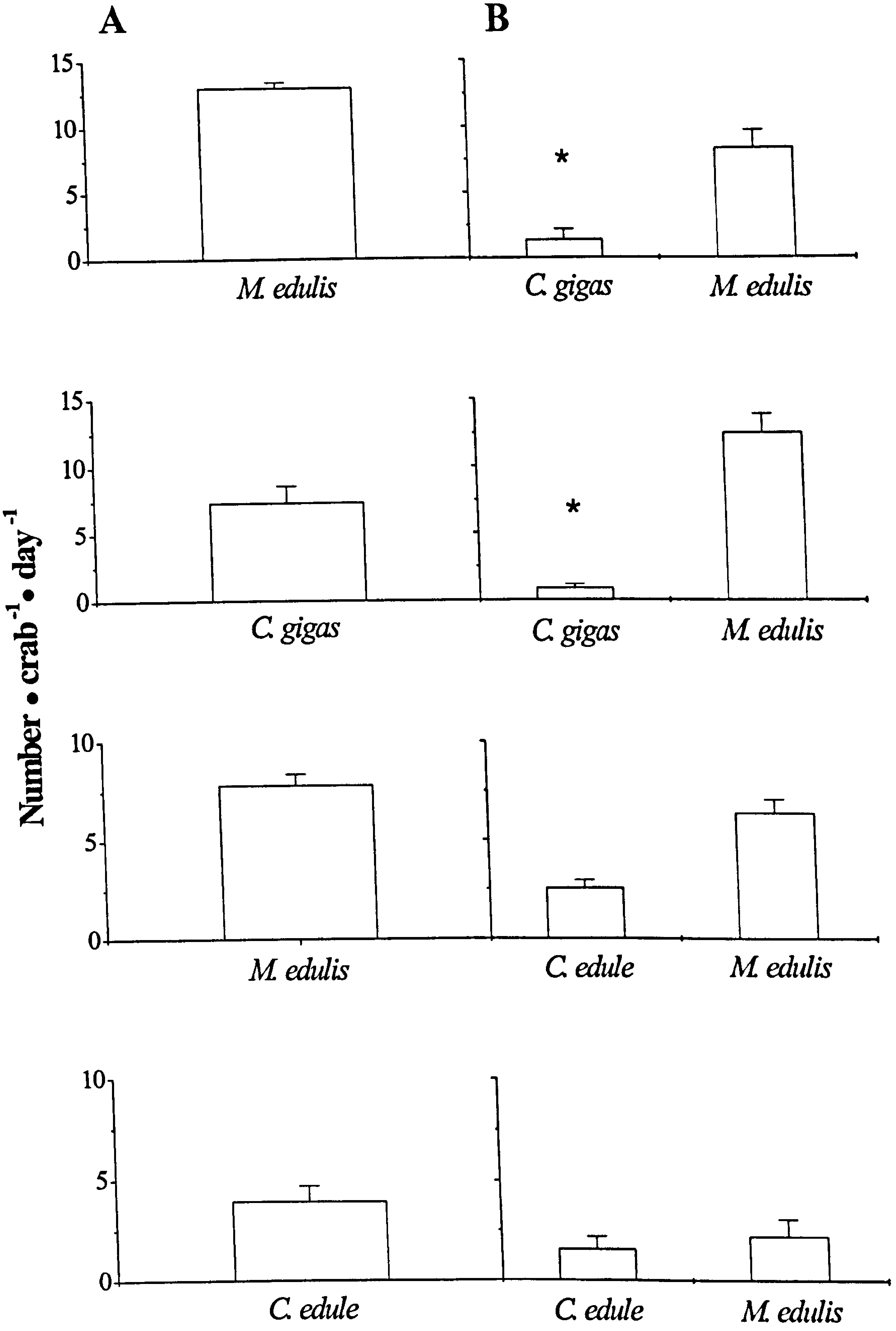

Figure 6.14. Mean number of prey (± se) consumed by *Carcinus maenas* of 60-65 mm CW after 5 days of an unlimited diet of the species shown in (A), and after 5 days of being subsequently presented with paired combinations of the species shown in (B); * denotes significant differences at $p < 0.05$

Taken overall, results of experiments with epoxy resin models indicate that crabs initially preferred those with a larger minimum dimension (i.e. models of mussels and cockles, and models in the shape of a sphere and a wedged rectangle). Persistence time, however, decreased with increasing number of models in the sequence in a similar rate regardless of model type, suggesting that shell shape does not influence the rate at which preference declines if crabs handle food items of zero profitability.

6.3.4. Learning experiments.

In experiments with mussels and cockles, the mean breaking time of 'naive' *C. maenas* (60-65 mm CW) feeding on *M. edulis* (156 ± 24 sec) and *C. edule* (56.5 ± 11 sec) was not significantly different from the mean breaking time of 'experienced' crabs (139 ± 20; $t = 1.60$; $p = 0.12$ and 71 ± 16 sec; $t = -0.76$; $p = 0.45$, respectively). In the learning experiments with *M. edulis* and *C. gigas*, no significant differences between mussel breaking times of 'naive' (64 ± 7.7 sec) and 'experienced' crabs could be detected (72.5 ± 7.8 sec, $t = -1.18$; $p = 0.24$). Curiously, however, 'naive' crabs took significantly less time to open oysters (67.9 ± 9.1 sec) than 'experienced' crabs (99.4 ± 12 sec, $t = -2.76$; $p < 0.001$).

The mean numbers of *M. edulis*, *C. gigas* and *C. edule* that were opened by *C. maenas* (60-65 mm CW) during the learning trials are shown in Figure 6.14. After crabs had experienced either mussels or cockles for a period of nine consecutive days, they did not exhibit any significant preference regardless of the species of prey to which they had been exposed ($\chi^2 = 2.82$; $p = 0.09$). However, in the trials with mussels and oysters, crabs opened significantly more mussels than oysters whether they had been exposed to *M. edulis* or *C. gigas* ($\chi^2 = 5.27$; $p < 0.05$).

Although these results do not demonstrate the acquisition of predatory skills that reduce handling time, they suggest that crab reluctance to feed on oysters is not modified by previous experience with this type of shell.

6.4. Discussion

6.4.1. Basis of prey size selection.

Selective feeding by brachyuran crabs has been extensively documented (e.g. Brown & Haight,1992; Du Preez, 1984; Hughes, 1989; Juanes, 1992; Rheinallt, 1986; Seed, 1990; Walne & Dean, 1972), and many studies have discussed their results in the framework of Optimal Foraging Theory (Hughes, 1980; Lawton & Zimmer-Faust, 1992). This theory assumes that predators are able to rank prey in the order of their dietary value, and predicts that they should select prey accordingly (Charnov, 1976; Pyke *et al.*, 1977). When crabs in the present study fed on *Mytilus edulis* and *Cerastoderma edule*, there was an optimum size of prey, above and below which profitability (= dry flesh weight per unit of handling time) decreased. The size ranges of *M. edulis* and *C. edule* selected by *Carcinus maenas* and *Cancer pagurus* of all size categories either closely corresponded to or were slightly smaller than the size ranges of prey with the highest profitability (Figures 6.2-6.5). Results similar to these have previously been demonstrated for *C. maenas* (Akumfi & Hughes, 1987; Elner & Hughes, 1978) and *C. pagurus* (Lawton, 1983) feeding on mussels, and for *C. maenas* feeding on cockles (Sanchez-Salazar *et al.*, 1987a) where crabs selected prey close to or slightly smaller than the predicted optimum size. Elner and Hughes (1978) suggested that the feeding strategy exhibited by *C. maenas* maximised net energy intake, and Sanchez-Salazar *et al.* (1987a) suggested that preference for smaller size classes of prey could reflect shorter absolute breaking times.

Profitability values in the present study, however, showed considerable variation, particularly from the preferred to the largest size ranges of prey. Since the biomass of a prey of any given shell length is approximately constant within each prey species (Chapter 4), variations in profitability are due mainly to variations in handling time, and more specifically, individual crab breaking times. Variations in breaking time of a narrow size range of prey could be due to differences in hunger levels (Hughes & Elner, 1979), or as a result of learning mechanisms developed by crabs to manipulate prey of a particular shape (Cunningham & Hughes, 1984). Age specific differences in shell strength and morphology of individual prey items (Boulding, 1984; Seed, 1980) can also influence size-related preferences (Lawton, 1983; Lin, 1990) and predation by crabs feeding on different populations of the same species (Ebling *et al.*, 1964; Elner & Raffaelli, 1980; Hughes & Elner, 1979). Variations in growth rates due to severe and varying environmental conditions especially on wave-exposed shores can result in individual *M. edulis* of similar shell length but of a different age, shell thickness and gross morphology (Seed, 1968; Seed, 1973).

A detailed examination of the present data showed that small differences in shell size, could result in large variations of handling time, suggesting that differences in the thickness and fracture resistance between individual prey items of similar linear length could account for much of the observed variation in handling time and profitability. Moreover, the patterns of variation appear to be the result of behavioural strategies that crabs present when feeding on prey that increase little in size, yet vary markedly in vulnerability. When crabs opened the smaller prey within the size range offered, breaking time was approximately constant, since the outright crushing techniques used by crabs are equally effective on small size classes of shells (Chapter 4). This resulted in short handling times and low profitability values, though they constantly increased with prey size as a result of small increments in flesh weight. When crabs attempted to open a prey item of an intermediate size, the shell would sometimes yield in a short period of time, making that prey item highly profitable due to its relatively larger biomass. However, when the shell did not yield in the first few crushing attempts, crabs took a considerably longer time to access the flesh. Microfractures in the shell that had started to break probably constituted a reinforcing cue for crabs causing them to persist on that prey item, thereby increasing handling time. Thus, prey of an intermediate, but similar shell length had extremely variable profitability values, although amongst them were the highest ones. Because flesh weight increases approximately as the cube of shell length (Chapter 4), whilst handling time increases exponentially with respect to shell length, the time taken by crabs to handle prey ultimately increased more rapidly than the biomass that crabs obtained in return. Thus, the lowest profitability values often corresponded to prey items of a larger shell length, which although offering the greatest biomass, could only be opened by crabs using more complex and time consuming handling techniques (Figures 6.2-6.5). A similar trial and error procedure by which crabs search for weak spots in the umbonal region of the shell has previously been described by Elner (1977).

It has been stated previously that the factors involved in the selective feeding behaviour of crabs, and the complex interactions between them, make the dietary value of a certain prey item variable and difficult to predict theoretically (Hughes & Seed, 1995). These results indicate that the lack of precision in predicting prey value could be due to a wide variety of factors that influence the time taken by crabs to open successfully and eat individual prey items, rather than to experimental designs that fail to measure handling time accurately. Furthermore, they support the view that size selection may be the result of a mechanical process in which all encountered prey are attacked but rejected if unbroken after a certain number of opening attempts (Elner & Raffaelli, 1980; Hughes & Elner, 1979; Lawton & Hughes, 1985). According to the latter view, the decreasing order of crab preference for different size classes of prey should reflect the decreasing order of their vulnerability to crab attack. A pattern of size selection that decreases monotonically as prey increase in size corresponds to the behavioural strategy described above, and has been reported for several brachyuran crabs feeding on a variety of molluscan prey (e.g. Davidson, 1986; Juanes & Hartwick, 1990; Pearson *et al.*, 1981; Seed, 1982). In addition, authors have suggested that selection of small size classes of hard-shelled prey can minimise handling time (Hughes & Seed, 1981; Seed, 1986a) as well as the risk of claw damage (Juanes & Hartwick, 1990), increasing the possibility of survivorship of foraging crabs that may themselves be subject to predation (see also Sih, 1980). In the present study, however, large *C. maenas* selected intermediate size classes of *M. edulis*, and small-medium *C. pagurus* selected intermediate size classes of *Crassostrea gigas*. According to previous reports (e.g. Elner & Hughes, 1978; Lawton, 1983; Rheinallt, 1986), larger prey may be less preferred because of their robustness to crab attack, whilst the smallest size classes of prey are less preferred simply because they are encountered less frequently, misidentified amongst shell debris, or frequently dropped. This latter would be particularly true for crabs with large, somewhat clumsy chelae that do not allow for efficient manipulation of small prey (Elner & Lavoi, 1983; Rheinallt & Hughes, 1985). Although the present work did not include experiments which presented crabs with altered proportions of different size classes of prey, observations during handling time experiments showed that large crabs often had difficulty encountering, identifying, and grasping small prey items within their chelae.

