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The impact of Carcinus Maenas on commercial mussel beds

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THE IMPACT OF *CARCINUS MAENAS* ON COMMERCIAL MUSSEL BEDS

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Ph.D. Thesis

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SUMMARY

This thesis examines the impact of the shore crab, *Carcinus maenas*, on commercial mussel beds. The seasonal abundance of *C. maenas* was determined in the Menai Strait, where densities varied from around 0.2 crabs m^{-2} in winter to 1.5 crabs m^{-2} in summer. Day length showed a strong seasonal correlation with crab abundance and may be the cue which initiates migration offshore by crabs.

Laboratory experiments showed that the number of mussels consumed by *C. maenas* decreased exponentially as the size of mussels presented was increased. The number of mussels eaten was greatest at 13°C, decreasing at higher and lower temperatures. Catch per unit effort by the commercial shore crab fishery in the Menai Strait did not accurately reflect abundance but co-varied with temperature due to the temperature-dependence of feeding rates, which were the main influence on catches. Thus, baited trap catches are likely to be a relatively poor estimator of crab abundance.

Shore crabs foraged more efficiently in the presence of conspecifics, by foraging optimally sized mussels, and were able to identify the most profitable patches of mussels in which to forage. This behaviour presumably influences the distribution of crabs in the wild. Mixing larger mussels, above the size most often selected by crabs, with smaller, more vulnerable, mussels may help to reduce losses by increasing foraging time.

The biodiversity of mussel assemblages was examined in the commercial mussel beds in the Menai Strait and in natural and cultivated mussels in Maine, USA. Rope-grown mussels possessed a significantly greater biomass of associated macrofauna than cultivated subtidal mussels or natural intertidal mussels. There were significantly fewer individuals associated with subtidal mussels than with intertidal or rope-grown mussels in Maine. Twenty-seven taxa were found among cultivated intertidal mussels in the Menai Strait, while 15 taxa were associated with naturally occurring intertidal mussels in Maine.

A predation model is presented that is used to estimate mussels lost to crab predation during the cultivation process. This model can also potentially be applied to other areas of mussel cultivation subject to shore crab predation. The model may also be more generally applicable to other bivalve species subject to crab predation, although further work will be necessary to determine appropriate coefficients for other species.

It is concluded that *Carcinus maenas* is a major predator of mussels during the three year cultivation process, consuming approximately 10% of the mussels re-laid to the Menai Strait. The main factor influencing the numbers of mussels lost to crab predation is the growth of mussels; thus most effort to reduce the impact of crabs should be expended on protecting mussels during the first year of cultivation.

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CHAPTER 1

GENERAL INTRODUCTION

The blue mussel, *Mytilus edulis* (Linnaeus), is a member of the family Mytilidae, class Bivalvia. The genus *Mytilus* also includes *M. galloprovincialis*, *M. californianus* and *M. trossulus* (Gosling, 1992). In mussels food is acquired by filtering seston – phytoplankton, bacteria and particulate matter – from the water column; particles without nutritional value are rejected as pseudofaeces (Hawkins and Bayne, 1992). Seston availability is a major factor in determining mussel growth (Jorgensen, 1976; Bayne *et al.*, 1987). *M. edulis* is a facultative anaerobe and has been shown to tolerate extremely low oxygen concentrations (0.21 mg L^{-1}) for up to 35 days at 10 °C (Theede *et al.*, 1969) although survival is heavily dependent on temperature. *M. edulis* can tolerate temperatures ranging from below freezing (Williams, 1970) to 29 °C (Read and Cumming, 1967) depending on the period of exposure. Consequently, mussels can survive over a wide geographical range and in varied habitats and are well suited to both extensive and intensive cultivation.

Mytilus edulis is competitively a superior species on rocky shores (Seed, 1996) and a model organism in studies of physiology (Hawkins and Bayne, 1992), biochemistry (Zwaan and Mathieu, 1992) and genetics (Gosling, 1992). *M. edulis* beds have also been identified as hotspots of biodiversity in numerous studies (Tsuchiya and Nishihira, 1985; Seed and Suchanek, 1992; Seed, 2000; Saier, 2002). *M. edulis* is most often found in the intertidal zone attached to rocky, gravely or other hard substrates by byssus (Seed, 1969a; 1976; Yonge, 1976), strands of protein secreted from glands in the foot. However, it can also be found attached to macroalgae and stones in soft sediments, often in clumps that provide a more secure anchorage. Mussel patches on rocky shores are important habitats for a wide variety of macrofauna, which includes polychaetes, cnidarians, poriferans, crustaceans, molluscs and nemerteans, and exhibit high spatial and temporal diversity (Seed, 1996). Likewise, mussel beds on sand and muddy

substrata may be inhabited by barnacles, hydrozoans, bryozoans, and polychaetes (Enderlein and Wahl, 2004).

Mussels are cultivated and fished worldwide for human consumption, with a world mussel catch of 1.94 million tonnes in 2005, of which the United Kingdom catch constituted 11,158 tonnes (FAO, 2007). Mussels of the genus *Mytilus* are the most commonly cultivated species globally, but species of *Perna* are also cultivated in East Asia and Australasia (Hickman, 1992). The main methods of mussel cultivation are raft, pole and bottom culture (Mason, 1972; Hickman, 1992; Garen *et al.*, 2004) in addition to artisanal harvesting from naturally occurring populations. Pole and rope culture are the predominant methods of cultivation in southern Europe, both of which involve raising mussels off the seabed. Rope cultivation is most suited to deep water areas and produces fast growing, clean mussels, and is the predominant method of cultivation in Spain and Scotland, for instance (Smaal, 2002). The cultivation of mussels on the seabed is more suited to shallow extensive areas but mussels are subjected to heavier predation and are slower growing than on ropes; on-bottom cultivation is the only mussel cultivation method used in the Netherlands (Dijkema, 1997).

Small mussels (~20 mm length) may be harvested from natural populations to stock on-bottom or suspended cultivation sites. These seed mussels may be taken from recently settled beds, or from more established populations (Murray *et al.*, 2007). Although the harvesting of seed mussel could lead to a decrease in naturally occurring mussel populations, Kaiser *et al.* (1998) suggested that if mussel seed beds were not exploited then the mussels would be lost to predators and storms. *Asterias rubens* and juvenile *Carcinus maenas* are major predators of small mussels (Dolmer, 1998; Burch and Seed, 2000; Saier, 2001). However, clearly some mussel seed does survive to sustain natural populations, and the potential to overexploit seed mussels does exist. Furthermore, introducing *M. edulis* into a habitat where the species may not be present naturally, or where it exists only in small numbers, has a potential major impact on the local ecosystem.

As a valuable resource, seed mussel stocks should be used as efficiently as possible to allow the greatest yields to be obtained from fisheries. Predation is a

major source of mussel losses in natural and cultivated populations. The predominant predators of *M. edulis* are the common starfish *Asterias rubens*, the shore crab *Carcinus maenas*, the dogwhelk *Nucella lapillus* and many bird species including gulls, diving ducks and waders. *A. rubens* has been shown to reduce *M. edulis* abundance by half in the Wadden Sea (Saier, 2001), while yields of seed mussels may be increased eight-fold when protected from *C. maenas* (Davies *et al.*, 1980). Oystercatchers *Haematopus ostralegus* may consume up to three mussels per five minutes (Goss-Custard *et al.*, 1984), and herring gulls *Larus argentatuts* can also feed extensively on seed mussels (Sibly and McCleery, 1983).

Although studies have estimated predator feeding rates on mussels, including the predators *A. rubens* (Saier, 2001), *H. ostralegus* (Ens and Goss-Custard, 1984), and *C. maenas* (Beadman *et al.*, 2003), no studies have made specific estimates of the mussel losses resulting from crab predation during the cultivation process, and mussel size, crab size and abundance have not been related to predation estimates. Dare and Edwards (1976) measured total predation on intertidal mussels in the Menai Strait throughout a two year period of growth, attributing most mussel losses to *C. maenas* or *H. ostralegus*. Furthermore, Caldow *et al.* (2004) estimated that over-wintering *H. ostralegus* consumed 3.5% of the autumn stock of mussels on intertidal mussels beds in the Menai Strait, United Kingdom. Predation is influenced by the preference of the predator (Elner and Hughes, 1978; Jubb *et al.*, 1983; Jackson and Underwood, 2007), the available size distribution of prey (Burch and Seed, 2000), the prey species (Mascaro and Seed, 2000) and environmental variables, such as temperature (Wallace, 1973; Elner, 1980). Thus, to estimate effectively the impact of a predator on a prey species some measure of the influence of each of these variables is necessary.

Carcinus maenas is a member of the family Portunidae, the swimming crabs, class Crustacea. It is found in the intertidal and subtidal zones and has a preferred salinity range of around 20 to 40 (Thomas *et al.*, 1981; Ameyaw-Akumfi and Naylor, 1987; McGaw and Naylor, 1992). *C. maenas* is omnivorous but smaller individuals (<30 mm Carapace Width, CW) consume more vegetation, while larger crabs feed predominantly on molluscs (Crothers, 1968). During the first 130 days of life *C. maenas* moults around six times, but the frequency of moulting

is increased at higher temperatures (Breteler, 1975). After the first year of life moulting occurs approximately once a year (Crothers, 1967). For around one to two weeks after moulting the crab ceases feeding until the exoskeleton hardens, and is highly vulnerable to predation during this period. It has been suggested that *C. maenas* moves into deeper water (>6 m) when temperatures are below ~8 °C (Atkinson and Parsons, 1973) but returns to intertidal waters when the temperature increases (Naylor, 1962; Welch, 1968). Thus, shore crabs are generally absent from the intertidal zone during winter (Crothers, 1968; Gascoigne *et al.*, 2005). On mussel beds in the Wadden Sea, Saier (2002) found that *C. maenas* was significantly more abundant in the intertidal zone than in the subtidal zone; however, juvenile crabs (<10 mm CW) accounted for around 90 % of specimens in both zones.

Although *M. edulis* can form a major part of the diet of *C. maenas*, the prey consumed by shore crabs is varied and includes molluscs, polychaetes and crustaceans (Ropes, 1968; Raffaelli *et al.*, 1989). Temperature has a major influence on overall food consumption, and is 2.4 times higher in *C. maenas* acclimated at 24 °C than in those acclimated at 10 °C, though metabolism does not vary proportionally with feeding rates (Wallace, 1973), which are dependent on several factors. *C. maenas* exists in green and red forms; this colouration is visible on the abdomen, thorax and chelae, ranging from a dark red and orange to pale yellowish green. Red forms of *C. maenas* are all in late inter-moult, evident from a greater level of fouling and limb autonomy than in green forms (Kaiser *et al.*, 1990) but carapace colour is not an indicator of moult stage (Reid *et al.*, 1997).

There have been several studies of *C. maenas* in the Menai Strait where the species occurs commonly (Dare and Edwards, 1976; Sanchez-Salazar *et al.*, 1987a; Hunter and Naylor, 1993; Gascoigne *et al.*, 2005). The Menai Strait is a 20 km mile long stretch of water that separates the Isle of Anglesey from mainland Wales. The depth of the Strait ranges from just a few metres to 22 m. The tide flows towards the northeast on the flood, and to the southwest on the ebb; the residual flow is to the southwest (Tweddle *et al.*, 2005). Temperatures in the Strait range from 5°C to 17°C. The commercial mussel fishery is located at the north-

eastern end of the Strait and covers an area of 5.1 km^2, in the intertidal and subtidal zones.

Around half of the total UK production of mussels (*M. edulis*) is derived from extensive on-bottom culture in the Menai Strait (DEFRA, 2002), all of which is exported to mainland Europe. Mussel cultivation occurs exclusively on the seabed, as the shallow water depth at low spring tides, combined with shipping traffic, make any off-bottom culture economically unfeasible. In addition, slower growth rates in the UK due to lower temperatures require higher yields to make off-bottom culture economically viable, with mussels taking ~2.5 years to reach marketable size (Mason, 1972). However, seston supply is of prime importance and growth rates sufficient to be economically viable are achieved with raft culture in Scottish waters. Dare and Edwards (1976) recorded growth of re-laid seed mussels from a mean of 27 mm length to 50 mm over 15 to 20 months in the Menai Strait.

C. maenas is also fished commercially in the Menai Strait; though the effectiveness of this fishery has not been quantified. Furthermore, many studies of *C. maenas*, in the Menai Strait and elsewhere, deal with population dynamics mainly within the intertidal zone (e.g. Naylor, 1962; Hunter and Naylor, 1993; Gascoigne *et al.*, 2005). Most studies also give estimates of relative abundance (Welch, 1968; Dare and Edwards, 1976; Rewitz *et al.*, 2004). Although such studies are useful in initial assessments of the population structure of *C. maenas*, baited trap catches are influenced by the activity of crabs and may be size and sex biased (Williams and Hill, 1982) and therefore are not useful in determining the impact of *C. maenas* as a predator of mussels.

Numerous behavioural studies have been conducted involving *C. maenas* feeding on *M. edulis*, which have greatly elucidated the feeding behaviour of this species; however, these studies cannot generally be applied to practical problems in the natural environment. In the Menai Strait knowledge of the population dynamics of the shore crab is surprisingly poor. The only information on when crabs copulate and moult, and when eggs hatch is anecdotal, and there is no general consensus among stakeholders (Morris *et al.*, 2007). There are currently no estimates of the

absolute abundance of shore crabs anywhere in the Menai Strait. Mussel fishermen estimate that 90% of mussels are lost during the cultivation process but the contribution of shore crabs to these losses has been unknown to date. It has been assumed that crabs are major predators of mussels based on the observed losses and the regular presence of crabs on the mussel beds. Furthermore, the relationship between crab and mussel size, temperature, and crab morphology must be considered for any realistic estimate of the impact of this predator on local mussel stocks to be made.