Furthermore, when prey items were spread over bare aquaria floors, crabs could consume prey over a wide size range (Elner & Hughes, 1978), but more realistic laboratory conditions have shown that group living in mussels (Bertness & Grosholz, 1985; Lin, 1990), or deep burial of infaunal prey in soft substratum (Blundon & Kennedy, 1982b) can considerably enhance prey survivorship. Work on the blue crab, *Callinectes sapidus*, feeding on the marsh mussel, *Geukensia demissa*, showed that crabs did not actively search for juvenile mussels when these were located in the centre of the mussel clumps, and smaller items were consumed only as by-products when crabs preyed upon adult mussels to which juveniles where attached (Lin, 1991). Present results emphasise the passive nature of size-selective feeding in both *C. pagurus* and *C. maenas*, and further support the findings of previous studies on the foraging tactics used by these species of crabs (e.g. Lawton, 1983; Lawton & Hughes, 1985 for *C. pagurus*; and Elner & Raffaelli, 1980; Hughes & Elner, 1979 for *C. maenas*). Since diets in which crabs selected both the smallest and the intermediate sized items corresponded approximately to those predicted by optimal foraging theory, this behavioural strategy probably maximises feeding efficiency.

Despite the variability in handling time, results show that profitability curves varied with the species of bivalve on which crabs were being fed. Crabs abandoned large cockles more frequently than large mussels, reflecting the greater difficulty in successfully attacking large cockles with methods other than crushing (Chapter 4). Differences between the patterns of cockle and mussel size selection described in Chapter 5 further support this idea, since crab preference for cockles decreased more abruptly as cockles than as mussels increased in shell length, and crabs always preferred smaller size classes of cockles than of mussels. The more convex, thicker shell of cockles is probably less vulnerable to crab crushing than the more elongate shell in mussels, particularly amongst the larger size classes of prey where differences in shell width are greater (Chapter 4). These results accord with those previously reported by Sanchez-Salazar *et al.* (1987a), who attributed differences in the size selection of *M. edulis* and *C. edule* to variations in shell morphology and strength per unit length between these two bivalve species. These authors showed that the shell dimensions of cockles that could be opened by crabs of a given chelal strength were less, but the energy obtained was greater, than when feeding on mussels.

Accordingly, they suggested that crabs could obtain better yields by consuming cockles than mussels of a smaller linear size. In the present study, profitability values for adult *C. maenas* feeding on cockles were overall higher than when feeding on mussels (Figures 6.2 & 6.5). However, the selected size classes of both prey species yielded similar biomass per unit time for all but the smallest crabs (Table 6.2), suggesting that differences between the linear size of cockles and mussels preferred by adult *C. maenas* were large enough so that differences between biomass, handling time, and hence prey value were negligible (Figure 6.7). These results further emphasise the importance of shell shape in determining the vulnerability of different prey species, and suggest that prey species can be transposed in their value to predators depending on their size and relative abundance (Boulding & Hay, 1984; Elner & Hughes, 1978; Hughes & Elner, 1979), especially when one considers the wide diversity of prey types to which crabs are exposed in their natural environments (Lake *et al.*, 1987).

Variability in handling time and profitability, was even more pronounced amongst crabs feeding on *Ostrea edulis* and *C. gigas* (Figures 6.3-6.4). Although profitability curves could be obtained for crabs in most size categories, the size ranges of *O. edulis* and *C. gigas*, at which profitability attained its highest values, were not so clearly delimited. The precise orientation of the shell within the chelae when force is first applied might have further influenced oyster handling time, probably as a result of their irregular shell shape and resistance at different points of the shell, as well as, the greater variability in the handling methods used by crabs to open oysters (Chapter 4). Furthermore, large variations in oyster profitability might explain the size-related preferences of crabs feeding on these bivalve species. Adult *C. maenas* and small-medium *C. pagurus* did not show any size-related preference when feeding on *O. edulis*, whereas juvenile *C. maenas* and small *C. pagurus* selected the smallest size classes of flat oysters offered, and never included oysters > 15 and > 10 mm SL, respectively (Chapter 5). If crabs attempted to open oysters as they encountered them, rejecting those that would not yield to the first few crushing attempts, then the size classes of *O. edulis* selected would be those that took the least time to open. The smaller crabs of both species selected only the smallest *O. edulis*, probably because their more narrow chelal gapes did not allow for easy manipulation and efficient crushing of the higher shells of flat oysters > 15 mm (Chapters 4 & 5). Indeed the highest profitability values of *O. edulis* were always obtained when juvenile *C. maenas* and small *C. pagurus* fed on prey < 15 and < 10 mm SL, respectively. Crabs with larger chelal gapes, on the other hand, could more easily manipulate *O. edulis* from all the size classes offered (Chapter 4), thus probably explaining the more uniform distributions found in both the profitability values and the size selection of flat oyster obtained for the larger size categories of crabs (Chapter 5).

During size-selection experiments with *C. gigas*, small, small-medium, and medium *C. maenas* also selected the smallest individuals. Large *C. maenas* and small *C. pagurus* consumed *C. gigas* of all size classes in similar numbers, whereas small-medium *C. pagurus* preferred intermediate size classes of *C. gigas*. Crabs in all size categories, however, were able to open oysters of all the size range offered (Chapter 5). The profitability values obtained for these crabs were highly variable, probably reflecting a greater variation in Pacific oyster vulnerability. A feeding strategy which involves accepting or rejecting oysters in the order in which they yield to attack would eventually result in the patterns of size selection observed for *C. gigas*, since larger and/or stronger crabs can more readily open a wider size range of prey than smaller and/or weaker ones.

Previous studies comparing prey size selection between crabs of different carapace width have frequently reported that the preferred size classes of prey increase as crabs increase in size (e.g. Chilton & Bull, 1986; Kaiser *et al.*, 1990; Lee & Seed, 1992; Whetstone & Eversole, 1981). These authors have explained their findings in terms of increased strength of larger crabs and their ability to open a wider size range of prey. Similarly, previous reports on the feeding preferences of several brachyuran crabs have shown that variations in prey size selection amongst crabs of different species but similar carapace width could be related to differences in chelal morphology and occlusive geometry (e.g. Bisker & Castagna, 1987; Seed & Hughes, 1995; Lake *et al.*, 1987; Rheinallt & Hughes, 1985; Whetstone & Eversole, 1981). The master chela in *C. maenas* is at a lower mechanical advantage than the monomorphic chelae in *C. pagurus* (Chapter 3; Warner & Jones, 1976), allowing edible crabs to exert greater compressive forces than shore crabs of comparable body size (Lawton, 1983).

Differences in the foraging strategies between crab species are partly determined by specific morphological features of the mouthparts and chelipeds, but can also be related to differences in behavioural adaptations (e.g. adaptations to swimming or burrowing) that influence crab preference for certain foraging areas (Sponaugle & Lawton, 1990). Monomorphic crabs from the genus *Cancer* are typically burrowing species (Brown & Bennett, 1980; Hall *et al.*, 1993; Howard, 1982), with a general retiring, relatively quiescent, habit (Chapter 4; Lawton, 1983), and have been reported to persist with prey for up to several hours, even when alternative items were available (Lawton & Hughes, 1985). *C. maenas*, like other portunids, is a tidally migrating species, which explores and forages actively on the shore (Hunter & Naylor, 1993; Naylor, 1958), and readily replaces prey that have not quickly yielded. An active exploring behaviour might increase the probability of *C. maenas* to encounter and attempt to open a wider diversity of prey types, whereas the more sedentary and tenacious nature of *C. pagurus* might confine crabs to persevere in attacking prey in their immediate surroundings. Moreover, a comparison between the foraging efficiency of *C. maenas* and *C. pagurus* suggested that the voracious feeding behaviour exhibited by *C. maenas* could be due to their relative inefficiency as predators, since the rate of energy return obtained by shore crabs was below that obtained by edible crabs (Lawton, 1983). Differences between the profitability obtained by *C. maenas* and *C. pagurus* feeding on *M. edulis*, *C. edule*, and *C. gigas* in the present study confirm this view, and help to explain differences between the patterns of size selection of prey species whose shell shape makes crushing resistance an important factor in determining its vulnerability to crab attack. However, profitability was similar for both crab species feeding on *O. edulis*, probably because the higher shell of this prey species constitutes a shape-related restriction making flat oysters equally unprofitable for both the relatively stronger *C. pagurus* and the more voracious *C. maenas*.

6.4.2. Basis of prey species selection.

Whilst prey size selection by *C. maenas* and *C. pagurus* appears to be based on mechanisms that minimise handling time, crab selection amongst the preferred size classes of each prey species seems to be more strongly associated with differences in prey value. Comparisons between mean profitability of the preferred size ranges of each prey species showed that crabs in all but the smallest size categories obtained similar profitabilities when consuming *M. edulis* and *C. edule*, and obtained higher profitabilities when consuming mussels and cockles rather than *O. edulis* or *C. gigas* (Table 6.2). The rank order of prey profitability clearly paralleled the order in which prey species were ranked according to consumption rates during single prey species experiments (Figures 6.6-6.8), providing a first indication that prey value could influence crab selection regarding these four bivalve species. Results from prey species selection experiments described in Chapter 5 further supported this idea, since *C. maenas* of 25-70 mm and *C. pagurus* of 30-40 mm CW selected mussels over oysters, and did not show any feeding preferences either between mussels and cockles, or between the two oyster species. Previous studies have suggested that some brachyuran crabs are capable of exhibiting a flexible foraging behaviour, allowing crabs to maximise their feeding efficiency (Creswell & McLay, 1990; Micheli, 1995). For example, when offered a variety of prey sizes, *Cancer novaezelandiae* selected those items that minimised foraging time, but when presented with four different molluscan species, crabs maximised their energy intake by choosing the optimum prey species (Creswell & McLay, 1990).

Differences in shell shape and thickness determine prey vulnerability, and hence breaking times, and are therefore expected to influence prey value (Elner & Raffaelli, 1980; Griffiths & Seiderer, 1980). Comparisons between breaking times in the present study showed that crabs generally spent increasingly more time opening prey through the sequence *C. edule* → *M. edulis* → *O. edulis* → *C. gigas*. However, statistical differences in pairwise comparisons of prey breaking times were generally not significant (Table 6.3), suggesting that the four bivalves were opened in approximately similar times, and only differences between extreme values were able to be detected (Appendix C2). Conversely, comparisons between the increment of dry flesh weight with respect to shell length in *M. edulis*, *C. edule*, *O. edulis*, and *C. gigas* revealed that amongst prey of the size ranges used during feeding trials, the biomass in mussels and cockles is similar, but significantly greater than the biomass in both oyster species (Chapter 4). These results indicate that differences in profitability between the selected size ranges of prey were mainly due to differences in their biomass. Nonetheless, there is sufficient evidence to suggest that differences in vulnerability, and hence breaking times could also have influenced the position of prey species as ranked in their value to crabs. For example, a combination of short breaking times and high flesh content as in *C. edule* might have further raised its value to larger crabs.

It is interesting to note that shell shape was also related to dry flesh weight, since the relatively flatter oyster species had significantly less biomass than the more voluminous shells of cockles and mussels (Chapter 4). Moreover, observations of crab handling techniques indicated that both *C. maenas* and *C. pagurus* had more difficulty grasping the relatively higher, flatter, and more irregular shell of *O. edulis* than those of mussels and cockles (Chapter 4), whose more globular shells fitted within the chelae in a position that allowed the predator to exert a greater compressive force. These observations support the view that variations in shell shape and strength are closely associated with the way crabs manipulate prey which in turn can influence handling techniques, and might therefore constitute an important factor determining crab preference for certain prey species (Boulding, 1984; Sanchez-Salazar *et al.*, 1987).

When the feeding behaviour of the smallest size categories of crabs is examined, however, prey value did not always parallel the consumption rates of the preferred size classes of the four prey species. Whilst *C. maenas* of 15-25 mm CW and *C. pagurus* of 20-30 mm CW selected mussels and oysters as predicted by their ranked profitabilities (Chapter 5), small crabs obtained a significantly higher profitability when feeding on the preferred size classes of *M. edulis* than on *C. edule* (Table 6.2), but consumed mussels and cockles in similar rates (Figures 6.6 & 6.8; Chapter 5). Since both small *C. maenas* and *C. pagurus* selected similar size classes of *M. edulis* (2-8 mm and 4-8 mm SL) and *C. edule* (2-4 mm and 2-6 mm SL, respectively), and mussel and cockle breaking times were not statistically different for the smallest crabs of both species (Table 6.3), a strategy of prey species selection based solely on prey value or time minimisation fails to explain entirely these results. Variation in crab strength relative to size can result in the size range of prey that is accessible to larger, and hence stronger, crabs to be greater than for smaller and weaker ones (Lee & Seed, 1992; Elner, 1980). *C. maenas* > 25 mm CW actively forage up and down the shore during high tide (Dare & Edwards, 1976, 1981; Naylor, 1962). Most shore crabs < 20 mm, however, tend to be sedentary and do not make these tidal migrations (Dare *et al.*, 1983). Food restrictions and the risk of predation are probably most severe for smaller crabs, whose already limited food resources are depleted by larger individuals (Lawton, 1989; Ropes, 1968; Klein-Breteler, 1975a). That the smallest crabs consumed *M. edulis* and *C. edule* in similar numbers despite the lower profitability of the latter, might be explained by the need to gain sufficient energy in the least time possible in order to satisfy their metabolic requirements and escape predation by larger crabs of the same or other species.