The aim of this study was to determine the losses of mussels resulting from *Carcinus maenas* predation during the cultivation process. This thesis begins with a brief overview of mussel biology and cultivation, and the potential impact of *C. maenas* as a predator of mussels (this chapter). Chapter 2 examines the abundance of *C. maenas* in the Menai Strait over a period of 18 months. Spatial and temporal variation in the number of crabs is considered. It was then necessary to determine the feeding rates of these local crab populations. Thus, in Chapter 3 mussel size selection and crab feeding rates are examined. The relationships between crab size, feeding rates and prey selection, and between mussel size frequency distribution, feeding rates and prey selection are described. The effects of temperature and crab sex and colour were also assessed. Having examined prey selection by *C.maenas*, in Chapter 4 the ability of shore crabs, maintained either individually or in groups, to select the most profitable mussel patches in which to forage is examined. In Chapter 5 the fauna associated with the mussel beds in the Menai Strait was identified and the contribution of these species to the diet of *C. maenas* was ascertained. However, natural and cultivated mussel beds are found worldwide; thus, the relevance of the work presented in this thesis on a wider scale is dependent on the variability found in mussel assemblages under different cultivation or environmental regimes. Therefore, natural intertidal and cultivated subtidal mussel beds were also examined, together with raft-grown mussel assemblages in Maine, USA, the results of which are presented in Chapter 6.

In the first five research chapters all the necessary data was compiled and hypotheses tested to make predictions regarding the effects of *C. maenas* on the cultivated mussel beds in the Menai Strait. In Chapter 7 a predation model is

developed that allows the number of mussels consumed by crabs to be estimated throughout the cultivation process. Catches of shore crabs by the crab fishery in the Menai Strait are also considered in relation to the results presented in Chapters 2 and 3 concerning abundance and feeding rates, respectively. A general discussion is presented in Chapter 8. The financial costs of mussel losses due to *C. maenas* are estimated, and methods to mitigate crab predation suggested. The wider applicability of this work is also discussed.

CHAPTER 2

MUSSEL CULTIVATION AND THE POPULATION DYNAMICS OF *CARCINUS MAENAS*

ABSTRACT

Cultivated mussel beds provide a major food resource for *Carcinus maenas* throughout the year. Crabs can consume all but the largest mussels, which are found towards the end of the cultivation process that takes approximately three years. The aim of the present study was to determine the abundance of *C. maenas* throughout the year in relation to temperature and mussel cultivation sites, and to identify changes in the crab population structure. *C. maenas* abundance was measured using video surveys of the cultivated mussel beds and surrounding areas in the Menai Strait for a period of 18 months. The structure of the *C. maenas* population was assessed based on samples collected from dredging vessels and the crab fishery. Data were also collected on temperature, mussel population structure, and the number of crabs removed by the local *C. maenas* fishery. Male crabs moulted predominantly in April, followed by female crabs in June. Most ovigerous females were found during January. The maximum *C. maenas* abundance was ~150,000 crabs ha^{-1} in July 2006, falling to <2,000 crabs ha^{-1} during the winter. The peaks in crab abundance in 2006 and 2007 preceded the maximum temperature by around two months in both years. Based on the results of video surveys, *C. maenas* was absent from the intertidal zone during the winter, but migrated extensively over and around the mussel beds during the rest of the year. The high numbers of *C. maenas* over the mussel beds and their effect through predation were found during most of the year undoubtedly represent a major source of mussel losses in the Menai Strait. The number of crabs found in the *C. maenas* population throughout the year can be modelled using a sine wave function, reducing the requirement for regular monitoring of the population in order to determine the potential economic costs of crab predation on cultivated mussel beds.

2.1 INTRODUCTION

Mussel cultivation involves growing mussel from seed of around 20 mm in length to marketable size of around 50 mm, a process which takes around 3 years. During this time mussels may be subjected to heavy predation. The predominant predators of *M. edulis* in the United Kingdom are the common starfish (*Asterias rubens*), the shore crab (*Carcinus maenas*), the dogwhelk (*Nucella lapillus*) and many bird species including gulls, diving ducks and waders. *A. rubens* has been shown to reduce *M. edulis* abundance by half in the Wadden Sea (Saier, 2001), while yields of seed mussels may be increased by eight times when protected from *C. maenas* predation (Davies *et al.*, 1980).

Seed mussels used to stock cultivated mussel beds are usually dredged from natural stocks, and the time and extent of natural settlement determines when seed mussels can be harvested and how much can be imported to cultivation sites. In extensive on-bottom culture seed is laid on the seabed at approximately 10 % of natural densities and left to grow (Hickman, 1992). Many other species may also be transported with the seed mussels, including *C. maenas*, *Cancer pagurus*, *Asterias rubens*, and *Nucella lapillus* (Davies, 2003), thus exacerbating the level of predation at the cultivation sites. *C. maenas* is an invasive species that can survive under a wide range of environmental conditions (Roman and Palumbi, 2004) and is considered detrimental to both molluscan (Walton *et al.*, 2002; Miron *et al.*, 2005 and crustacean (Rossong, 2006; Williams *et al.*, 2006) fisheries.

C. maenas is found in the intertidal and subtidal zones and has a preferred salinity range of around 20 to 40 (Thomas *et al.*, 1981; Ameyaw-Akumfi and Naylor, 1987; McGaw and Naylor, 1992). *C. maenas* is omnivorous with younger individuals (<30 mm carapace width, CW) consuming more vegetation, and mature animals feeding predominantly on molluscs (Crothers, 1968). During the first 130 days of life *C. maenas* moults around six times (Breteler, 1975). After the first year of life growth decreases with moulting occurring approximately once a year (Crothers, 1967) and for around one to two weeks after moulting the crab ceases feeding until the exoskeleton hardens.

Hunter and Naylor (1993) observed extensive tidal migration by *C. maenas* in the Menai Strait, in particular by green male crabs >30 mm in carapace width. During winter months *C. maenas* poses less of a problem to mussel cultivation sites as the crabs move into deeper water (>6 m) when temperatures fall below 8 °C, but return to intertidal waters when temperature increases (Naylor, 1962). Although *M. edulis* may form a major part of the diet of *C. maenas*, the prey consumed by *C. maenas* is varied, including molluscs, polychaetes and crustaceans (Elner, 1981). However, Raffaelli *et al.* (1989) found that *C. maenas* had a significant effect on the abundance of *Hydrobia ulvae* but not polychaetes, oligochaetes, nematodes or crustaceans in enclosure experiments, indicating that although a scavenger, *C. maenas* can also be a highly selective predator.

Several methods have previously been used to assess the relative abundance of *C. maenas* including baited (Rewitz *et al.*, 2004) and unbaited traps (Hunter and Naylor, 1993; Gascoigne *et al.*, 2005). Baited traps are likely to overestimate abundance whilst traps without bait will underestimate abundance, and in both cases the activity levels of crabs will affect the numbers caught. *C. maenas* exists in both green and red forms that reflect the stage of intermoult, with most red crabs being in the late intermoult stage (McGaw and Naylor, 1992; Styrishave *et al.*, 2004). Immediately after moulting crabs are pale green, then over time develop a light orange colouration which later develops into a dark red colour. Red *C. maenas* have thicker carapaces and stronger chelae than green forms but are less tolerant of low salinities and reduced oxygen concentrations (Reid *et al.*, 1997). However, red forms exert greater chelal force than green *C. maenas* (Kaiser *et al.*, 1990), possibly giving red crabs a feeding advantage. Moreover, red *C. maenas* are further advantaged by having heavier chelae allowing them to win more fights than green crabs (89 %) (Sneddon *et al.*, 2000). Green *C. maenas* are tolerant of a wider range of salinities (McGaw and Naylor, 1992) and temperatures (Wallace, 1973) than red crabs. Shore crabs inhabit a diverse range of environments including rocky shores, sand and mud flats (Jensen *et al.*, 2002; Rewitz *et al.*, 2004) and mussel beds (Beadman *et al.*, 2004). *C. maenas* gather at mating 'hotspots' shortly before females moult (Van der Meeren, 1994). Following copulation, egg maturation takes several months (Naylor, 1962).

The aim of the present study was to establish the size ranges of mussels present on commercial mussel beds in the Menai Strait throughout the year, and to estimate the seasonal abundance and size of *C. maenas* (>30 mm CW). Both spatial and temporal variations in numbers were assessed. It was hypothesised that *C. maenas* abundance would increase in parallel with temperature. Sex ratios and colour ratios were also determined to identify when moulting and copulation occurred.

2.2 MATERIALS AND METHODS

Mussel populations

Mussel cultivation in the Menai Strait follows a regular timetable under which seed mussels are imported annually during July and August, the exact timing depending on when natural stocks of newly settled mussels are located. These seed mussels are laid in the intertidal zone, where they are left to grow for around 2 years. The two-year old mussels are then moved to the subtidal zone for a final period of more rapid growth for 6 to 12 months. Mussels are harvested from October to March after between 28 and 33 months of growth. To determine the growth of mussels during the cultivation process, mussels were collected from three cohorts approximately every three months, each representing a distinct year class of mussels, at sites I1, I2 and S1-3 (Figure 2.1) from September 2005 to March 2007. Five 10 cm diameter cores of mussels were collected from the lower and upper limits of the intertidal mussel beds approximately every three months. Subtidal mussels were collected haphazardly from commercial dredges. All mussels were measured along the antero-posterior axis to 0.1 mm.

Crab population

To establish the abundance and size of *C. maenas* on the cultivated mussel beds in the Menai Strait, still images were extracted from video recordings of the seabed. A Mobitronic RV-2 Marine underwater camera was mounted on a steel frame at a height of 55 cm, giving a 50 cm x 50 cm field of view. The video images were recorded onto mini DV tape via an A/V cable using a Canon MV850i camcorder.

Three sites on the intertidal mussel beds and three on the subtidal mussel beds, together with three sites without mussels were identified (Figure 2.1). Sampling was conducted during the 2 hour period before high water during tides intermediate between neaps and springs once per month from April 2006 to September 2007. Sites were located using a handheld GPS receiver. Seabed images were recorded by lowering the camera frame from a boat onto the seabed and lifting and re-lowering it at intervals as the boat drifted with the tide. Transects of ~100m were recorded and 20 images extracted at random from the video. Still images were extracted using Video2Photo software. Image J software was used to enhance and analyse the images (Appendix A1). Mussel coverage and crab abundance were recorded, and the CW of crabs measured using Image J.

During the winter, from November until February, visibility on the subtidal mussel beds was poor due to a combination of high turbidity and low light levels. During these months crab abundance was estimated by collecting samples from commercial mussel dredging vessels. Start and finish points of trawls (Appendix A2) selected at random were recorded using a GPS receiver. Dredges were emptied into hoppers before mussels and crabs were passed up a conveyor belt where all visible crabs were removed, counted and measured. Six trawls (~250 – 1000 m long) were conducted each month from October 2006 to March 2007. During October, abundance as measured by dredging was compared to abundance measured using the video system. Carapace width (CW) was measured, and crab sex and colour were recorded. Trawls were also conducted from January to March 2006 (see Appendix A2 and A3). Crab abundance was also considered in relation to day length[1].

During April 2005, drop nets baited with mackerel were used to catch *C. maenas*. A drop net was deployed from the end of Bangor Pier (Figure 2.1) in the shallow

[1] Day length was calculated using an online day length and photoperiod calculator: Currah (2007) *Dawn to Dusk*. http://www.qpais.co.uk. Last accessed: 8th December 2007.

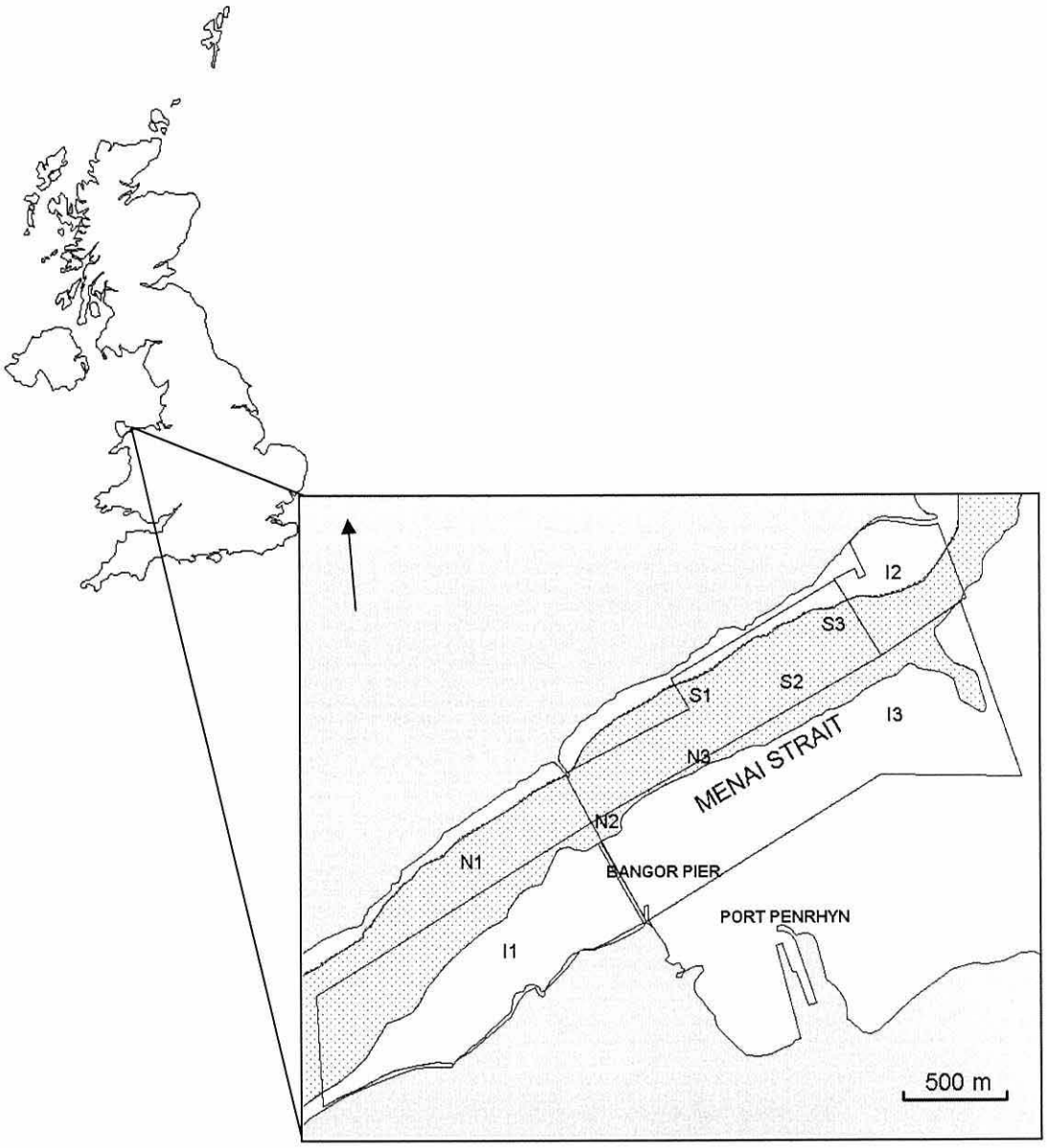


Figure 2.1. The intertidal (I), subtidal (S) and non-mussel sites (N) studied in the Menai Strait. Subtidal (dotted) and intertidal (white) zones are demarcated. Boxes show the legal limits (Several Order areas) of the mussel cultivation areas studied.

subtidal zone, and another halfway along the pier in the intertidal zone which remained submerged (<1 m depth at low water) at the time of sampling. The net was retrieved every 30 minutes for six hours from low water to high water. A net was also deployed and retrieved in the same manner from RV Prince Madog over the subtidal mussel beds for three days during April.

Data on monthly catches from the commercial *C. maenas* fishery in the Menai Strait were obtained[2]. *C. maenas* fishing occurs on and around the commercial mussel beds using traps baited with fish. The number of traps deployed and hauled, and the weight of crabs landed are recorded by fishermen; therefore, numbers of crabs were estimated from the relationship between CW and weight across the size range of crabs found on the mussel beds, based on the weights of a sub-sample of 50 crabs selected at random from traps and CW of crabs throughout the year. Seawater temperature was measured from January to October 2006 using a Valeport CTD mounted 0.5 m above Chart Datum at Ynys Faelog, 2 km south of the mussel beds [3]. From November 2006 to February 2007 temperature averaged from previous years' data was used due to equipment failure; from March 2007 onwards a Tinytag temperature logger was deployed at Ynys Faelog, in the same location as the CTD. A sub-sample of ~150 crabs was collected from commercial crab pots each month from April to September 2007 and carapace width, sex and colour of each crab was recorded.

Seed mussels

Seed mussels were collected from a commercial mussel dredging vessel (Valente) harvesting seed from Morecambe Bay during August 2006. The number of *C. maenas* collected with the seed mussels was estimated by sampling from the dredges after 30 separate trawls selected at random during four hours. Immediately after each dredge was emptied into the hold of the vessel, four buckets full of mussels were collected haphazardly within the hold from a position located by throwing a marker at random. The contents were emptied into a sorting

[2] Crab catch data were collected by Trevor Jones.
[3] The CTD was maintained by Gwynne Parry Jones and data made available by Dave Bowers and Graham Worley.

container, where all *C. maenas* were removed and measured. A sub-sample of 20 mussels was collected randomly from each of the 30 dredges. The total weight of mussels contained within each sample (4 buckets full) was estimated based on the mean weight of sub-sampled mussels and used to calculate the number of crabs per unit weight of mussels, and the number of mussels was estimated based on the mean size and weight of mussels in each sub-sample (Appendix A4). The mean weight of mussels ±1 S.D. per four-bucket sample was 9 ±0.06 kg.

2.3 RESULTS

Mussel populations

The mean length of mussels harvested in March, at the end of the harvesting period, did not differ significantly between 2006 and 2007 ($t = -0.19$, $p = 0.849$). All length frequency distributions approximated normal distribution. However, the mean length of seed mussels imported did differ significantly between 2006 and 2007 ($t = -3.44$, $p = 0.001$), and there was also a significant difference in length between the 2006 and 2007 year-classes of seed mussels after one year of growth ($t = 10.4$, $p<0.001$; Figure 2.2). The mean length of mussels harvested in January 2006 and 2007 was also significantly different ($t = 5.75$, $p<0.001$). However, it should be noted that the differences in mean lengths between 2006 and 2007 were small at 1.3, 3.4, 2.5 and 0.1 mm, respectively, during each stage of the cultivation process, from seed to final harvest, as shown in Figure 2.2.

On the commercial mussel beds in the Menai Strait, at any time during high water *C. maenas* has access to mussels ranging from around 20 mm up to 50 mm or greater (Figure 2.3). At low water crabs are restricted to feeding in the subtidal where mussels have a mean length >45 mm. During the first year of growth mussels increase in length by around 10 mm, by around 20 mm during the second year of growth, and by around 5 mm during the final 6 months of growth. Rapid growth occurs after mussels are laid (losses of small mussels to predators may also cause an apparent increase in size, as small mussels are eaten preferentially), while no or little growth occurs from October to March in either the first or second year of growth. Rapid growth occurs when mussels are moved

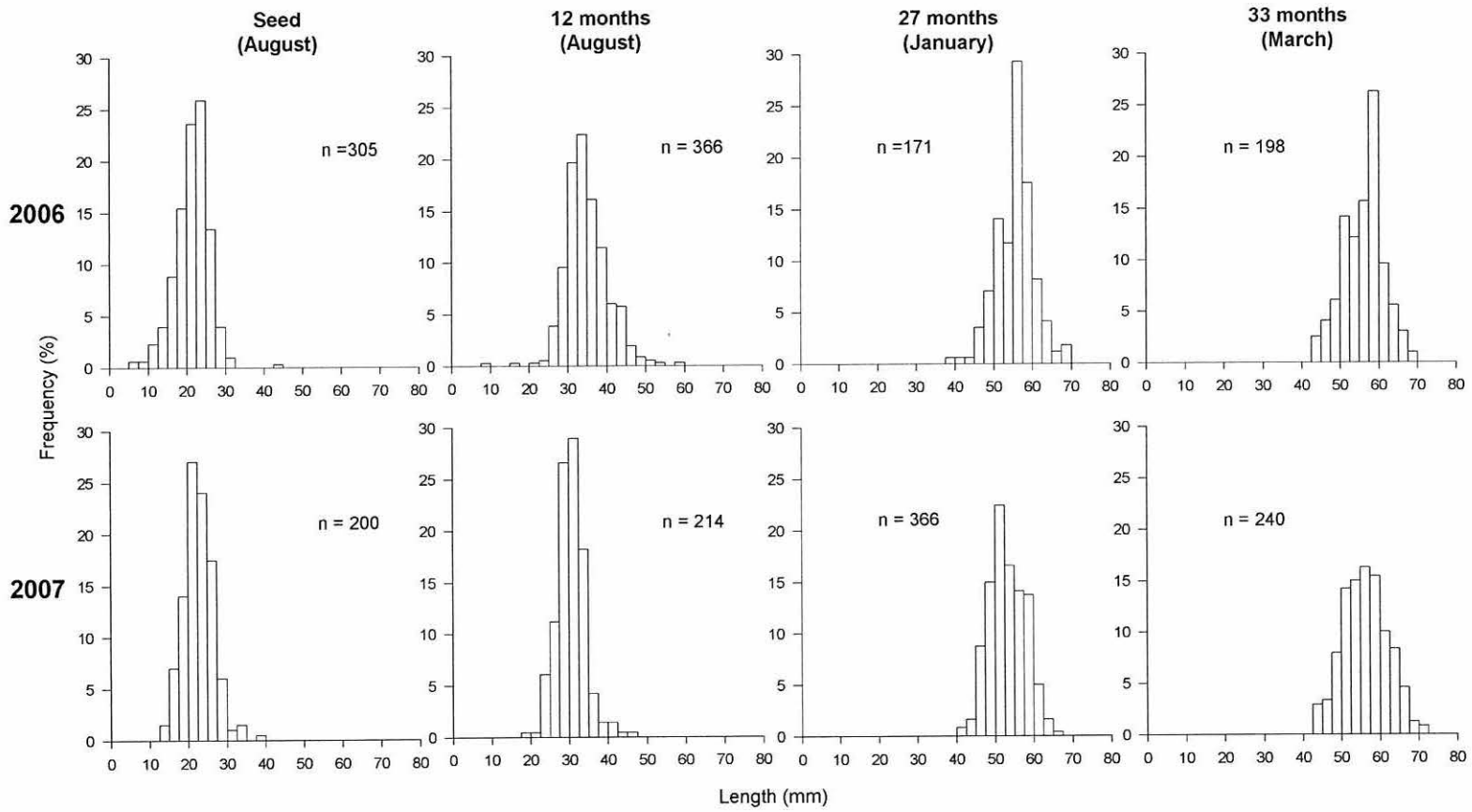


Figure 2.2. Length frequency distributions of mussels at different stages of the cultivation process during 2006 and 2007 at site I1 and on subtidal beds at the beginning and end of the harvesting period. Times shown are measured from when seed mussels were laid; months show when mussels were collected during each year.

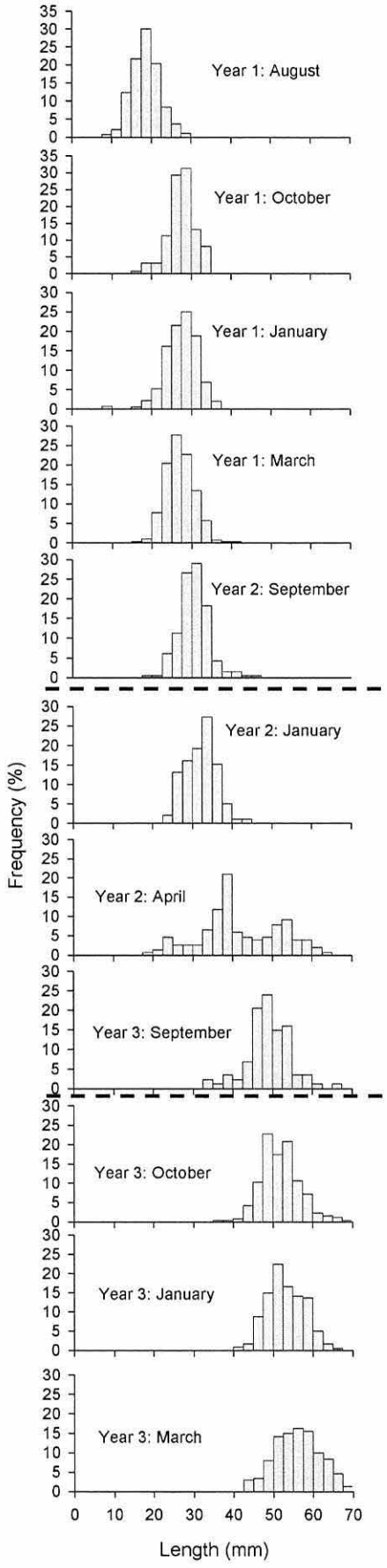


Figure 2.3. Mussel growth in the Menai Strait from seed to marketable size during three years of cultivation. Size frequency distributions were measured from three separate cohorts which are demarcated by dashed lines (Year 1 Aug – Sept 2006; Year 2 Jan – Sept 2007; Year 3 Oct – March 2007). NB. Year 2: April includes mussels from three cohorts, which are also apparent in Year 3: September.

to the subtidal zone between April and September. Overlapping of cohorts on the mussel beds is also apparent at certain times (see Figure 2.3) due to seed mussels being laid on existing older mussels and other mussels being missed by the dredging process and reaching a larger body size in the intertidal than most of the mussels present there.

Crab abundance

The mean number (±1 S.E.) of *C. maenas* per hectare measured by dredging (n = 6) in the subtidal zone ranged from 1,949 ±393 crabs ha^{-1} (0.19 ±0.04 crabs m^{-2}) in October to 324 ± 37 crabs ha^{-1} (0.03 ±0.004 crabs m^{-2}) in March. The mean number of crabs recorded in the video survey of the subtidal mussel beds one week before dredge sampling (Day 269) was 3,400 ±1,410 crabs ha^{-1} (0.34 ±0.14 crabs m^{-2}) and one week after dredge sampling in October 2006 (Day 283) was 2,536 ±1,239 crabs ha^{-1} (0.25 ±0.12 crabs m^{-2}). Both intertidal and subtidal video surveys showed a decline in abundance between September and October; thus it was estimated that dredging underestimated crab abundance by 33% and abundance estimates were increased by a factor of 1.5 accordingly. The number of crabs on the intertidal mussel beds, and overall, peaked during July 2006 (Day 190; Figure 2.4a) but no such peak was apparent intertidally in 2007.