The dietary value of a prey item can be influenced by the crab's physiological condition (i.e. age, hunger level, reproductive and moulting stage, etc.), and previous feeding experience (Cunningham & Hughes, 1984; Jubb *et al.*, 1983). Results in the present study suggest that the degree of crab selectivity amongst different species of bivalves can be much lower in smaller than in larger crabs probably as a result of the restrictions imposed on small individuals that have limited access to larger prey items. The reasons why small crabs excluded oysters from their diets, however, remain unexplained. Differences in shell shape associated to the difficulty in handling the relatively flatter oyster species, and the ability to learn to identify more rewarding prey might explain the reluctance of even the smallest crabs to consume *O. edulis* and *C. gigas* throughout these and other (Dare *et al.*, 1983; Richardson *et al.*, 1993) experiments.

Patterns of prey selection are the result of a sequence of specific behavioural components that a predator performs during a predation event, including the location, attack, capture or attack success and ingestion of prey (Hughes, 1980). Feeding preferences can be partially attributable to mechanistic consequences of physical properties in a predator-prey system which determine encounter rates and prey vulnerability (Hughes, 1980; Rodrigues *et al*, 1987; Sponaugle & Lawton, 1990). However, decisions by predators on whether to attack an encountered prey item or continue searching, or to reject or accept a prey item that is being manipulated are still the result of an active choice (Barbeau & Scheibling, 1994a; Ibrahim & Huntingford, 1989; Sih & Moore, 1990). Extrinsic factors, such as hunger, experience, and stimuli from alternative prey can modify predator selectivity, thus affecting these decisions (Croy & Hughes, 1991a; Hughes, 1979; Jubb *et al.*, 1983; Kislalioglu & Gibson, 1976). Nevertheless, intrinsic factors such as the information gained by manipulating the prey in chelae and mouthparts are crucial in deciding whether to continue or abort an attack (Akumfi & Hughes, 1987; Cunningham, 1983; Elner, 1978; Kaiser *et al.*, 1993). In the present work, species-related preferences exhibited by crabs feeding on prey near the optimal size suggest that active selection might have taken place at some point in the predation cycle, and that this selection was related to the amount of dry flesh weight gained per unit of handling time. For crabs to be able to rank prey in the order of their profitability, mechanisms must exist by which crabs are able to recognise prey characteristics which are correlated with their potential value. A series of experiments testing the importance of shell shape, volume and flesh odour/flavour in prey species selection investigated which of these characteristics mainly determined the recognition of potentially profitable prey and these will now be discussed.

Effects of flesh odour or flavour

Decapod crustaceans are highly sensitive to chemical substances in solution (Case, 1964; Derby & Atema, 1982a). Chemoreceptors on the first pair of antennae can detect stimuli by olfaction at a distance (Hirtle & Mann, 1978; Zimmer-Faust, 1989), whereas receptors on the tips of the legs and mouthparts are able to taste the prey when this is directly encountered by the crab (Ache, 1982; Laverack, 1963). Chemical substances, such as amino acids can be readily differentiated by *C. maenas* during both searching (Shelton & Mackie, 1971) and feeding phases (Case & Gwilliam, 1961). Results showed that crabs were not attracted any more often to gel cylinders made from mussel-flesh filtrate then to those containing oyster-flesh filtrate (see page 118). Crabs attacked both types of cylinders whenever these were encountered and this behaviour persisted throughout the duration of the trials, suggesting that preference for either type of odours/flavours was not modified after crabs had experienced the gels.

A study on the factors affecting diet selection in *C. maenas* demonstrated that shore crabs are sensitive to different concentrations of mussel flesh filtrate, and suggested that, despite dilution effects, crabs may be able to distinguish mussels of varying quality by responding to odour (Kaiser *et al.*, 1993). In addition, these authors indicated that olfactory stimuli had a reinforcing effect on crab preference, since crabs readily picked up and manipulated both models with and without mussel filtrate, but more quickly rejected those models that did not incorporate the chemical stimulus. Present experiments did not include any examination of different concentrations of flesh filtrate, but results strongly suggest that decisions by crabs on whether to attack or reject oysters were not influenced by the odour or flavour of their flesh (Table 6.2; Figure 6.9). Consequently, both mussel and oyster flesh filtrates had a similar reinforcing effect on the perseverance to open prey, since crabs appeared to be equally stimulated (i.e. antennular and maxilliped activity increased, prey were rotated more rapidly within the chelae, and crabs tore off pieces of shell with increased tenacity and effectiveness) when models had started to crack and the gel was broken down by chelae and mouthparts. These results provide further evidence of the reinforcing effect of olfactory and taste stimuli, and comparisons with previous reports suggest that the concentration, rather than the specific chemical composition, of flesh might be involved in prey attractiveness to crabs and other crustaceans (Crisp, 1967; Shelton & Mackie, 1971). By contrast, results suggest that certain characteristics in the shells of *M. edulis* and *O. edulis* might provide mechanical stimuli which influence decisions by crabs to both initially attack and to persist with prey that is already being manipulated (Figure 6.9).

Effects of shell shape and volume

When attacking hard-bodied, resistant prey, crabs show relatively stereotyped patterns of behaviour (Chapter 4; see also Cunningham, 1983; Heller, 1976; Lau, 1987; Shoup, 1968; Seed, 1993), but details of this behaviour can be influenced by specific morphological characteristics in prey of different size (Elner & Hughes, 1978). Over a narrow range of prey sizes, however, shape assumes a relatively stronger influence on the handling process (Boulding, 1984; Griffiths & Seiderer, 1990; Lawton & Hughes, 1985), and information gained by crabs while revolving prey with the chelae and mouthparts can be crucial in deciding whether to continue or abort an attack (Akumfi & Hughes, 1987). In experiments where adult *C. maenas* were offered paired combinations of model species of zero profitability, crabs exhibited species selective behaviour only at the beginning of trials. On days 1 and 2, both medium and large crabs attempted to open a greater number and proportion of *M. edulis* and *C. gigas* models when either prey type was offered in combination with *O. edulis*. In addition, when offered a sequence of five models of each type, crabs persisted longer with the first model of a mussel than with the first model of oysters, and they also persisted longer with the first model of a Pacific oyster than with a flat oyster. These results suggest that the initial reluctance of crabs to attack flat oysters, and the propensity to attack mussels, are not associated with differences in the ultimate energetic reward, but could be based on an evaluation of the overall shape and/or volume of the shells of these bivalves during a first recognition phase.

Experiments with bivalve shells filled with epoxy resin were carried out by presenting crabs with the preferred size classes of each prey species. Results, therefore, do not take into account differences in volume between the models offered. Further investigation of the importance of shell volume in species-selection by crabs, showed that when all models were of similar volume, *C. maenas* persisted much longer with the first models that resembled both the shape of a cockle (sphere) and a mussel (wedged rectangle) than with the first model that resembled a flat oyster (disc). These results suggest that amongst prey of similar volume, contrasting differences in shell shape can significantly influence crab persistence, and hence subsequent prey selection. Moreover, the resin models used had a similar maximum length, but differed in maximum height and width. If crabs evaluate shell volume on the basis of shell width rather than length, they would be expected to persist longer on those with the greatest shell width. Since measures of volume of the four bivalve species were not recorded, it could not be established whether shell width was more strongly correlated to volume than shell length. However, a strong association between shell width and volume was indicated by the significantly greater increase in shell width as cockles and mussels rather than, as flat oysters increase in shell length, and by flat oysters having significantly less flesh weight than both mussels and cockles of comparable shell length (Chapter 4). Furthermore, both *C. edule* and *M. edulis* were included in crab diets much more frequently than *O. edulis* throughout the experiments (Chapter 5), and adult *C. maenas* obtained the highest profitabilities when feeding on cockles and mussels (Figures 6.2-6.5). These results suggest that shell width constitutes an important morphological characteristic, which crabs might be able to recognise and associate with potential prey value.

Previous works have reported that the minimum dimension of the shell is an important characteristic determining prey size and species selection in crabs (Boulding, 1984) and other decapods (Griffiths & Seiderer, 1980). In experiments where *C. maenas* was presented with Perspex models of different shape and size, Kaiser *et al.* (1993) found that changes in the length of models had little influence on handling time since mechanical efficiency of the chelae was determined by the cross-sectional profile of the prey. These authors further suggested that those models which more closely resembled the shape of a mussel (tapered rectangle) allowed the chelae to work with greatest mechanical advantage and improved handling efficiency. Furthermore, the relative prey size (RPS = shell width /chelal height) preferred by crabs in each prey species consistently had a value of < 1, suggesting that the position in which the width of the shell fitted within the chelae assumed a great importance in determining attack success of the preferred size classes of prey. The flat disc model had a slightly smaller width, but had a much greater height than the wedged rectangle, suggesting that crabs did not persist with the flat disc as long as with the wedged rectangle probably because a large absolute height can reduce handling efficiency (see also Griffiths & Seiderer, 1980).

Foraging decisions by crabs based on shell characteristics associated with volume (i.e. shell width) might explain the patterns of species selection by *C. maenas* observed in the present study. The observed similarity in crab preference for *M. edulis* and *C. edule*, might be the result of the similarity in the volumes of the (different) size classes of both prey species that were selected. When crabs were offered similar size classes of *M. edulis* and *O. edulis*, they preferentially consumed mussels probably as a consequence of the differences in volume between the (similar) size classes of prey presented.

Effects of learning

The absence of significant differences between breaking times before and after crabs had experienced a particular species of live prey suggested that handling efficiency was not improved after a period of five days. Cunningham and Hughes (1984) presented data showing that mean breaking times taken by *C. maenas* to open individual *M. edulis* and *Nucella lapillus* could decrease to up to 30 % of the initial value after 5 to 6 mussels and dogwhelks had been eaten. According to these authors, skills were gained only within 1 or 2 h but were lost at a much slower rate. Results in the present study do not contradict these findings, since comparisons were performed between mean breaking times calculated for all the items eaten within the four days prior to and following the period of exposure to prey. Thus, if crabs acquired predatory skills, they probably did so within the first two days of the trials, and differences between breaking times before and after the period of exposure to prey could not be detected. In addition, improvement in handling efficiency after these relatively long periods of time was probably not detected, because the size classes of prey used for learning trials were those selected by crabs during single prey species experiments. If the preferred size classes of prey were those that yielded in the least time, handling efficiency was probably near to its maximum, and differences in breaking times amongst these size classes of prey were more strongly influenced by variations in individual hunger levels or prey vulnerability than by an increased effectiveness in attack methods.

That oyster breaking times were actually longer after, rather than before, the period of exposure to this prey species might partially be explained by a lack of hunger in crabs that had been constantly feeding during five consecutive days. However, breaking times for mussels and cockles did not increase in a similar way. In addition, experiments showed that previous exposure to either *M. edulis* or *C. edule* did not appear to affect selection between these bivalves, since crabs exposed to either prey species continued to consume both species in approximately equal numbers (Figure 6.14). All crabs, however, consumed significantly more mussels than oysters irrespective of whether they had been exposed to *M. edulis* or *C. gigas*. These results indicate that crab reluctance to feed on *C. gigas* was not modified by continuous exposure to this species. Moreover, they suggest that this reluctance might be related to the low efficiency with which oysters were handled even after crabs had experienced them during five consecutive days. *C. gigas* possesses an irregularly shaped shell associated with a high degree of variability in strength, fracture resistance and vulnerability (Dare *et al.*, 1983; Yamada *et al.*, 1993). These characteristics probably make the value of *C. gigas* to crabs highly unpredictable (Figure 6.4). In addition, if crab attacks on *C. gigas*, when successful, only yielded a low amount of dry flesh weight per unit of handling time (Table 6.2), it is reasonable to suggest that crabs learn to avoid oysters, particularly if mussels of a higher and more predictable profitability are available.