There was an approximate inverse relationship between the number of crabs recorded in the intertidal and subtidal zones during the spring and summer months (Figure 2.4a and b) reflecting tidal migration by *C. maenas*. There was a slight decrease in mean CW during July 2006, probably due to smaller crabs being imported with seed mussels during this month. Overall, numbers of crabs decreased from July until the end of November (Day 354; Figure 2.4c). No crabs were recorded on intertidal mussel beds from the end of November 2006 to February 2007 (Day 418) and, based on estimates made by dredging, numbers remained steady in the subtidal zone during these months. During March 2007, numbers of crabs increased sharply in the intertidal zone. Mean CW remained between 40 and 50 mm on both intertidal and subtidal beds from March 2006 to April 2007, excluding the decrease in mean CW recorded during July and there

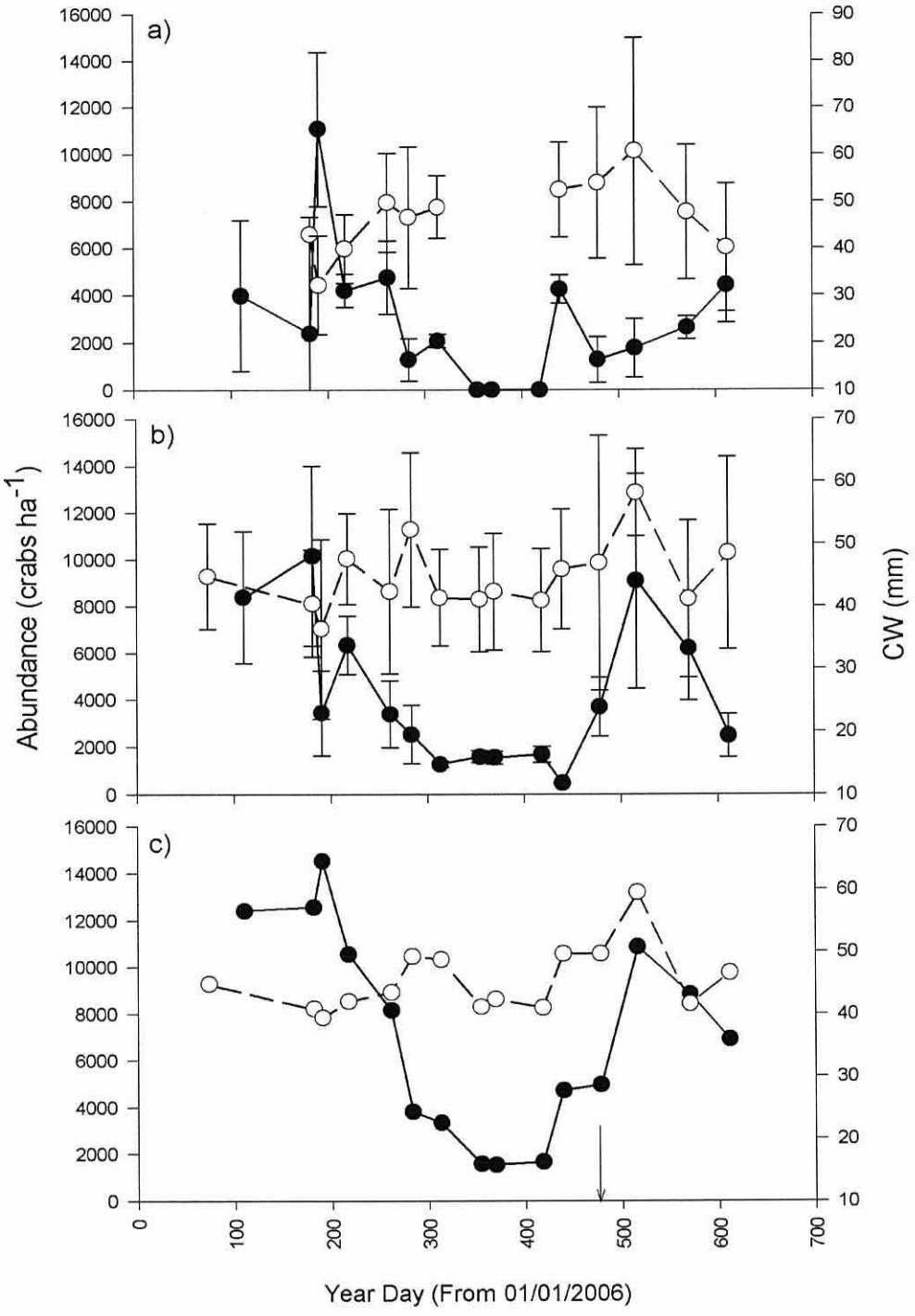


Figure 2.4. Abundance of *Carcinus maenas* (solid circles/line) and mean carapace width (CW, open circles/dashed line) on a) intertidal and b) subtidal mussel beds, and c) total numbers and mean CW on intertidal and subtidal mussel beds combined. Error bars show ±1 S.E. for abundance and ±1 S.D. for CW. Video surveys were conducted ~once monthly from 23/4/2006 to 3/9/2007. Arrow marks the beginning of the second year of surveys.

was also an increase in mean CW during May 2007, corresponding to the increase in abundance at these times.

Winter was defined as January to March, when seawater temperatures were lowest; spring, as April to June; summer, as July to September; and autumn as October to December. Crabs were mostly absent from the sites without mussels during the spring, but as total numbers increased, crabs were found at N1 and N2 (Table 2.1) in 2006 and at N1-3 during spring 2007. Site I2 had the highest abundance of crabs during any time of the year in 2006 (13,846 ±6,300 crabs ha^{-1}; 1.38 ±0.63 crabs m^{-2}), although sites I1 and S2 also exhibited abundances >10,000 crabs ha^{-1} during the summer, and there were >10,000 crabs ha^{-1} at S3 during the autumn. Numbers of *C. maenas* were low at I1 and I3 during spring 2006, when mussels were being moved to the subtidal zone, and at I1 and I2 during 2007. Site S2 had the highest mean abundance of crabs in 2007, during the summer months, with a value of 15,6000 ± 4,900 crabs ha^{-1} (15.6 ±0.49 m^{-2}).

Mean abundance across all sites from Spring to Autumn ranged from 3,256 ±1,901 to 4,059 ±1,244 crabs ha^{-1} (0.33 ±0.19 – 0.41 ±0.12 crabs m^{-2}); the biggest decrease in abundance occurred during the winter, when numbers fell to 510 ±88 crabs ha^{-1} (0.05 ±0.01 crabs m^{-2}). Site S3 had the highest annual mean abundance, at 5,188 ±1,553 crabs ha^{-1} (0.52 ±0.16 crabs m^{-2}). Sites N1-3 had the lowest mean annual abundance, ranging from 537 ±266 (0.05 ±0.02 crabs m^{-2}) at N1 to 1,212 ±522 (0.12 ±0.05 crabs m^{-2}) at N3. Of the three sites classified as being without mussels, site N3 was closest to the mussel beds. The mean abundance of crabs was similar during summer 2006 and 2007, at 4,100 ±1,400 crabs ha^{-1} (0.41 ±0.14 crabs m^{-2}) and 3,900 ±1,600 crabs ha^{-1} (0.39 ±0.16 crabs m^{-2}), respectively. Throughout the sampling period, sites I1 and S2 had the highest mean abundance of crabs, with 3,800 ±1,500 and 6,300 ±2,000 crabs ha^{-1}, respectively (0.38 ±0.15 and 0.63 ±0.2 crabs m^{-2}).

Both temperature and crab abundance exhibited pronounced annual maxima and minima (Figure 2.5). Two potential models of temporal variation in temperature and crab abundance can be adopted, both showing highly significant correlations

Table 2.1. Mean seasonal abundance ±1. S.E. of *Carcinus maenas* (crabs m^{-2}) on subtidal (S) and intertidal (I) mussel beds, and sites without mussels (N). Sampling was conducted three times per season. ND indicates no data.

Site	Spring 2006	Summer 2006	Autumn 2006	Winter 2006	Spring 2007	Summer 2007	Autumn 2007	Mean
N1	0 -	0.11 ± 0.05	ND	ND	0 -	0.08 ± 0.08	0 -	0.05 ± 0.02
N2	0 -	0.13 ± 0.06	ND	ND	ND	0.09 ± 0.06	0.12 ± 0.09	0.11 ± 0.03
N3	0 -	0 ± 0.00	0.36 ± 0.31	ND	0.06 ± 0.06	0.21 ± 0.14	0.37 ± 0.18	0.20 ± 0.07
I1	0.29 ± 0.20	1.08 ± 0.31	0.31 ± 0.09	0 -	0.05 ± 0.05	0.22 ± 0.11	0.65 ± 0.23	0.38 ± 0.15
I2	1.38 ± 0.63	0.5 ± 0.21	0.11 ± 0.06	0 -	0 -	0.25 ± 0.25	0 -	0.14 ± 0.19
I3	0 ± 0.00	0.16 ± 0.07	0.39 ± 0.11	0 -	0.35 ± 0.21	0.3 ± 0.13	ND	0.24 ± 0.07
S1	0.52 ± 0.52	0.1 ± 0.10	0.15 ± 0.15	0.1 ± 0.03	0 -	0.15 ± 0.15	0.37 ± 0.18	0.15 ± 0.07
S2	0.36 ± 0.22	1.06 ± 0.20	0.23 ± 0.16	0.09 ± 0.01	0.52 ± 0.31	1.56 ± 0.49	0.32 ± 0.13	0.63 ± 0.20
S3	0.38 ± 0.15	0.52 ± 0.12	1.07 ± 0.35	0.11 ± 0.01	0.18 ± 0.13	0.63 ± 0.17	0.13 ± 0.07	0.44 ± 0.13
Mean	0.33 ± 0.15	0.41 ± 0.14	0.37 ±0.12	0.05 ± 0.02	0.14 ± 0.07	0.39 ± 0.16	0.25 ± 0.08	

between time and temperature, and time and abundance. Over a single year temperature can be described using a cubic model (Figure 2.5a) where:

$$y = y_0 + ax + bx^2 + cx^3$$

And, y_0 = -75.3698, a = 0.9382, b = -0.0030, and c = 0.00001 (R^2 = 0.977, $F_{3,8}$ = 112.071, p<0.0001). Abundance can also be described using a cubic model, where y_0 = -11246.14, a = 387.953, b = -1.8121, and c = 0.0023 (R^2 = 0.965, $F_{3,7}$ = 64.271, p<0.0001). The parameters a and b control the axis of symmetry of the parabola, b is the curve of the parabola, and c determines the y-axis intercept. Assumptions of normality were met for temperature (K-S = 0.203, p = 0.654) and abundance (K-S = 0.132, p = 0.984) residuals, and residual variance was also equal for both temperature (p = 0.766) and abundance (p = 0.839). Beyond one year's data it is necessary to fit either a different cubic regression line for each year, or if abundance and temperature remain consistent between years then a sine wave function can be fitted (Figure 2.5b). Residuals were normally distributed for both temperature (K-S = 0.249, p = 0.267) and abundance (K-S = 0.222, p = 0.406), and variance was equal for both temperature (p = 0.873) and abundance (p = 0.853).

The relationship between time and temperature is best described by the function:

$$y = y_0 + a\sin\left(\frac{2\pi x}{b} + c\right)$$

Where, y_0 = 11.9461, a = 5.2611, b = 359.0206, and c = 3.4342 (R^2 = 0.973, $F_{3,11}$ = 133.184, p<0.0001). The coefficients relating time and abundance are y_0 = 6346.6918, a = 5403.6519, b = 387.4755, and c = -1.1890 (R^2 = 0.8154, $F_{3,11}$ = 16.201, p = 0.0002). The parameter b is the frequency and should be close to 365 days, as crab abundance and temperature follow an annual cycle. The parameter a is the amplitude, or magnitude of oscillation about the mean value of temperature or abundance, while y_0 is the displacement, and thus the mean abundance or temperature. The parameter c accounts for the differences in timing of the maximum and minimum abundance or temperature between years, and

thus must be adjusted between any two years. The peak abundance occurred earlier in 2007 than 2006, while the maximum temperature occurred slightly later in 2007 than 2006. It is clear from both the cubic model and sine wave model, that changes in abundance occur before changes in temperature but follow a similar pattern.

There was no significant correlation between mean monthly seawater temperature and *C. maenas* abundance (Figure 2.6a; $y = 467.1x + 438$, $R^2 = 0.229$, $F_{1,11} = 3.2635$, $p = 0.098$). However, there was a significant linear correlation between the temperature and the abundance measured one month earlier (Figure 2.6b; $y = 874.6x + 4222.2$, $R^2 = 0.679$, $F_{1,11} = 23.305$, $p = 0.0005$). This correlation was closer still between temperature and the abundance measured two months earlier (Figure 2.6c; $1018.6x + 5748.5$, $R^2 = 0.828$, $F_{1,11} = 53.101$, $p<0.0001$), suggesting a response to change in temperature rather than the temperature at any particular time. Residual variance was equal for all regressions ($p>0.583$) and residuals were normally distributed (K-S<0.173, $p>0.722$).

Day length ranges from only ~7.5 hours (in December) up to ~17 hours (in June) in the Menai Strait (Figure 2.7a). Unlike temperature, day length did show a significant correlation to *C. maenas* abundance without any lag ($y = 802.808 + -396.353x + 64.552x^2$; $R^2 = 0.805$, $F_{2,12} = 24.842$, $p<0.0001$; Figure 2.7b). This correlation between day length and crab abundance could be described using a linear relationship but the rate of increase in crab numbers is slightly greater during the longest days; thus a quadratic function provides the best fit. Residual variance was equal ($p = 0.257$) and residuals were normally distributed (K-S = 0.144, $p = 0.889$).