Previous studies have shown that encounters with alternating prey of different and unpredictable value can retard crab learning, since encounters with less profitable prey can raise handling time for the next prey item (Cunningham & Hughes, 1984). Furthermore, these studies have reported that learning by crabs can affect the profitability of a prey species which can become transposed if eaten in rapid succession during a foraging bout (Cunningham & Hughes, 1984). Results obtained during the present study do not provide sufficient evidence to suggest that crabs acquire skills that make handling of either mussels or cockles more efficient. However, they do suggest that the presence of an irregular shell associated with unpredictable profitability in *C. gigas*, might impede the acquisition of skills by crabs that consumed this oyster species in small numbers even when it was presented alone. A method of prey value assessment in which crabs base predictions on recent, rather than on more distant, experience (Akumfi & Hughes, 1987), might help to explain the subsequent preference of crabs for mussels as soon as they become available. Studying the effect of experience on the selection of shells by the hermit crab, *Calcinus tibicen*, Hazlett (1992) found that larger crabs, which had a longer experience with natural shell availability, were not as readily influenced by 1-week exposure to laboratory conditioning as smaller, younger crabs. Whether the rate of learning to manipulate and successfully attack bivalve prey is higher amongst younger *C. maenas*, that have not yet been under prolonged natural conditions of prey availability, is a question that remains unanswered, and constitutes an interesting topic for future research.

When *C. maenas* were presented with a sequence of several models of zero profitability, they became less selective and reluctant to attempt any further attacks on any model type (Figure 6.12). These results provide evidence to support that, despite intermittent stimuli from edible items, crabs may eventually learn to avoid items that do not provide an energetic reward (Kaiser *et al.*, 1993). Since models and live prey did not differ significantly in their total wet weight, results suggest that crabs learned to disregard prey when they do not get any energetic reward. Furthermore, the similarity in the decrease of persistence times regardless of the model type suggests that learning rates are independent of shell shape or volume when the profitability of the items is zero. Results of the learning trials, however, did not outrule the possibility that differences in shell morphology amongst live prey could influence the acquisition of predatory skills. The apparent disparity between these results might be explained if the amount of flesh obtained in return acts as a reinforcing factor of the skills learned by crabs through experience, rather than a factor directly involved in the initial decision to attack prey types that have

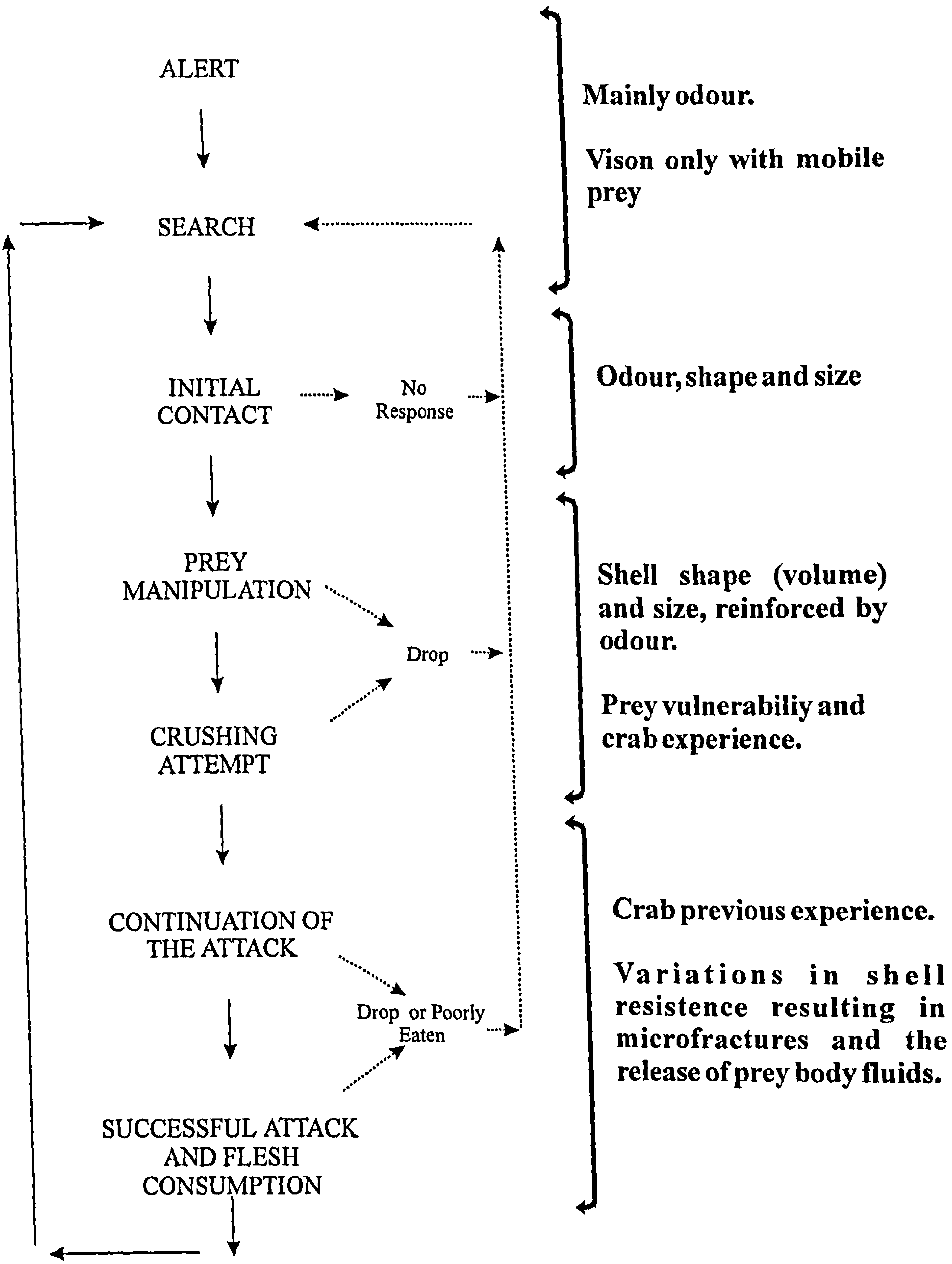

Figure 6.15. Diagram of the behavioural sequence of *Carcinus maenas* when feeding on hard-shelled prey, showing the most important factors affecting foraging decisions at various moments in the predation cycle.

not been previously experienced. If crabs are capable of increasing their handling efficiency on a particular prey type, and obtain flesh in return, then they should continue to select, whether actively or not, those prey items whose characteristics improved prey profitability. If, on the other hand, crabs do not obtain an energetic reward regardless of the different shell types experienced, any shell characteristic that could have been associated with prey value loses its significance, and crabs learn to avoid all shell types at a similar rate.

Although some portunids can use vision to locate their prey (Seed & Hughes, 1997; Rheinallt & Hughes, 1985; Hughes & Seed, 1981), shore crabs are essentially non-visual predators. This makes olfactory stimuli the predominant factor directing crabs towards potential prey (Barber, 1961). Although different concentrations of chemical compounds elicit different components of the searching response (i.e. locomotory or probing and grasping reflexes; Zimmer-Faust & Case, 1982; Derby & Atema, 1982b), results in the present study suggest that during this initial phase, differences in flesh odour/flavour between different prey species are not relevant in prey selection (Figure 6.15). Once crabs have physically encountered a prey item, shape and size of the shell assume a greater significance, interacting with chemical and mechanical stimuli from alternative prey touched by the pereiopods (Jubb *et al.*, 1983). Present results emphasise the importance of certain shell characteristics, and suggest that those dimensions more strongly associated with prey volume (e.g. shell width), and hence the amount of flesh obtained in return, might be predominant in deciding whether to attempt an attack (Figure 6.15). Once an item has been recognised as profitable and an attack has been initiated, further decisions can be influenced by several factors, including microfractures within the shell structure (Boulding & LaBarbera, 1986; Elner, 1978) and leakage of body fluids that encourage crabs to continue the attack. Stimuli from alternative prey may also deter crabs in their opening attempt. Moreover, it is at this stage, where a prey item that does not yield easily to the crab's crushing efforts, can be abandoned, suggesting that at this point of the encounter, prey vulnerability, together with the tenacity and experience of crabs might be particularly relevant (Figure 6.2). In a study of the hierarchical responses to prey stimuli by the fifteen-spine stickleback, *Spinachia spinachia*, Croy and Hughes (1991b) found that movement and size could be seen as coarse-tuning stimuli, and colour and location as finetuning stimuli affecting prey selection. Although the results presented in this chapter do not allow for such definition of the hierarchical order of crab responsiveness to various prey stimuli, they do nevertheless, emphasise that odour and shape assume different importance at several decisive moments of the foraging bout, and that by using a variety of stimuli to assess prey quality, crabs probably enhance their predatory efficiency.

6.5. Summary

1. The size ranges of *Mytilus edulis* and *Cerastoderma edule* selected by crabs either clearly corresponded to or were slightly smaller than the size ranges of prey with the highest profitability (= dry flesh weight per unit of handling time). Profitability values of *M. edulis* and *C. edule*, however, showed a considerable degree of scatter, whilst those of *Ostrea edulis* and *Crassostrea gigas* were even more variable. In addition, the size ranges of *O. edulis* and *C. gigas* at which profitability attained its highest values were not clearly delimited.

2. Differences in the thickness and fracture resistance between individual prey items of similar length could account for much of the variation in handling time and profitability. The patterns of variation appear to be the result of behavioural strategies that crabs present when feeding on prey that increase little in size, yet vary markedly in vulnerability. This strategy is based on a trial and error procedure by which crabs attack all encountered prey but reject those that remain unbroken after a certain number of opening attempts. Present results, thus, emphasise the passive nature of size-selective feeding in both *Cancer pagurus* and *Carcinus maenas*. Since diets in which crabs selected both the smallest and the intermediate-sized items corresponded approximately with those predicted by optimal foraging theory, this behavioural strategy probably maximises feeding efficiency.

3. Differences between the profitability obtained by *C. maenas* and *C. pagurus* feeding on *M. edulis*, *C. edule* and *C. gigas* were partly determined by their contrasting chelal morphology and biomechanics, but were also related to behavioural differences that make *C. maenas* a voracious but less efficient predator, than the more sedentary and tenacious *C.*

pagurus. However, profitability was similar for both crab species feeding on *O. edulis*, since its significantly higher shell constitutes a shape-related restriction making flat oysters equally unprofitable for both crab species. These results confirmed that differences in size-selective foraging strategies between crab species can vary depending on the prey species on which they feed.

4. The ranking order of prey profitability for large crabs clearly paralleled their ranking order according to consumption rates during feeding experiments. Results indicated that differences in profitability between the selected size ranges of prey were mainly due to differences in the biomass contained in their shells. Nonetheless, evidence suggested that differences in vulnerability, hence breaking times also influenced the position of prey species as they ranked in their value to crabs. Thus, variations in shell shape and strength closely associated to the way crabs manipulate prey can influence handling techniques, and might constitute an important factor determining crab preference for certain bivalve species.

5. Prey value did not always parallel the consumption rates of the preferred size classes of the four bivalve species. Variations in crab strength related to size accounted for certain differences between the foraging behaviour of juvenile *C. maenas* compared to adult crabs, but there can be other factors involved, such as the need of energy intake for rapid growth during live stages of active moulting. Results suggested that the degree of crab selectivity amongst different species of bivalves is considerably lower in smaller than in larger crabs as a result of the restrictions imposed on small individuals that have limited access to larger prey items.

6. Species-related preferences exhibited by crabs feeding on prey near the optimal size suggested that active selection can take place at some point of the predation cycle, and that crabs decisions were based on prey characteristics correlated with prey value.

a) Decisions by crabs on whether to initially attack or reject oysters and mussels were not influenced by the flavour or odour of their flesh. Both mussels and oyster flesh filtrates had a similar reinforcing effect on crabs perseverance to open prey. By contrast, characteristics in the shells of *M. edulis* and *O. edulis* constituted mechanical stimuli influencing decisions by crabs to both initially attack and persist to open prey that were already being manipulated.

b) Since crabs exhibited similar trends in their preference for mussels over oysters, whether these provided a higher (live prey) or equal (epoxy model prey) profitability, the initial reluctance of crabs to attack *O. edulis* was not associated with the ultimate energetic reward, but could be based on evaluations of the overall shape and/or volume of the shells of these bivalves during a first recognition phase. Results of experiments with epoxy models of various geometric shapes, but similar volumes showed that contrasting differences in shell shape could influence crab persistence, and hence prey selection. Moreover, they suggested that shell width constitutes an important morphological characteristic, which crabs might be able to recognise and associate with prey value. An adequate match between an item of a certain shell width and chelal gape allowed chelae to work with greatest mechanical advantage, improving handling efficiency, and hence profitability. By contrast, a combination of small shell width and large shell height as in *O. edulis* reduced handling efficiency, and partly determined its rejection by crabs.

c) Improvement of the handling efficiency by *C. maenas* feeding on mussels, cockle and oyster combinations was not detected in the course of this study. Handling efficiency of the preferred size classes of prey was probably near its maximum, and differences in breaking times amongst prey species were more strongly influenced by variations in individual hunger levels or prey vulnerability than by an increased effectiveness in attack methods. However, whilst previous exposure to either *M. edulis* or *C. edule* did not affect subsequent crab selection of these bivalve prey, crabs consumed greater numbers of *M. edulis* than of *C. gigas*, whether they had been previously exposed to mussels or oysters. A mechanism of prey value assessment in which crabs base predictions on recent rather than on more distant experience, can explain the subsequent preference of crabs for mussels as soon as they became available. Results further suggested that successful and energetically rewarding attacks act as reinforcers of foraging stimuli, increasing the efficiency with which crabs subsequently detect and consume prey.