Crab fishery

The mean height of the intertidal mussel beds in the Menai Strait above Chart Datum (Lowest Astronomical Tide) is 2.1 m (UKHO, 2004). Consequently, they are on average immersed for 79 % of the time. The number of *C. maenas* removed by the crab fishery was predicted, based on a mean CW of 45.7 mm,

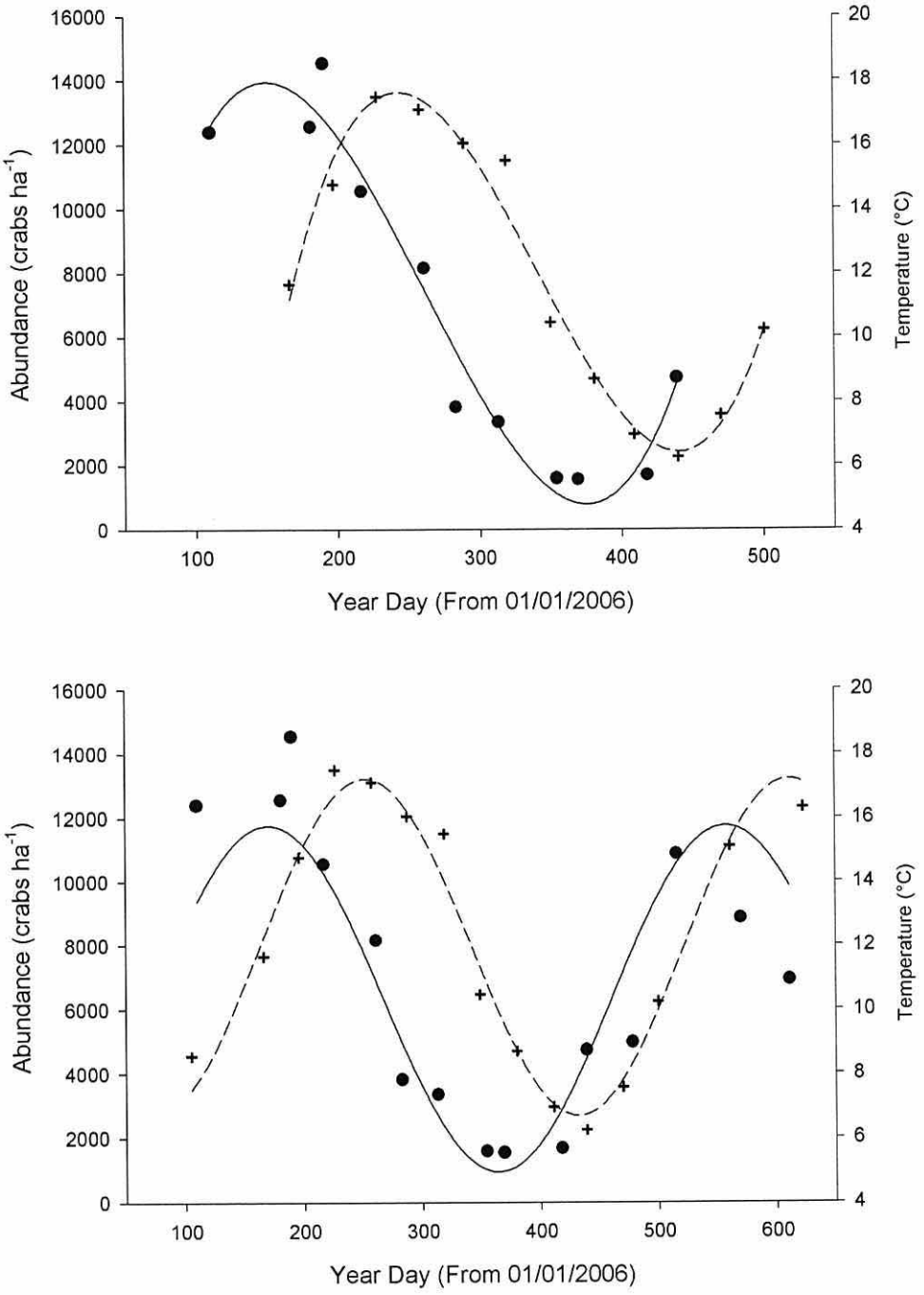
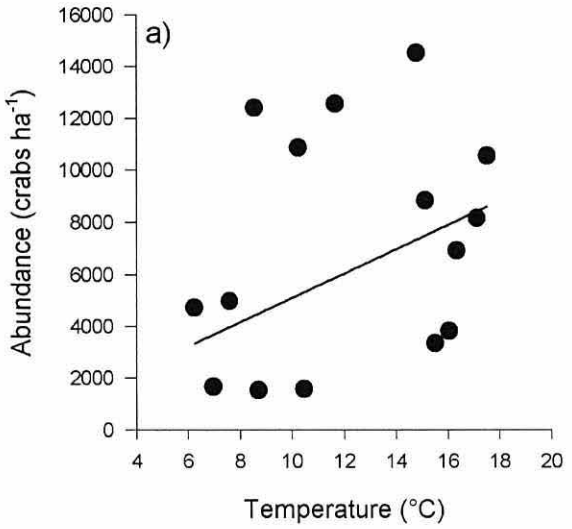
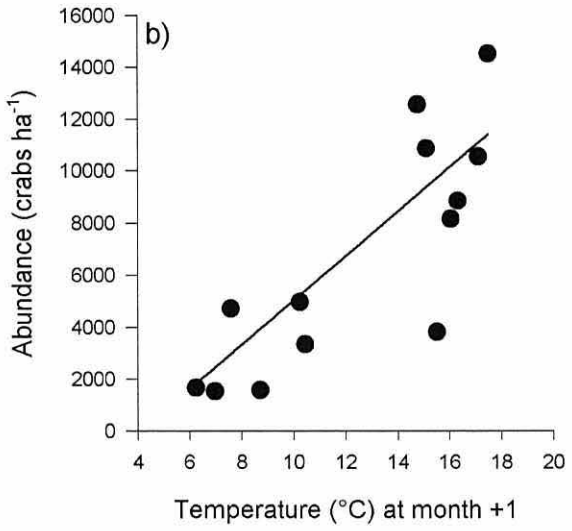


Figure 2.5. Changes in *Carcinus maenas* abundance and temperature with time in the Menai Strait. a) Cubic model fitted to data spanning one year, and b) sine wave model fitted to data spanning 18 months. Abundance (●/solid line) and temperature (+/dashed line).





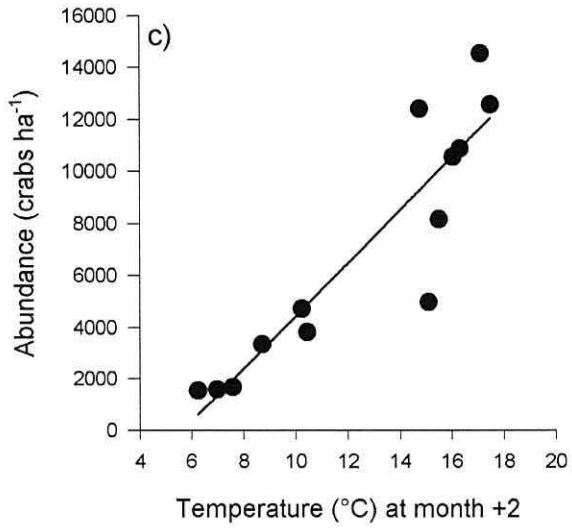


Figure 2.6. Correlations between temperature and *Carcinus maenas* abundance a) within the same month, b) temperature one month after abundance was measured, and c) temperature two months after abundance was measured.

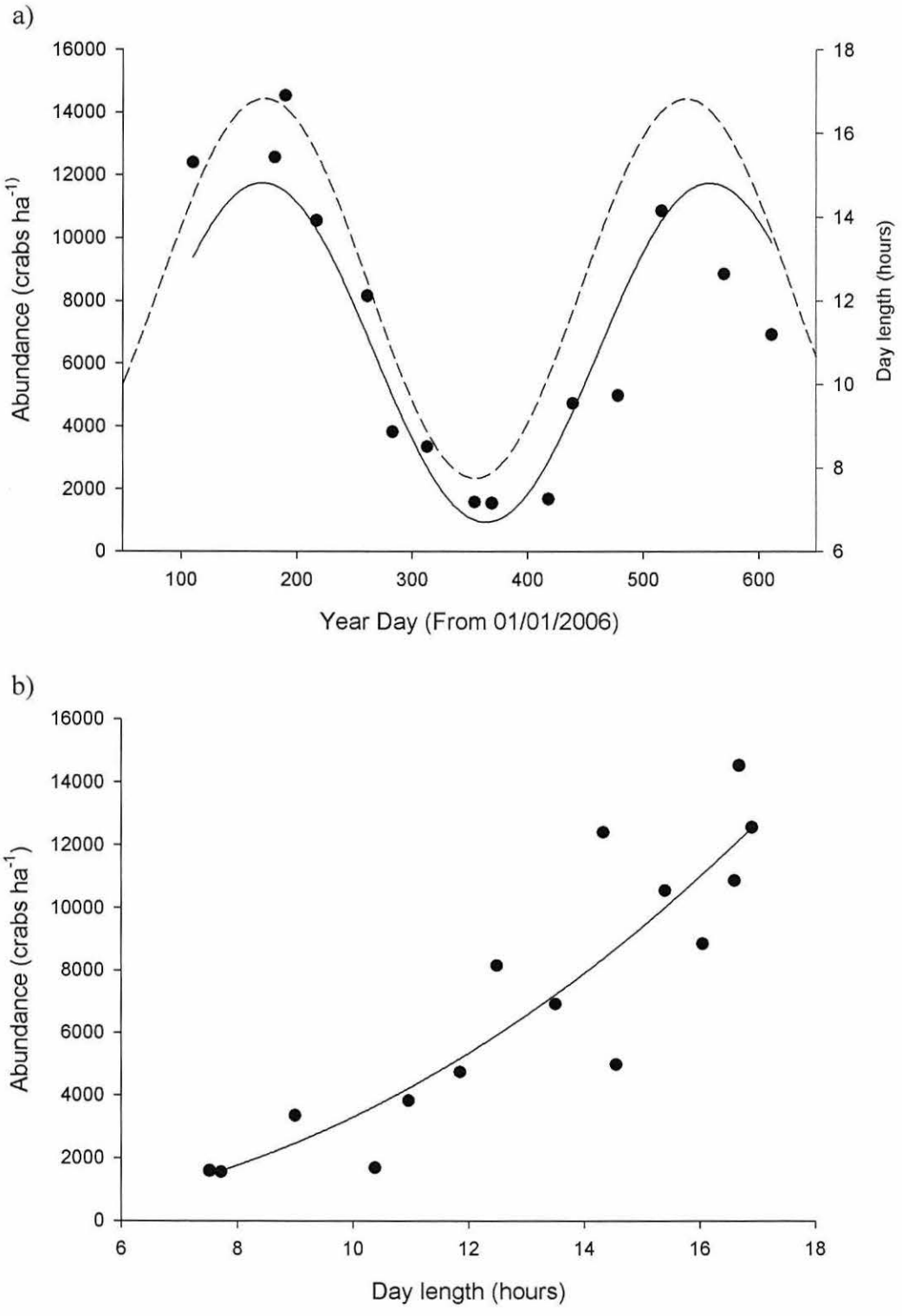


Figure 2.7. a) *Carcinus maenas* abundance (solid line) and day length (dashed line) in the Menai Strait, and b) the relationship between day length and *Carcinus maenas* abundance fitted with a quadratic regression line.

with a mean wet weight of 20.5 g based on the relationship between CW and weight in the annual commercial catch ($y = 0.0003x^{2.912}$; also see Appendix A5). Thus catch per unit effort (CPUE) was expressed as the number of *C. maenas* per trap. The CPUE of *C. maenas* increased during the summer months before declining from September 2006 to January 2007 (Figure 2.8). The maximum CPUE was recorded during September 2006, and the minimum during March 2006 and 2007. Seawater temperature ranged from ~5°C in March to 17°C in July (Figure 2.8). There was a significant quadratic correlation between temperature and CPUE ($y = -0.9892x^2 + 32.1x - 122.7$, $F_{2,9} = 26.14$, $p<0.001$, $R^2 = 0.853$; Figure 2.9); residual variances were equal ($p = 0.921$) and residuals were normally distributed (K-S = 0.115, $p = 0.995$). There was a decline in CPUE during June, which was also the time when female *C. maenas* moulted (see Figure 2.14 and 2.15). CPUE did not peak until September, despite the peak in abundance estimated from the video footage occurring in July. It was also during July that seed mussel, and associated crabs, were imported into the Menai Strait.

The minimum catch during any one month in 2006 was 19,000 crabs, compared to a minimum of 62,000 during 2004 (Figure 2.10), in both years during March when temperatures were lowest. The number of crabs removed in July 2006 amounts to the number of crabs present on approximately 38 hectares (0.38 km^2) of mussel beds and thus to around 1.9 % of the crabs present over the entirety of the mussel beds. During March, when *C. maenas* abundance was lowest, the fishery removed crabs equivalent to what would be found on 4 hectares at that time of the year. During 2006, a total of 162,250 kg of *C. maenas* were caught, amounting to approximately 3,328,000 crabs. The total number of *C. maenas* removed by the crab fishery comprised quite a small percentage of the total population throughout the year when considered as the percentage of crabs removed from the population each month (Figure 2.11), ranging from 0.8% in March to 20% in October, but then increasing sharply to 61% in February. The mean percentage of the population removed was 19%. The percentage of the *C. maenas* population removed generally increased from July to February 2006, due largely to a decline in abundance during this time.