7. Results of experiments in the present chapter emphasise that odour and shape/volume assume different importance at several decisive moments of the foraging bout, and that crabs use a variety of stimuli to assess prey quality, thus, enhancing their predatory efficiency.

Chapter 7

General Discussion

During the course of this study it was observed that the shell length of prey items preferred by crabs increased with increasing carapace width (Chapter 5). Since the occlusive geometry of the chelae did not vary markedly amongst juvenile and adult *Carcinus maenas*, these differences were presumably due largely to variations in chelal size, strength and dexterity as crabs increased in size (Chapter 3). Changes in the sexual and agonistic behaviour of juvenile *Carcinus maenas* as they grow into adults account for differences in the growth patterns of a variety of chelal size parameters (Hartnoll, 1978), which amongst other factors, such as the availability of suitable food types, determine the natural diet and distribution patterns of different parts of the local crab population.

Large, adult *C. maenas* had difficulties both finding and handling small prey items, but were able to open larger items by applying a variety of relatively complex attack methods. Juvenile crabs, on the other hand, could easily handle small prey, but were rarely successful in opening larger prey items (Chapter 4). Throughout the summer, juvenile *C. maenas* remain on the shore (Chapter 2) where their foraging activity increases as the result of elevated sea temperatures (Chapter 5). In addition, these juvenile crabs need to satisfy their energy requirements for rapid growth during life stages where moulting makes them especially vulnerable to predation (Klein Breteler, 1975a; 1975b). In order to compensate for the limited power of their chelae, juvenile *C. maenas* increase their energy intake by including a wider diversity of prey of a smaller size range than adult crabs. Thus, the degree of prey species selectivity is lower in juvenile than in adult *C. maenas* as a result of restrictions imposed on small individuals that have limited access to larger prey items. These results are in accordance with those reported by previous authors (Rangeley & Thomas, 1987; Ropes, 1968), who found that the natural diet of juvenile *C. maenas* consisted of a high variety of food types, whereas that of adult crabs was dominated by fewer prey species.

Differences in prey size preferences between *C. maenas* and *Cancer pagurus* were related to their contrasting chelal morphologies and biomechanics. However, differences in prey size preference varied with the species of prey offered to crabs as a result of variations in vulnerability between prey of different shape. The monomorphic chelae of *C. pagurus* operate at a much higher mechanical advantage than the master chela in *C. maenas* (Chapter 3), allowing edible crabs to readily crush larger *Mytilus edulis* and *Crassostrea gigas* relative to the size of their chelae than shore crabs of similar or even greater carapace width

(Chapters 4 & 5). By contrast, the relatively inflated shell of large *Cerastoderma edule* constituted a highly effective barrier to even the most powerful chelae of *C. pagurus*, whereas the reluctance of the smallest crabs of both species to feed on large *Ostrea edulis* reflected the equal difficulties of these crabs to manipulate the relatively wide shell of flat oysters (Chapters 4 & 5).

Differences in prey profitability obtained by *C. maenas* and *C. pagurus* when feeding on several bivalve prey were partly determined by specific morphological features of mouthparts and chelipeds, but were also related to the behavioural adaptations that influence the foraging strategies of these two brachyuran crabs. Monomorphic crabs of the genus *Cancer* are known for their burrowing behaviour (Brown & Bennett, 1980; Hall *et al.*, 1993; Howard, 1982), their general retiring habit, and their persistence with one prey item even when alternative prey are available (Chapters 4 & 5). *C. maenas*, by contrast, is a tidally migrating species that explores and forages actively on the shore (Hunter & Naylor, 1993; Naylor, 1958), and readily replaces prey that do not yield after a few opening attempts (Chapters 4 & 5). An active exploring behaviour might increase the probability of *C. maenas* encountering and attempting to open a wider diversity of prey types, whereas the more sedentary and tenacious nature of *C. pagurus* might constrain crabs to persevere with attacking prey in their immediate vicinity. These findings accord with those reported by Lawton (1983), who suggested that the voracious feeding behaviour exhibited by *C. maenas* could be due to the relative inefficiency of this crab as a predator, since the rate of energy return obtained by shore crabs was below that obtained by edible crabs.

Inter-specific differences in crab foraging behaviour can account for the distribution patterns of their prey populations (Boulding & Hay, 1984; Elner & Raffaelli, 1980), and certain crab-resistant features in prey shells are known to be partly determined by crab predation (Blundon & Kennedy, 1982b; Boulding, 1984; Hughes & Elner, 1979). Moreover, chelal morphology (Vermeij, 1977), as well as the ability of crabs to modify their foraging tactics (Creswell & McLay, 1990; Davidson, 1986; Micheli, 1995), have in turn probably evolved in response to prey characteristics. In this context, comparisons between the foraging behaviour of *C. maenas* and *C. pagurus* contribute to a more comprehensive understanding of the ecological, morphological and ethological characteristics that distinguish these two brachyuran species.

Variations in handling time and profitability throughout the size ranges of prey examined in this study appeared to be the result of behavioural strategies that crabs present when feeding on prey that may increase little in size, but vary markedly in vulnerability. This strategy is based on a trial and error procedure by which crabs attack all encountered prey but reject those that remain unbroken after a persistence time. These results emphasise the passive nature of size-selective feeding in *C. maenas* and *C. pagurus*, and confirm the findings of previous authors (e.g. Hughes & Elner, 1979; Lawton & Hughes, 1985). The broad correspondence between the size ranges of prey selected by crabs and those predicted by profitability curves suggest that this behavioural strategy maximises feeding efficiency, and thus, can be easily confounded with a strategy where crabs actively select prey of an energetically optimal size. In order to distinguish between active and passive selective feeding, future studies on crab foraging behaviour must examine the various components of predation rate (i.e. encounter rate between predator and prey, probability of capture upon encounter, and probability of consumption upon capture), and take into consideration that active selection occurs when a predator selects a prey type more often when given a choice of prey types than when not given a choice (Barbeau & Scheibling, 1994a).

The number of attempts, and hence the amount of time that a crab will persist with a prey item, is a function of several factors including hunger levels, availability of alternative prey, and crab experience. The shape of a prey item and the way it fits into the chelal grip has a marked effect on crab persistence time (Chapter 6). Furthermore, the shell width of the bivalves examined in this study constituted an important morphological characteristic which crabs were able to recognise and associate with prey value, and it therefore strongly influenced active decisions by crabs to initiate an attack (Chapter 6). At later stages of the predation cycle, however, the relationship between shell shape and chelal morphology affected persistence time thus mechanically determining the outcome of the attack. Results of the present investigation therefore suggest that species-related preferences exhibited by crabs when feeding on prey near to the optimal size involve an active component in the crabs initial decisions on whether to attack bivalve prey of contrasting shell morphology and strength.

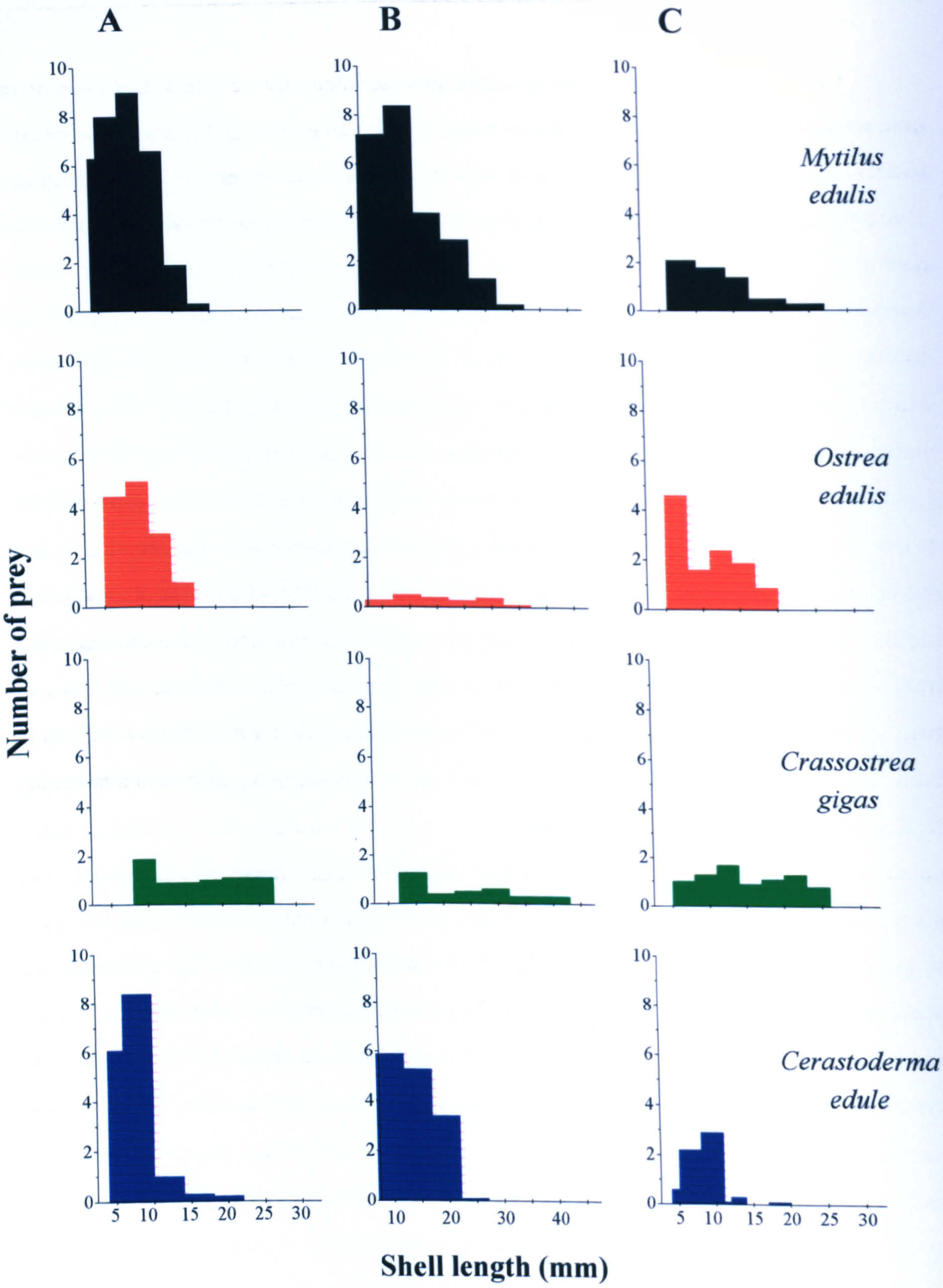

Figure 7.1. The number and size ranges of *Mytilus edulis, Ostrea edulis, Crassostrea gigas*, and *Cerastoderma edule* that are consumed daily (temperature 11-15 °C) by **(A)** a single juvenile *Carcinus maenas* in each of two size categories (15-25 and 25-35 mm CW); **(B)** a single adult *C. maenas* in each of two size categories (40-55 and 55-70 mm CW); **(C)** a single juvenile *Cancer pagurus* in each of two size categories (20-30 and 30-40 mm CW).

Crab predation can influence community structure by reducing the density of dominant species (Elner, 1981; Jensen & Jensen, 1985; Paine, 1966), and can also affect the distribution and abundance of the major prey populations (Du Preez, 1984; Muntz *et al.*, 1965; Gee *et al.*, 1985; Raffaelli & Milne, 1987). Moreover, size-selective predation can determine prey population structure and influence its dynamics (Wear & Haddon, 1987; Raffaelli *at al.*, 1989; Kent & Day, 1983). Laboratory experiments have shown that crabs consume large numbers of prey (Hill, 1979; Lin, 1990; Seed, 1980), but the impact on natural populations needs to be assessed by taking into account the abundance of predators and the importance of prey as natural components of their diet (Arnold, 1984).

M. edulis has been previously reported as the most frequent food item of *C. maenas* (Elner, 1981), and shore crabs are known to forage extensively on commercial *C. gigas* (Dare *et al.*, 1983), and natural populations of *C. edule* (Sanchez-Salazar *et al.*, 1987b) in North Wales. Cancrids have generally been associated with predation of gastropods, but various species of the genus *Cancer* have also been considered important predators of bivalve prey (Boulding & Hay, 1984; Elner & Jamieson, 1979; Elner & Lavoie, 1983). Although brachyuran crabs forage over prey populations depending on their local availability (Choy, 1986; Elner, 1981; Ropes, 1968), the consumption rates on *M. edulis* and *C. edule* obtained in the present study suggest that predation by both *C. maenas* and *C. pagurus* can potentially be an important cause of mortality in these bivalve species (Figure 7.1), particularly when those size ranges of prey that are easily accessible to predators are plentiful. Consumption rates of *O. edulis* and *C. gigas*, however, were always lower than those of *M. edulis* and *C. edule* (Figure 7.1), and crabs consistently selected mussels over oysters when prey were offered simultaneously. Results such as these are relevant in the context of aquaculture, since cultivators may be able to reduce predatory impact on certain bivalve species by artificially combining a variety of prey types that could offer natural predators an alternative, and sometimes preferred, source of food. Nonetheless, such multiple species interactions need to be investigated under field conditions in order to implement both adequate and economically viable culture strategies.

The abundance and size-frequency distribution of *C. maenas* and *C. pagurus* populations fluctuated markedly throughout the year (Chapter 2; Appendix A1, A2). Changes in the relative abundance of certain size groups (Chapter 2), temperature-dependent

Table 7.1. Estimated number and percentage of *Mytilus edulis*, *Cerastoderma edule*, *Ostrea edulis*, and *Crassostrea gigas* that several size categories of *Carcinus maenas* found at Aberffraw, Gallows Point and Traeth Melynog could potentially consume in one year. Calculations were made on the basis of mean daily ingestion rates (temperature = 12-15 °C) of each size category of crab, and the number of crabs found per transect (three shore levels) of baited traps during one year of seasonal sampling. Note that these figures serve only for gross comparisons between locations and do not represent prey consumption by the whole of the *C. maenas* populations at each site.

	M. edulis				*C. edule*		*O. edulis*		*C. gigas*	
Crab size	Aberffraw		Gallows Point		Traeth Melynog		Gallows Point [1]		Gallows Point [1]	
	Number	%	Number	%	Number	%	Number	%	Number	%
5-15 mm CW	-	-	28076	0.9	-	-	-	-	-	-
15-25 mm CW	69850	8.6	432254	13.7	4393	0.7	117200	12.3	62731	9.8
25-40 mm CW	166989	20.5	1418156	45.0	161974	27.6	719896	75.3	376339	58.8
40-55 mm CW	379246	46.5	1073276	34.0	290643	49.5	100188	10.5	165828	25.9
55-70 mm CW	199866	24.5	200441	6.4	130228	22.2	18840	2.0	35587	5.6
Total	815951		3152201		587238		956124		640485	

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[1] Since *O. edulis* and *C. gigas* do not occur naturally at Gallows Point, these figures represent expected consumption rates given a *C. maenas* population comparable to the one found at Gallows Point.

variation in ingestion rates (Chapter 5), and the possibility of switches in diet at certain times of the year make predatory impact seasonally variable. The present investigation has shown that estimates of crab abundance and population size composition depend to a large extent on the method used to collect crab samples (Chapter 2; Appendix A3). Thus, not only do seasonal fluctuations in crab abundance need to be considered when estimating predation impact, but also whether the crab population is being sampled realistically. Furthermore, crabs find a variety of prey species under natural conditions, and consumption rates may vary depending on the availability of alternative prey.

Taking into consideration the opportunistic feeding behaviour of crabs, and the difficulties in estimating crab abundance accurately, the following attempt to evaluate the potential impact of predation by *C. maenas* populations at selected sites around the Isle of Anglesey, North Wales constitutes only an initial approximation and the calculated values must therefore be viewed with some caution. The number of *M. edulis*, *O. edulis*, *C. gigas* and *C. edule* that could potentially be consumed by *C. maenas* in each of several size categories found at Aberffraw, Traeth Melynog and Gallows Point are shown in Table 7.1. Since *O. edulis* and *C. gigas* do not occur naturally at any of the study sites, the numbers of both oyster species represent the expected consumption rates given a crab population comparable to that found at Gallows Point. These figures were calculated by multiplying daily ingestion rates (temperatures 12-15 °C) of different size categories of *C. maenas* feeding on each of several size classes of prey (Chapter 5), by the number of crabs in each size category that were found in each of four seasonal sampling periods (Chapter 2). Note that crab abundance estimated in this way can only be analysed in relative terms (i.e. the number of crabs found along a transect at one site relative to those along the transect in another), and that these figures serve merely to compare the potential predatory impact between different sites. Results suggest that the crab population at Gallows Point could consume four times as many mussels as the crab population at Aberffraw. At Aberffraw, 47 % of the mussels consumed would be accounted for by crabs of 40-55 mm CW, whereas a similar percentage of the mussels consumed at Gallows Point (45 %) would be eaten by crabs 25-40 mm CW. At Traeth Melynog, 50 % of the total number of *C. edule* consumed would be predated by crabs 40-55 mm CW. Results in Table 7.1 also show the potential impact that a crab population like the one found at the commercial mussel bed at Gallows

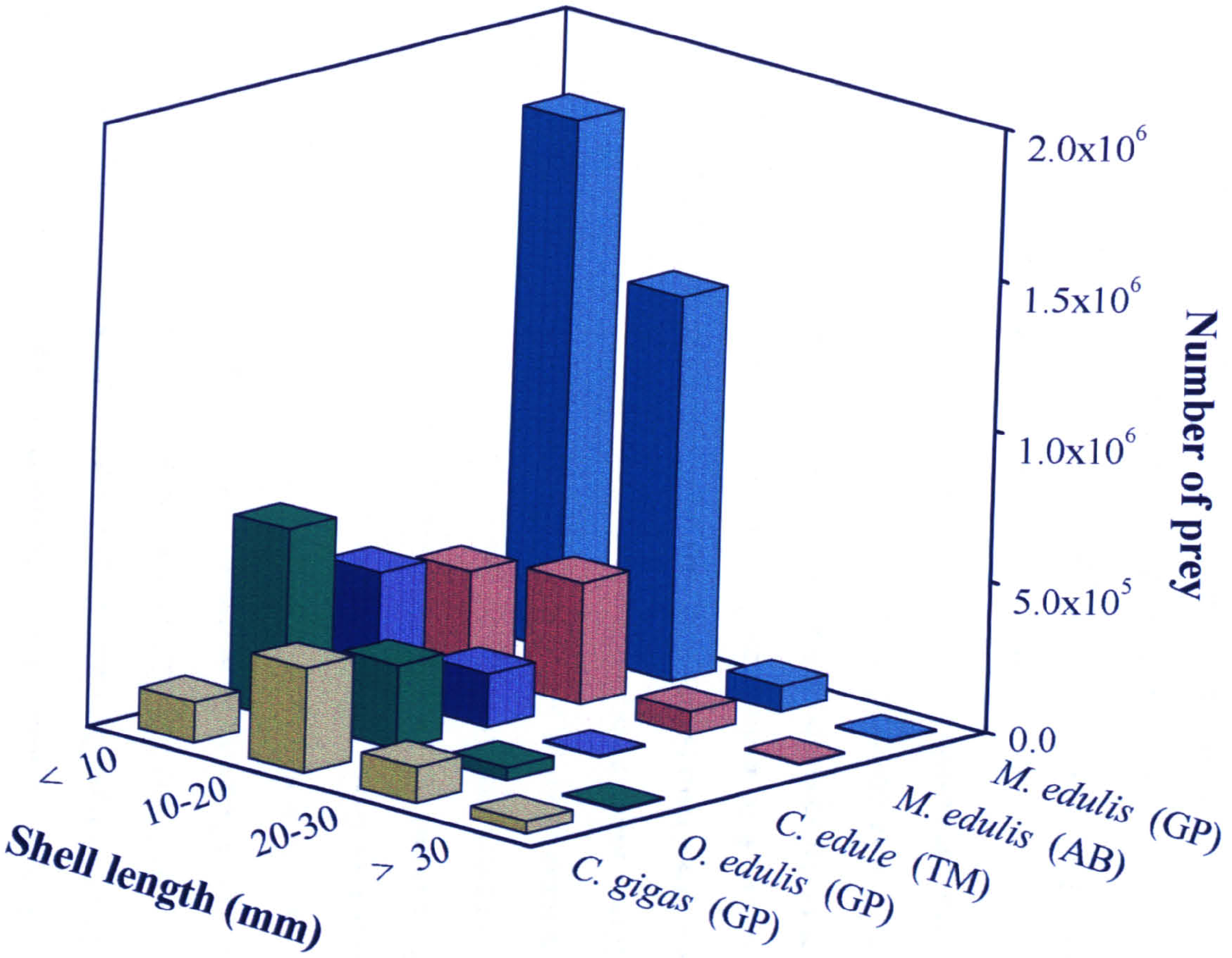

Figure 7.2. Estimated number of *Mytilus edulis*, *Ostrea edulis*, *Crassostrea gigas*, and *Cerastoderma edule* of four size classes (mm in shell length) that could potentially be consumed over a 1 yr period by *Carcinus maenas* at Aberffraw (AB), Gallows Point (GP), and Traeth Melynog (TM). Calculations were made on the basis of mean daily ingestion rates (temperature = 11-15 °C) of different size categories of crabs, and the number of crabs found per transect (three shore levels) of baited traps during one year of seasonal sampling. Note that these figures serve only for gross comparisons between locations, and do not represent prey consumption by the whole of the *C. maenas* populations at each site.

Point could have on commercially reared *O. edulis* and *C. gigas*. Whilst the number of *O. edulis* consumed by crabs would be 0.96 × 10 ^{6} • year $^{-1}$, those of *C. gigas* would be 0.64 × 10 ^{6} • year $^{-1}$, 30 % and 20 % of the number of mussels estimated to be consumed by crabs at Gallows Point, respectively. Up to 75 % and 59 % of the total number of *O. edulis* and *C. gigas*, respectively, would be accounted for by crabs 25-40 mm CW.

The size distribution of prey that could potentially be consumed by *C. maenas* at Aberffraw, Traeth Melynog and Gallows Point (Figure 7.2) indicates that the largest predatory impact would fall on *M. edulis* at Gallows Point. According to these estimates, crabs could have a major impact on *M. edulis*, *O. edulis*, *C. gigas* and *C. edule* < 20 mm SL. However, the proportion of *C. gigas* > 20 mm SL that could be consumed by crabs at Gallows Point (24.8 %) is higher than the proportion of *M. edulis* (9.6 %) and *O. edulis* (4.9 %) that could be consumed by crabs at the same sampling site. Even though the crab population at Traeth Melynog contained individuals of 55-70 mm CW in approximately similar numbers to the crab populations at the other sites, the number of *C. edule* > 20 mm SL that could be consumed by these crabs is minimal. Whilst the size distribution pattern of *O. edulis* that could be consumed by crabs at Gallows Point is similar to that of *C. edule* consumed by crabs at Traeth Melynog, crabs at Gallows Point could consume a higher number and proportion of flat oysters > 20 mm SL (4.9 %) than the crabs at Traeth Melynog could consume cockles > 20 mm SL (0.6 %). The number of *M. edulis* < 10 mm SL and between 10-20 mm SL that could be consumed by the crab population at Gallows Point is in the order of 2 × 10 ^{6} • year $^{-1}$ and 1.5 x 10 $^{-6}$ • year $^{-1}$, respectively. Very few mussels > 20 mm SL could be consumed by these crabs. The crab population at Aberffraw could consume similar numbers of mussels < 10 mm and 10-20 mm SL.

Because ingestion rates of *C. pagurus* were only recorded for crabs 20-40 mm CW (Chapter 5), comparisons between the potential predatory impact of *C. pagurus* and *C. maenas* were only made for crabs 20-40 mm and 15-40 mm CW, respectively. Estimates of the number of prey that could potentially be consumed by both crab species at Treborth were calculated as mentioned above, but were based on the number of crabs found at the low intertidal per standard search time (Chapter 2). Since density is not constant across the intertidal gradient, these figures serve only for comparisons between crab species and do not represent prey consumption by the whole of the *C. maenas* and *C. pagurus* populations at Treborth. Whilst *C. maenas* could consume 2350 *M. edulis* • m $^{-2}$ year $^{-1}$ and 988 *C. edule* • m $^{-2}$ year $^{-1}$, *C. pagurus* of comparable size could consume only 125 mussels • m $^{-2}$ year $^{-1}$ and 114 cockles • m $^{-2}$ year $^{-1}$. These results indicate that *C. pagurus* could potentially consume only 5.3 % of the mussels and 11.5 % of the cockles that *C. maenas* at the same site could consume. *C. pagurus* could consume 217 *O. edulis* • m $^{-2}$ year $^{-1}$ and 154 *C. gigas* • m $^{-2}$ year $^{-1}$, representing 25.1 % of the *O. edulis* (864 • m $^{-2}$ year $^{-1}$) and 33.8 % of the *C. gigas* (456 • m $^{-2}$ year $^{-1}$) that *C. maenas* could consume. Differences between the number of prey that *C. maenas* and *C. pagurus* could consume over a one year period largely reflect differences in crab species density at the low intertidal zone at Treborth. However, differences in ingestion rates between crab species can vary markedly depending on the species of prey considered (Figure 7.1), and thus can strongly influence estimates of the predatory impact on different prey populations.