The number of *C. maenas* caught during the first half of 2007 was slightly lower in 2007 than at the same time of year in 2006, possibly due to a change in the bait used from *Limanda limanda* to *Trachurus trachurus* from May to July 2007. There was a clear decline in the number of crabs caught during winter, when the water temperature was lowest, followed by a rapid increase in CPUE with increasing water temperature. Winter water temperature was around 1°C higher in 2007 than in 2006 but a much lower CPUE from January to March was evident in both years, after which there was a sharp increase in numbers.

Crab population structure

Female crabs were more abundant over subtidal mussel beds and in the intertidal zone; similar numbers of males and females were observed in the shallow subtidal zone (Figure 2.12). Over the subtidal mussel beds, female crabs comprised almost 100 % of the population of crabs <60 mm CW, and the majority of both male and female crabs were red. In the shallow subtidal zone, there were more males, although females still comprised ~65 % of the population from 45 mm to 65 mm CW. Most crabs from 35 to 65 mm CW were red. More crabs <30 mm CW were present in the intertidal zone and >80 % of these were green. The minimum size of crabs caught in the intertidal zone was also lower, at 15 mm CW, while the maximum size caught was only 65 mm CW compared to 70 mm CW in the subtidal zone.

All methods used to collect *C. maenas* over the mussel beds showed females to be predominant in the population. Mean CW was between 40 and 50 mm, as shown by the video surveys. There does not appear to be any size or sex bias created by using baited traps as opposed to dredging; however, both dredging and baited traps will underestimate the number of juvenile crabs. From October to March 2006 (Figure 2.13a-f), female crabs were predominant from around 30 mm to 55 mm CW, comprising >70 % of the crab population. Female *C. maenas* were more abundant throughout the year, but there were more males in the smallest (<30 mm CW) and largest size classes (>55 mm CW). Sex ratios of *C. maenas* collected from baited traps from April to September 2007 (Figure 2.13g-

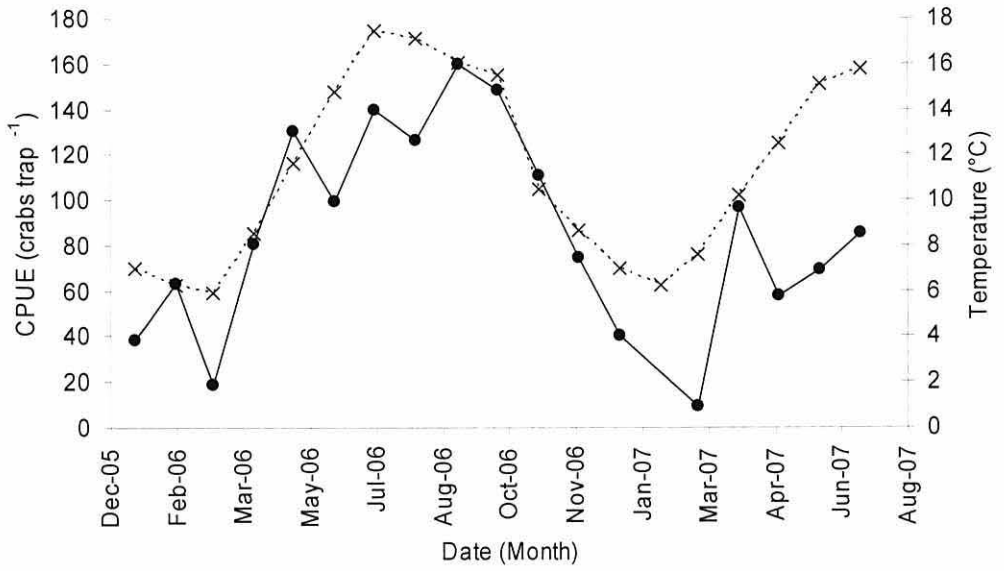


Figure 2.8. Mean number of *Carcinus maenas* caught per trap per day on cultivated mussel beds (•), and mean monthly seawater temperature (×) in the Menai Strait during 2006 and 2007.

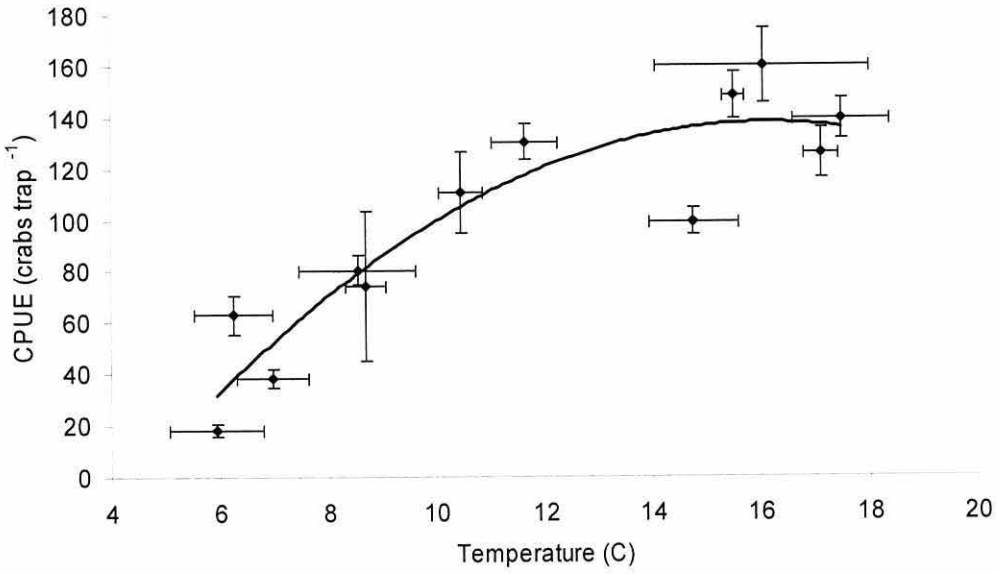
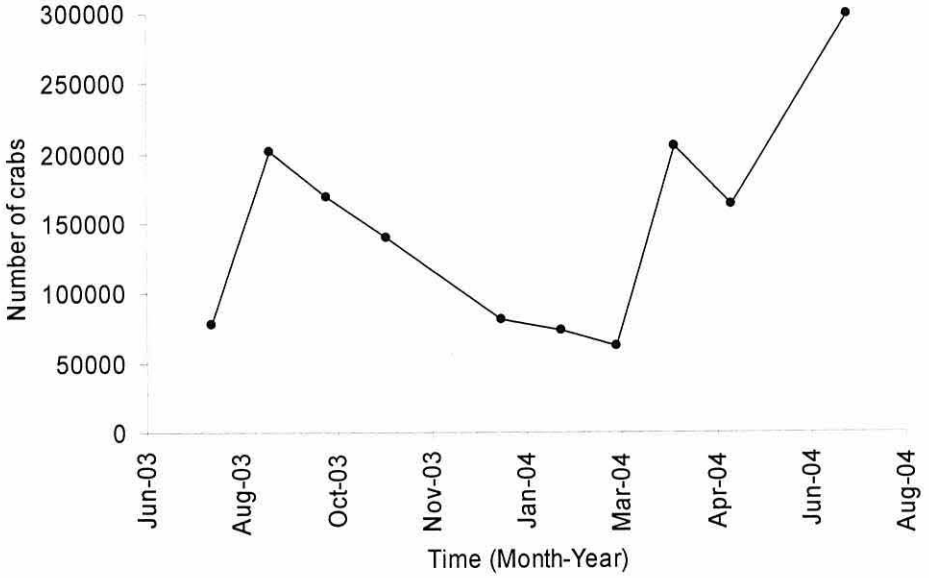


Figure 2.9. Mean seawater temperature (±1. S.D.) in the Menai Strait during 2006 versus catch per unit effort (CPUE) of *Carcinus maenas* (±1 S.E.) over cultivated mussel beds.

a)



b)

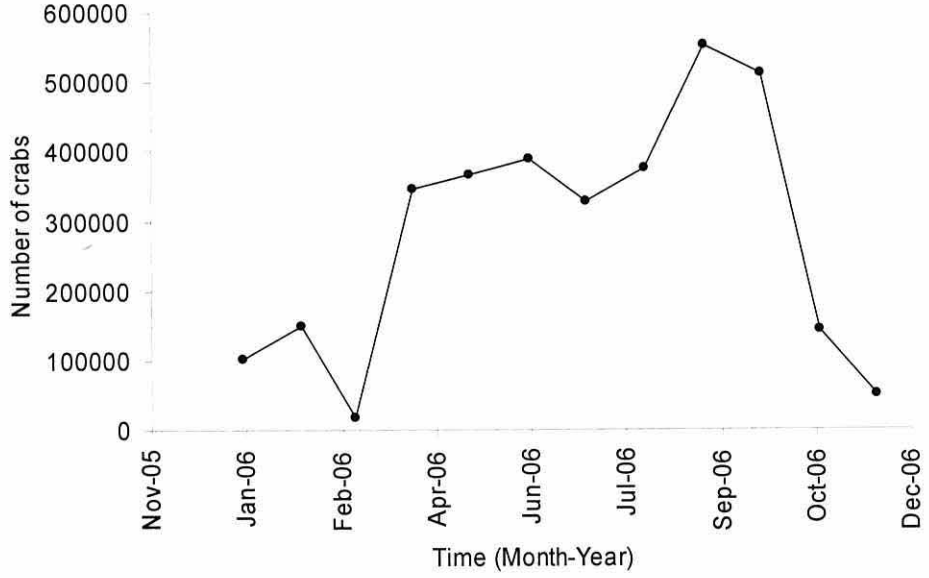


Figure 2.10. Total commercial catch of *Carcinus maenas* per month over mussel beds in the Menai Strait from a) July 2003 to July 2004 and b) January 2006 to December 2006.

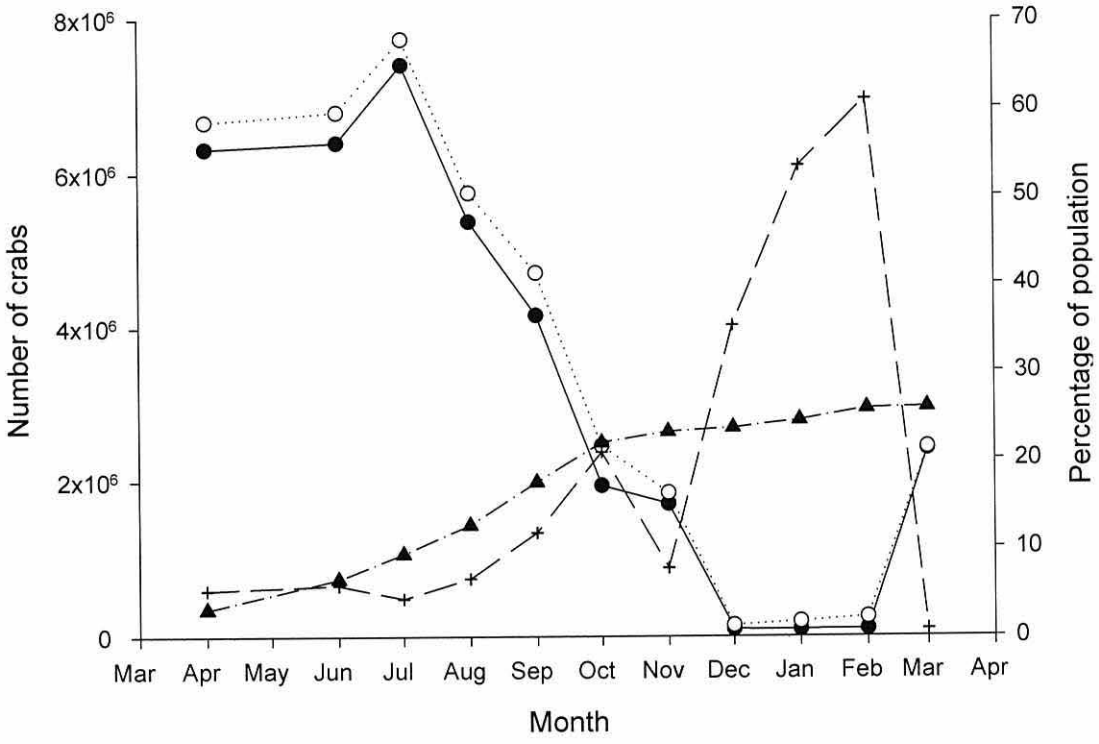


Figure 2.11. Estimated *Carcinus maenas* population size over cultivated mussel beds in the Menai Strait from April 2006 to March 2007 (•), population size plus crabs removed by crab fishery (○) and cumulative catch (▲), and percentage of the population removed by the fishery each month (+).