These results demonstrate that variations in the local abundance of crabs and their population dynamics can result in marked differences when calculating predatory impact from one site to another. Thus, they emphasise the need for accurate estimates of crab abundance and population size composition, features which must be considered when predation impact on prey populations is being investigated. Differences in diet and migratory behaviour associated with crab size (Chapter 2), as well as differential growth rates, and hence ingestion rates (Chapter 5), indicate that it is essential to consider juvenile crabs in future studies. Furthermore, juvenile *C. maenas* are generally far more abundant on the shore than adult crabs (Chapter 2; see also Crothers, 1970), and may, therefore, contribute significantly to prey mortality. For example, the presence of large numbers of juvenile shore crabs at Traeth Melynog and their co-occurrence with cockle spat at all shore levels (Chapter 2), suggests that predation by even the smallest crabs could play an important role in the impact of *C. maenas* predation on the *C. edule* population at this site. In addition, results reveal that predation rates can vary markedly from one species of prey to another, and that direct extrapolations may result in unrealistic assessments of the influence of crab predation on prey abundance and size composition.

Estimates of the extent to which crabs determine the abundance of their prey is difficult because of their mobility, their broad diet and the potential complexity of their responses to the relative abundance of their various prey species (Sponaugle & Lawton, 1990). In natural conditions, populations are subject to environmental and ecological pressures that modify crab feeding habits. Information on this topic involves complex interactions between a number of environmental and ecological factors that can strongly influence crab predation rates. Future research must include direct field observations and experiments that more closely resemble natural conditions in order to obtain accurate conclusions regarding the impact of crab predation and its role in determining the ecological features of prey populations within the intertidal shore. Furthermore, detailed information on inter- and intra-specific interactions between populations can be used to improve management strategies in extensive and semi-extensive polyculture of aquatic resources.

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The Biology of Crustacea

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(7)

Integrated biological and chemical monitoring: *In situ* responses of *Pacifastacus leniusculus* to fluctuations in environmental ammonia concentrations.

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A portable battery powered computer aided physiological monitoring system (CAPMON) has been developed in conjunction with an automated spectrophotometric field monitor which permits the continuous long term recording of both cardiac activity in selected aquatic organisms and total ammonia concentration in the surrounding environment. Physiological monitoring of cardiac activity in the fresh water crayfish *Pacifastacus leniusculus* was achieved using non-invasive infrared emitter/detectors to transduce heart beat from 8 animals simultaneously. Data was collected continuously and stored on a micro-computer. The automated flow injection (FI) based photometric monitor incorporated a gas diffusion unit and an acceptor stream containing an acid-base indicator. The detection system utilised a solid state light emitting diode source and photodiode detector. Remote control and data processing was achieved by an in-house designed micro-computer system. The instrumentation was fully evaluated in the laboratory and was shown to operate unattended for periods of up to 1 week. A dose response experiment showed that 4 h exposures to concentrations of ammonia greater than 5 mg l^{-1} had a significant effect on heart rate (ANOVA F=7.6; df=5; $P<0.0005$). The feasibility of the system was demonstrated in a 3 day field trial when the monitors were successfully deployed *in situ* at a landfill leachate lagoon.

(8)

Inter- and intraspecific differences in prey vulnerability to predation by the shore crab *Carcinus maenas* L.

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The foraging behaviour of brachyuran crabs on marine molluscs has been the subject of considerable research. Both size and species preference have been demonstrated and as such, brachyurans have the potential to influence significantly the spatial distribution and abundance of their prey. In the field, alternative sources of food and variations in prey vulnerability will be important factors in determining the actual intensity of crab predation.

Laboratory experiments have shown that *Carcinus maenas* L. is both size and species selective in its choice of prey. The reasons for such selection are not entirely clear, but energy maximization, time minimization, and mechanical difficulties associated with prey handling have been suggested as causal factors. We have designed a series of laboratory experiments to determine prey selection over a variety of bivalve species with contrasting morphologies (*Crassostrea gigas, Ostrea edulis, Mytilus edulis*, and *Cerastoderma edule*). The main objective of these experiments is to establish how crabs select their prey, the possible causal factors underlying this preference, and the relationship between these and differences in interspecific prey vulnerability. Once the preferred size ranges had been established for each prey species, paired combinations of prey types were offered to two size classes of crabs and the preferences noted. In order to establish the basis of the observed selection, crabs were offered equal numbers of the preferred sizes of each prey species and the foraging behavioural sequences recorded. Handling times and prey profitabilities were calculated for a range of sizes of each prey species.

C. maenas is a tidally foraging species and therefore encounters changes in the abundance, distribution and morphology within individual prey species over a single foraging bout. Mussels from the high shore of a wave exposed location and from a low shore sheltered location were used to represent the extremes of variability within this species. Handling time, prey preference and profitability were calculated using these mussels to determine whether optimality of prey alters with morphology, and whether the crab adjusts its foraging behaviour accordingly. Handling times and profitability were also obtained for crabs feeding on a) mussels presented individually, b) mussels presented as five individuals in each of five size classes, and c) mussels presented in varying proportion with increased number of small individuals, in order to determine whether changes in availability of specific size classes of prey affects foraging behaviour.

Appendix A1. Total number of *Carcinus maenas* and *Cancer pagurus* captured per standard search time in each of three quadrats (30 m ^{2}), placed 100 m from each other at low-water mark of spring tides during monthly sampling at Treborth (Text-fig 2.1, A).

		1995							1996				
Species	Quad.	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May
C. maenas	I	11	14	18	36	5	20	21	2	9	5	13	17
	II	12	27	18	15	23	13	15	1	5	16	27	18
	III	7	10	13	10	17	14	17	5	0	3	16	6
	TOT	30	51	49	61	45	47	53	8	14	24	56	41
C. pagurus	I	6	4	14	4	10	4	9	10	1	15	7	18
	II	10	5	7	6	5	0	1	0	0	2	5	3
	III	9	9	2	5	5	1	1	4	1	1	10	13
	TOT	25	18	23	15	20	5	11	14	2	18	22	34

Appendix A3. Number of juvenile *Carcinus maenas* captured in baited and unbaited quadrats (623 cm ^{2}) set at high (HS), mid (MS) and low shore (LS) during the sampling period of June, 1997 at Traeth Melynog (Text-fig. 2.1, B).

Quad.	Type	HS	MS	LS
I	Baited	13	8	8
II	Baited	3	10	2
III	Baited	3	8	5
IV	Unbaited	6	5	6
V	Unbaited	7	2	4

Appendix A2. Total number of *Carcinus maenas* captured in each of three baited traps set at high (HS), mid (MS) and low shore (LS) during seasonal sampling at four different sites around the Isle of Anglesey (Text-fig. 2.1). The number of males (MAL)and females (FEM) in each case are also given. No traps were set at Treborth on May 1996.

	Shore-	May 1996			August 1996			November 1996			February 1997			June 1997		
Site	level	N	Fem	Mal	N	Fem	Mal	N	Fem	Mal	N	Fem	Mal	N	Fem	Mal
Aberffraw	HS	10	4	6	31	15	16	16	8	5	32	5	27	17	2	15
	MS	29	6	23	6	4	2	43	25	18	0	0	0	9	6	3
	LS	28	11	17	32	21	18	9	6	3	27	10	17	36	26	10
	TOT	67	21	46	69	40	36	68	39	26	59	15	44	62	34	28
Gallows Point	HS	45	19	26	85	28	57	44	12	32	19	6	13	21	6	15
	MS	35	21	14	82	25	57	60	23	37	52	10	42	89	52	37
	LS	29	7	22	119	63	56	147	74	73	63	13	50	69	36	33
	TOT	109	47	62	286	116	170	251	109	142	134	29	105	179	94	85
Treborth	HS	-	-	-	31	5	26	11	5	6	0	0	0	1	0	1
	MS	-	-	-	6	3	3	2	0	2	6	1	5	27	5	22
	LS	-	-	-	3	0	3	0	0	0	37	3	34	0	0	0
	TOT				40	8	32	13	5	8	43	4	39	28	5	23
Traeth Melynog	HS	0	0	0	9	7	2	9	4	5	0	0	0	2	2	0
	MS	0	0	0	78	36	42	3	1	2	3	3	0	7	4	3
	LS	30	21	9	88	51	37	111	56	55	0	0	0	65	16	49
	TOT	30	21	9	175	94	81	123	61	62	3	3	0	74	22	52

Appendix B1. Size range and number of *Mytilus edulis*, *Ostrea edulis*, *Crassostrea gigas*, and *Cerastoderma edule* that were individually offered to one *Carcinus maenas* and *Cancer pagurus* in each of several size categories during experiments to describe prey handling methods; CW: carapace width (mm), SL: shell length (mm).

		M. edulis		*O. edulis*		*C. gigas*		*C. edule*	
	CW	SL	n	SL	n	SL	n	SL	n
C. maenas	5-15	1-14	113	-	-	-	-	-	-
	15-25	1-14	130	3-24	11	3-24	6	1-14	26
	25-35	1-14	165	3-24	14	3-24	35	1-14	22
	40-55	5-40	144	5-40	25	5-40	25	5-40	22
	55-70	5-40	125	5-40	15	5-40	20	5-40	23
C. pagurus	10-20	2-17	55	-	-	-	-	-	-
	20-30	3-24	51	3-24	16	3-24	20	2-14	21
	30-40	5-30	68	3-24	21	3-24	20	3-21	26

Appendix B4. Size classes (mm in shell length) of *Mytilus edulis*, *Ostrea edulis*, *Crassostrea gigas*, and *Cerastoderma edule*, that were offered to various size categories (mm carapace width, CW) of *Carcinus maenas* and *Cancer pagurus* in trials with equal and altered proportions of prey species. Size classes were established on the basis of those selected by crabs in the highest number and percentage in experiments where prey species were presented both individually and in pair combinations.

	CW	*M. edulis*	*O. edulis*	*C. gigas*	*C. edule*
C. maenas					
	15-25	3-6	3-6	3-6	2-4
	25-35	6-9	6-9	6-9	6-9
	40-55	10-15	10-15	10-15	5-10
	55-70	15-20	15-20	15-20	10-15
C. pagurus					
	20-30	4-8	3-6	4-8	4-6
	30-40	10-15	9-12	10-15	6-9

Appendix B2. Size classes I-VII (mm in shell length) in which *Mytilus edulis*, *Ostrea edulis*, *Crassostrea gigas*, and *Cerastoderma edule* were offered to various size categories (mm carapace width) of *Carcinus maenas* and *Cancer pagurus* during the single prey species experiments.

Mytilus edulis									
	No.	Size	I	II	III	IV	V	VI	VII
C. maenas									
15-25	5	2 mm	2-4	4-6	6-8	8-10	10-12	12-14	-
25-35	6	3 mm	3-6	6-9	9-12	12-15	15-18	18-21	-
40-55	7	5 mm	5-10	10-15	15-20	20-25	25-30	30-35	35-40
55-70	7	5 mm	5-10	10-15	15-20	20-25	25-30	30-35	35-40
C. pagurus									
10-20[1]	5	3 mm	2-5	5-8	8-11	11-14	14-17	-	-
20-30	5	4 mm	-	4-8	8-12	12-16	16-20	20-24	-
30-40	5	5 mm	-	5-10	10-15	15-20	20-25	25-30	-

Ostrea edulis									
	No.	Size	I	II	III	IV	V	VI	VII
C. maenas									
15-25	5	3 mm	3-6	6-9	9-12	12-15	15-18	-	-
25-35	6	3 mm	3-6	6-9	9-12	12-15	15-18	18-21	-
40-55	6	5 mm	5-10	10-15	15-20	20-25	25-30	30-35	-
55-70	6	5 mm	5-10	10-15	15-20	20-25	25-30	30-35	-
C. pagurus									
20-30	5	3 mm	3-6	6-9	9-12	12-15	15-18	-	-
30-40	5	3 mm	3-6	6-9	9-12	12-15	15-18	-	-

Crassostrea gigas									
	No.	Size	I	II	III	IV	V	VI	VII
C. maenas									
15-25	5	3 mm	-	6-9	9-12	12-15	15-18	18-21	-
25-35	6	3 mm	-	6-9	9-12	12-15	15-18	18-21	21-24
40-55	6	5 mm	-	10-15	15-20	20-25	25-30	30-35	35-40
55-70	6	5 mm	-	10-15	15-20	20-25	25-30	30-35	35-40
C. pagurus									
20-30	6	3 mm	3-6	6-9	9-12	12-15	15-18	18-21	-
30-40	6	3 mm	-	6-9	9-12	12-15	15-18	18-21	21-24

Cerastoderma edule									
	No.	Size	I	II	III	IV	V	VI	VII
C. maenas									
15-25	5	4 mm	< 4	4-8	8-12	12-16	16-20	-	-
25-35	6	4 mm	< 4	4-8	8-12	12-16	16-20	20-24	-
40-55	5	5 mm	5-10	10-15	15-20	20-25	25-30	-	-
55-70	5	5 mm	5-10	10-15	15-20	20-25	25-30	-	-
C. pagurus									
20-30	6	2 mm	2-4	4-6	6-8	8-10	10-12	12-14	-
30-40	5	3 mm	-	3-6	6-9	9-12	12-15	15-18	-

[1] *C. pagurus* from 10-20 mm CW were exclusively used in experiments of the influence of temperature variations on ingestion rates of *M. edulis*.

Appendix B3. Size classes I-VI (mm in shell length) in which *Mytilus edulis*, *Ostrea edulis*, *Crassostrea gigas*, and *Cerastoderma edule* were offered to various size categories (mm carapace width) of *Carcinus maenas* and *Cancer pagurus* during trials where crabs were presented with a wide size range of paired combinations of prey species.

	Mytilus edulis -Ostrea edulis											
	M. edulis						*O. edulis*					
	I	II	III	IV	V	VI	I	II	III	IV	V	VI
C. maenas												
15-25	3-6	6-9	9-12	12-15	15-18	-	3-6	6-9	9-12	12-15	15-18	-
25-35	3-6	6-9	9-12	12-15	15-18	-	3-6	6-9	9-12	12-15	15-18	-
40-55	5-10	10-15	15-20	20-25	25-30	-	5-10	10-15	15-20	20-25	25-30	-
55-70	5-10	10-15	15-20	20-25	25-30	-	5-10	10-15	15-20	20-25	25-30	-
C. pagurus												
20-30	<4	4-8	8-12	12-16	16-20	-	3-6	6-9	9-12	12-15	15-18	-
30-40	4-8	8-12	12-16	16-20	20-24	-	3-6	6-9	9-12	12-15	15-18	-
	Mytilus edulis - Crassostrea gigas											
	M. edulis						*C. gigas*					
C. maenas												
15-25	3-6	6-9	9-12	12-15	15-18	-	6-9	9-12	12-15	15-18	18-21	-
25-35	3-6	6-9	9-12	12-15	15-18	-	6-9	9-12	12-15	15-18	18-21	-
40-55	-	10-15	15-20	20-25	25-30	35-40	-	10-15	15-20	20-25	25-30	35-40
55-70	-	10-15	15-20	20-25	25-30	35-40	-	10-15	15-20	20-25	25-30	35-40
C. pagurus												
20-30	<4	4-8	8-12	12-16	16-20	-	3-6	6-9	9-12	12-15	15-18	-
30-40	4-8	8-12	12-16	16-20	20-24	-	6-9	9-12	12-15	15-18	18-21	-
	Ostrea edulis - Crassostrea gigas											
	O. edulis						*C. gigas*					
C. maenas												
15-25	3-6	6-9	9-12	12-15	15-18	-	3-6	6-9	9-12	12-15	15-18	-
25-35	6-9	9-12	12-15	15-18	18-21	-	6-9	9-12	12-15	15-18	18-21	-
40-55	-	10-15	15-20	20-25	25-30	35-40	-	10-15	15-20	20-25	25-30	35-40
55-70	-	10-15	15-20	20-25	25-30	35-40	-	10-15	15-20	20-25	25-30	35-40
C. pagurus												
20-30	3-6	6-9	9-12	12-15	15-18	-	3-6	6-9	9-12	12-15	15-18	-
30-40	6-9	9-12	12-15	15-18	18-21	-	3-6	6-9	9-12	12-15	15-18	-
	Mytilus edulis - Cerastoderma edule											
	M. edule						*C. edule*					
C. maenas												
15-25	3-6	6-9	9-12	12-15	15-18	-	3-6	6-9	9-12	12-15	15-18	-
25-35	<4	4-8	8-12	12-16	16-20	-	<4	4-8	8-12	12-16	16-20	-
40-55	-	10-15	15-20	20-25	25-30	35-40	-	10-15	15-20	20-25	25-30	35-40
55-70	-	10-15	15-20	20-25	25-30	35-40	-	10-15	15-20	20-25	25-30	35-40
C. pagurus												
20-30	4-8	8-12	12-16	16-20	20-24	-	2-4	4-6	6-8	8-10	10-12	-
30-40	4-8	8-12	12-16	16-20	20-24	-	3-6	6-9	9-12	12-15	15-18	-

Appendix C1. Results of appropriate analyses of variance and pairwise comparisons on profitability data of *Mytilus edulis* (M), *Ostrea edulis* (O), *Crassostrea gigas* (C), and *Cerastoderma edule* (E), following homogeneity of variance tests (Hom.Var.). Diff. Mean=difference between means; SE=standard error of the mean; CI (Low)=low limit of confidence interval; CI (High)=high limit of confidence interval; * p < 0.05; ns = no significant difference between pairs of variables.

	Hom.Var.	Test	Pairwise Comp.	Diff. Mean	SE	CI (Low)	CI (high)	*p*
C. maenas 15-25 mm CW	Levene's	ANOVAR	M-O	0.76	0.088	0.50	1.02	*
	statistic	+ Scheffe	M-C	1.03	0.098	0.74	1.31	*
	2.26		M-E	0.37	0.085	0.12	0.62	*
	$p=0.10$	$F=48.19$	O-C	0.26	0.113	-0.07	0.59	ns
		$p<0.001$	O-E	-0.39	0.101	-0.69	-0.09	*
			C-E	-0.65	0.120	-0.97	-0.33	*
25-35 mm CW	Levene's	ANOVAR	M-O	0.31	0.081	0.072	0.54	*
	statistic	+ Scheffe	M-C	0.67	0.081	0.44	0.91	*
	2.26		M-E	-0.12	0.061	-0.30	0.05	ns
	$p=0.09$	$F=34.17$	O-C	0.36	0.100	0.07	0.65	*
		$p<0.001$	O-E	-0.43	0.085	-0.68	-0.19	*
			C-E	-0.80	0.085	-1.04	-0.55	*
40-55 mm CW	Levene's	ANOVAR	M-O	0.31	0.089	0.05	0.56	*
	statistic	+ Scheffe	M-C	0.58	0.070	0.37	0.78	*
	1.99		M-E	-0.12	0.065	-0.31	0.07	ns
	$p=0.13$	$F=30.98$	O-C	0.27	0.102	-0.03	0.56	ns
		$p<0.001$	O-E	-0.43	0.098	-0.72	-0.15	*
			C-E	-0.70	0.082	-0.94	-0.46	*
55-70 mm CW	Levene's	ANOVAR	M-O	0.60	0.072	0.39	0.80	*
	statistic	+ Scheffe	M-C	0.66	0.078	0.44	0.89	*
	2.44		M-E	-0.17	0.062	-0.35	0.004	ns
	$p=0.07$	$F=60.00$	O-C	0.07	0.083	-0.17	0.305	ns
		$p<0.001$	O-E	-0.77	0.068	-0.97	-0.57	*
			C-E	-0.84	0.075	-1.05	-0.62	*
C. pagurus 20-30 mm CW	Levene's	ANOVAR	M-O	0.48	0.071	0.27	0.68	*
	statistic	+ Scheffe	M-C	0.74	0.086	0.49	0.99	*
	0.43		M-E	0.29	0.068	0.10	0.49	*
	$p=0.73$	$F=33.75$	O-C	0.26	0.101	-0.03	0.56	ns
		$p<0.001$	O-E	-0.18	0.086	-0.43	0.07	ns
			C-E	-0.44	0.099	-0.73	-0.16	*
30-40 mm CW	Levene's	ANOVAR	M-O	0.63	0.079	0.40	0.86	*
	statistic	+ Scheffe	M-C	0.62	0.094	0.35	0.89	*
	0.44		M-E	0.18	0.089	-0.08	0.44	ns
	$p=0.73$	$F=29.47$	O-C	-0.01	0.109	-0.33	0.30	ns
		$p<0.001$	O-E	-0.45	0.105	-0.76	-0.15	*
			C-E	-0.44	0.117	-0.78	-0.10	*

Appendix C2. Results of appropriate analyses of variance and pairwise comparisons on breaking time data of *Mytilus edulis* (M), *Ostrea edulis* (O), *Crassostrea gigas* (C), and *Cerastoderma edule* (E), following homogeneity of variance tests (Hom.Var.). Diff.Mn.=difference between means; SE=standard error of the mean; CI (Low)=low limit of confidence interval; CI (High)=high limit of confidence interval; Diff.Md=difference between medians; SD=standard deviation; * p < 0.05; ns = no significant difference between pairs of variables.

	Hom.Var.	Test	Pairwise Comp.	Diff.Mn.	SE	CI (Low)	CI (High)	*p*
C. maenas 15-25 mm CW	Levene's	ANOVAR	M-O	-0.41	0.168	-0.91	0.08	ns
	statistic	+ Scheffe	M-C	-0.46	0.187	-0.101	0.08	ns
			M-E	0.25	0.162	-0.22	0.72	ns
	2.55	$F = 6.08$	O-C	-0.05	0.214	-0.68	0.58	ns
	$p = 0.07$	$p < 0.01$	O-E	0.66	0.193	0.10	1.23	*
			C-E	0.71	0.209	0.10	1.33	*
				Diff.Md.	SD	Diff Md/SD		
25-35 mm CW	Levene's	Kruskal-Wallis	M-O	5.8	6.67	0.87		ns
	statistic	+ Dunn	M-C	4.4	6.67	0.66	Stand. Err. Diff = 2.64	ns
			M-E	19.0	5.03	3.78		*
	2.90	$H = 14.67$	O-C	1.4	8.26	0.17		ns
	$p < 0.05$	$p < 0.01$	O-E	13.2	7.00	1.89		ns
			C-E	14.6	7.00	2.09		ns
40-55 mm CW	Levene's	ANOVAR	M-O	-0.17	0.138	-0.57	0.23	ns
	statistic	+ Scheffe	M-C	-0.23	0.109	-0.54	0.09	ns
			M-E	0.58	0.101	0.29	0.87	*
	2.54	$F = 16.92$	O-C	-0.05	0.158	-0.51	0.41	ns
	$p = 0.07$	$p < 0.001$	O-E	0.75	0.153	0.31	1.20	*
			C-E	0.81	0.128	0.44	1.18	*
55-70 mm CW	Levene's	ANOVAR	M-O	-0.19	0.136	-0.58	0.20	ns
	statistic	+ Scheffe	M-C	-0.24	0.148	-0.66	0.19	ns
			M-E	0.18	0.118	-0.16	0.52	ns
	0.59	$F = 4.30$	O-C	-0.05	0.157	-0.50	0.40	ns
	$p = 0.63$	$p < 0.01$	O-E	0.37	0.130	-0.0002	0.75	ns
			C-E	0.42	0.142	0.01	0.83	*
C. pagurus 20-30 mm CW	Levene's	Kruskal-Wallis	M-O	-	-	-		-
	statistic		M-C	-	-	-		-
			M-E	-	-	-		-
	3.52	$H = 2.44$	O-C	-	-	-		-
	$p < 0.05$	$p = 0.49$	O-E	-	-	-		-
			C-E	-	-	-		-
30-40 mm CW	Levene's	ANOVAR	M-O	-0.20	0.092	-0.46	0.07	ns
	statistic	+ Scheffe	M-C	-0.55	0.109	-0.86	-0.23	*
			M-E	-0.06	0.103	-0.36	0.23	ns
	2.59	$F = 8.84$	O-C	-0.35	0.126	-0.71	0.02	ns
	$p = 0.06$	$p < 0.001$	O-E	0.13	0.121	-0.22	0.48	ns
			C-E	0.48	0.135	0.09	0.87	*