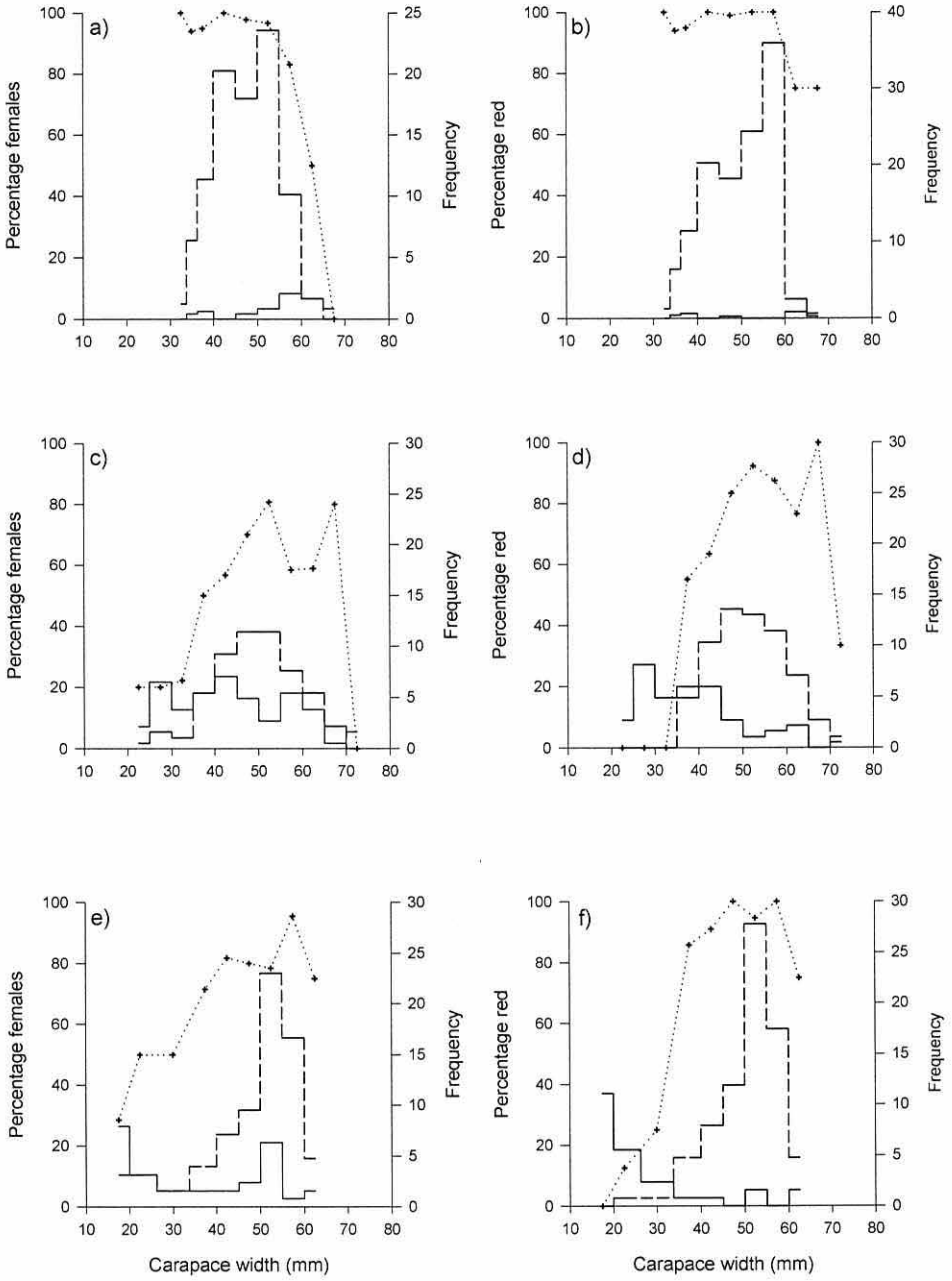


Figure 2.12. Number of *Carcinus maenas* caught using baited traps over three days in April 2005 in the subtidal zone over mussel beds (a and b), the shallow subtidal zone (c and d) and over intertidal mussel beds (e and f). Dashed line shows percentage females (a,c,e) or percentage red crabs (b,d,f); solid lines are percentage males (a,c,d) or percentage green crabs (b,d,f). Dotted line shows the proportion of females or red crabs within each size class.

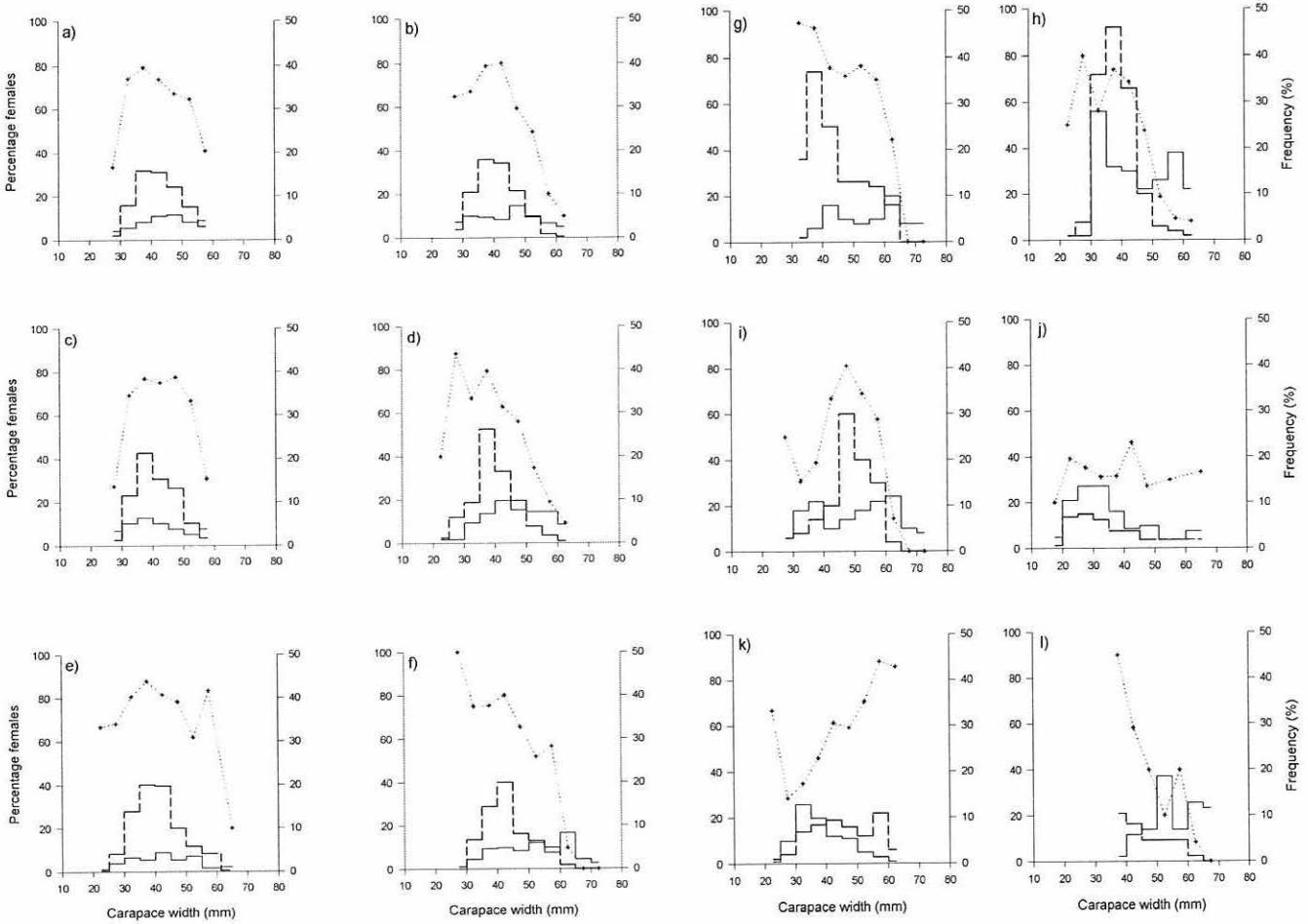


Figure 2.13. Number of female (dashed line) and male (solid line) *Carcinus maenas* collected monthly on subtidal mussel beds in the Menai Strait, and percentage of females in each sample (crosses/dotted line) from October 2006 to September 2007 (a – l). Samples were collected by dredging during the mussel harvesting season from October to March and using baited traps from April to September.

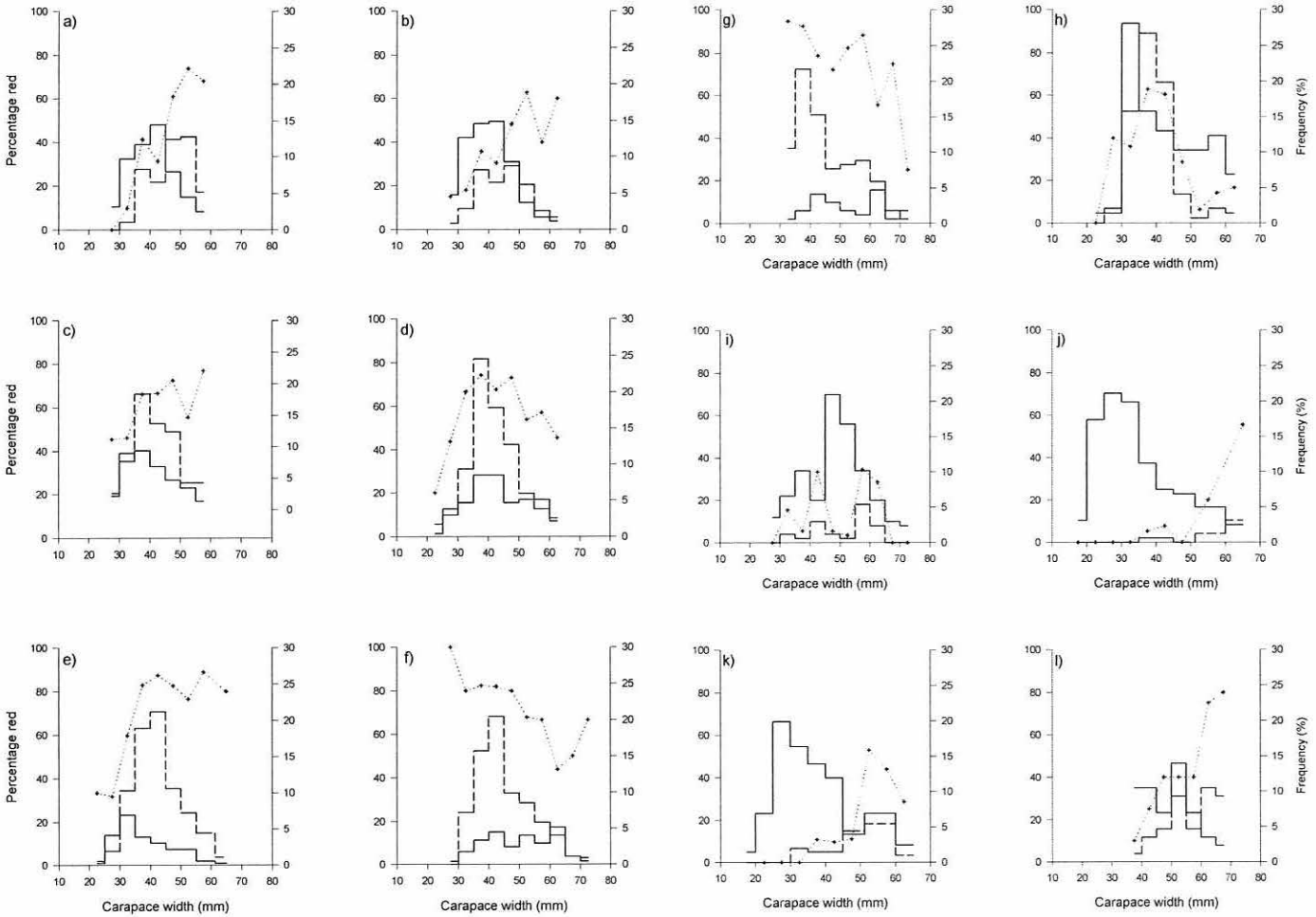


Figure 2.14. Number of green (solid line) and red (dashed line) *Carcinus maenas* collected monthly on subtidal mussel beds in the Menai Strait, and percentage of red crabs in each sample (crosses/dotted line) from October 2006 to September 2007 (a – l). Samples were collected by dredging during the mussel harvesting season from October to March and using baited traps from April to September.

l) showed a similar pattern to those collected during the dredging season. Male crab size frequency distributions were bimodal, with modes of ~40 mm and 60 mm CW. Female crab size frequency distributions were unimodal, with a mode of ~40 mm CW.

Red crabs were predominant in the population from December 2006 to March 2007 (Figure 2.14c-f); during October and November 2006 numbers of green and red crabs were approximately equal (Figure 2.14a-b). Females continued to be predominant in the population during the summer months, but the number of males increased markedly during May, comprising around 40 % of the population of crabs <45 mm CW and >90 % of the larger crabs. There was a shift back to a population dominated by female crabs during June. In April (Figure 2.14g), the proportion of red crabs in the population was of a similar level to that found from October to March, and was greater than the proportion of green crabs. However, the proportion of green crabs in the population increased substantially during May (Figure 2.14h), when 60 % of 25-35 mm CW crabs consisted of green crabs. Almost 100 % of crabs >50 mm CW were also green. The proportion of the population consisting of green crabs was even greater in June (Figure 2.14i), when red crabs did not comprise more than 40 % of any size class. This shift to a population consisting of predominantly green crabs reflects moulting during April and May.

On average, throughout the year, red female crabs comprised 48 % of the population, more than any other sex/colour group (Figure 2.15). The proportion of red females also varied most throughout the year, ranging from 7 % of the population in May to 72 % in March. Red male crabs were, on average, least abundant throughout the year, comprising 10 % of the population. The proportion of green females ranged from 2 % in March to 47 % in May, this rapid increase, together with the rapid decline in the proportion of red females, is indicative of moulting crabs in the population. The proportion of red females then steadily increased throughout the year, as the carapace developed the red colouration. There was also an increase in the proportion of green males during May, together with a decline in the proportion of red males. The proportions of red and green males remained steady throughout most of the year. The

percentage of female crabs which were egg-bearing increased from 1.8 % in October 2006 to 76.6% in January 2007, then fell to 22.9% in March, and 1.5 % in May (Figure 2.16). The mean CW of ovigerous females remained fairly constant throughout the year, ranging from 36.6 mm to 44.3 mm. The total range of the CW of ovigerous females caught on the mussel beds was 22.2 mm to 70 mm, spanning most of the size range of all *C. maenas* found on the mussel beds.

Imported crabs

Around 70 % of the crabs imported into the Menai Strait with seed mussel were of a size (30 mm CW) sufficient to consume at least some of the seed mussels imported (Figure 2.18). The mean mussel length (±1 S.D.) was 21.2 ±1.9 mm (Appendix A6). The largest crabs imported were of 76 mm CW, and the smallest 16 mm CW. The mean CW (±1 S.D.) was 37.3 ±9.1 mm, with a mean wet weight (±1 S.D.) of 13.3 ±9.9 g (Appendix A7). The mean number of *C. maenas* per tonne of mussels (±1 S.E.) was estimated at 445 ±72; thus, around 890,000 crabs would be imported with 2,000 tonnes of seed mussels, typical of the weight imported per year.

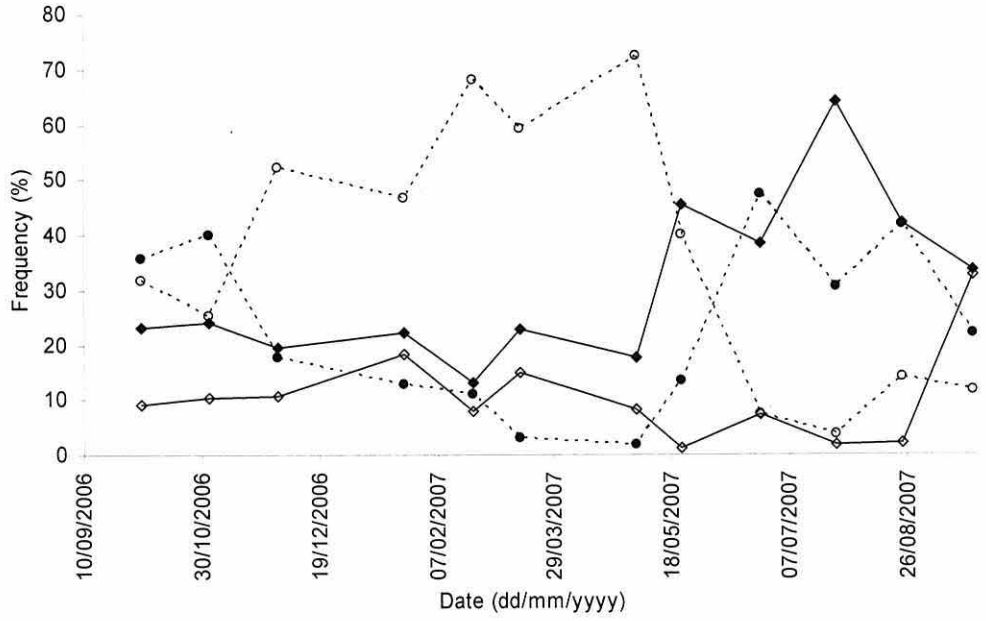


Figure 2.15. Percentage of *Carcinus maenas* population comprising green male (◆), red male (◇), green female (●) and red female (○) crabs.

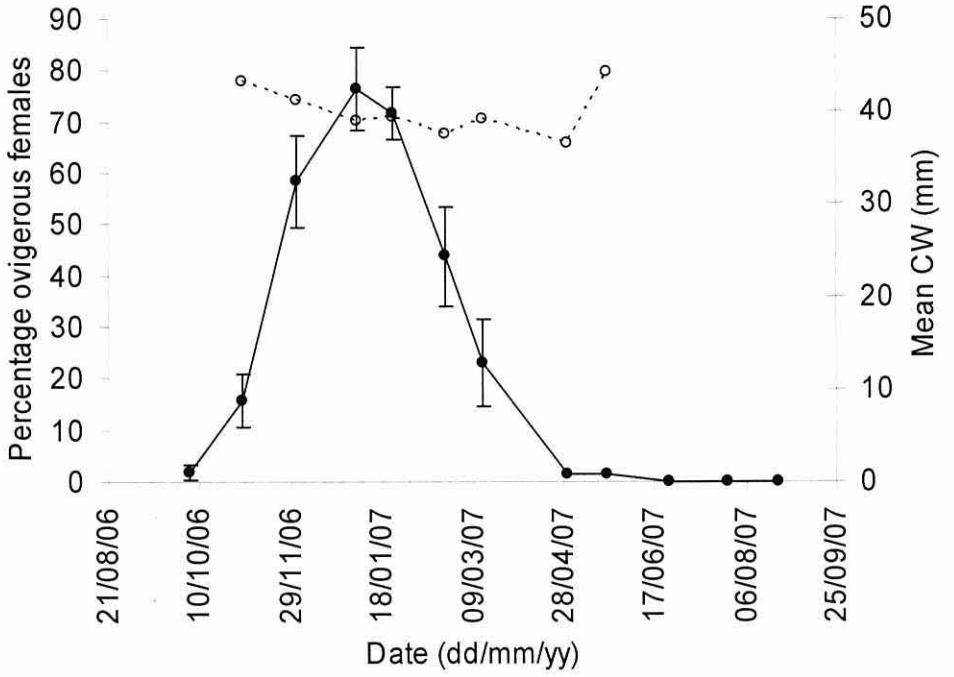


Figure 2.16. Percentage of female *Carcinus maenas* that were bearing eggs (●) and their mean carapace widths (○).

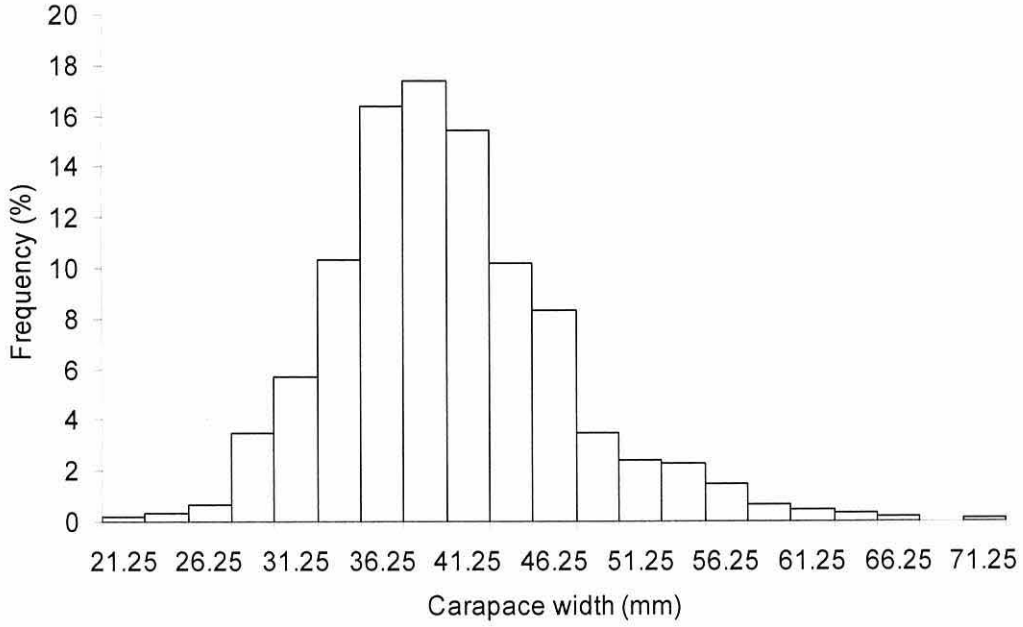


Figure 2.17. Size-frequency distribution of all ovigerous female *Carcinus maenas* caught in 2006 and 2007 on mussel beds in the Menai Strait (n = 888).

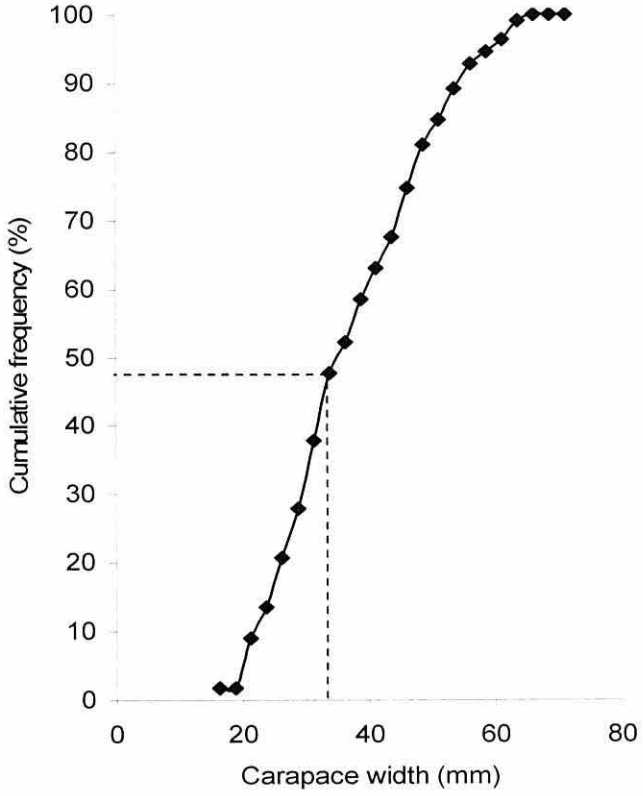


Figure 2.18. Cumulative frequency distribution of *Carcinus maenas* imported to the Menai Strait with seed mussels in July 2006. Dashed line indicates minimum size of crabs which consumed mussels in this study (see Chapter 3).

2.4 DISCUSSION

Seed mussels are imported annually to the Menai Strait during July or August, depending on the availability of natural mussel stocks. Typically, around 2000 tonnes wet weight of seed mussels are imported. Inevitably, many other species are also transported with the mussels, including predators such as *Carcinus maenas*, *Cancer pagurus*, *Asterias rubens*, and *Nucella lapillus* (Davies, 2003). Dare and Edwards (1976) recorded growth of re-laid seed mussels from a mean of 27 mm length to 50 mm over a 15 to 20 month period in the Menai Strait. The mean length of seed mussels imported in to the Menai Strait in 2006 was 19 mm, and these reached a mean length of 55 mm in 30 – 36 months. During the first year of growth mussels increase in length by around 10 mm, by around 20 mm during their second year of growth, and by around 5 mm during the final 6 months of growth. Therefore, on the commercial mussel beds in the Menai Strait, at any time during high water *C. maenas* has access to mussels ranging from around 20 mm up to 50 mm or greater, all of which would be available for consumption by *C. maenas* of varying sizes (Elner and Hughes, 1978; Ameyaw-Akumfi and Hughes, 1987; Burch and Seed, 2000; and Chapter 3).

At low water crabs are restricted to feeding in the subtidal zone where mussels are generally larger, and thus only available to larger crabs. However, the mean height of the intertidal mussel beds in the Menai Strait above Chart Datum (Lowest Astronomical Tide) is 2.1 m (UKHO, 2004). Consequently, they are on average immersed for 79 % of the time, and during this time are susceptible to crab predation. Rewitz *et al.* (2004) recorded widely varying densities of *C. maenas* in the Looe Estuary, Cornwall, which may be the result of movement of *C. maenas* due to salinity preference, food availability or avoidance of desiccation. *C. maenas* is tolerant of a wide range of salinities and does not exhibit any preference between 22 and 40 (McGaw and Naylor, 1992), much greater than the salinity range observed in the Menai Strait, which is usually around 31 – 34 (Buchan *et al.*, 1967; Tweddle *et al.*, 2005). Thus, salinity is unlikely to influence the distribution of *C. maenas* over the local mussel beds. Moreover, *C. maenas* shows great adaptability to differing environments. Brian *et al.* (2006) found that over 35% of *C. maenas* could be traced to their origin

based on morphology, due to phenotypic plasticity in the species. Given the ability of *C. maenas* to adapt readily to differing environments (Roman and Palumbi, 2004) the species is able to exploit the prevailing conditions. Therefore, even though cultivated mussel beds are comprised of mussels which are generally larger than would normally be selected by *C. maenas* given a choice of a full size range, crabs are clearly able to utilize the abundant food source that commercial mussel beds present. Smith (2004) found geographical differences in the crusher claw size of *C. maenas* that could be attributed to local shell thickness of *Littorina obtusata*, and crabs will undoubtedly show a similar response, over several generations, to larger prey items.

In the present study, CPUE peaked in September, whereas the peak in abundance of *C. maenas* occurred during July 2006 and May 2007. Seed mussels, and the crabs associated with them, were imported into the Menai Strait during July, thereby contributing substantially to the number of crabs present in the Menai Strait during this month and thereafter. The imported seed mussels will have provided an enormous food source to crabs during the summer months, when mussels were only around 20 mm in length and easily accessible, even to small crabs. Mean CW as measured in the samples collected by video, dredging or baited traps ranged from 43 to 46 mm (Table 2.2); thus, no one sampling method was obviously size biased relative to the other methods, although all the sampling techniques underestimated the abundance of small crabs, though these cannot feed on most of the cultivated mussels, which are too large to be opened. The mean CW of *C. maenas* was slightly greater on intertidal mussel beds (46 mm) than on the subtidal beds (43 mm), and the range of mean CW between months during the course of this study was also greater in the intertidal zone (37-62 mm) than in the subtidal zone (39-58 mm). Larger crabs are known to migrate more frequently than small crabs (Hunter and Naylor, 1993), which remain in the intertidal zone. The mean CW of crabs recorded in the current study ranged from 43 mm in winter to 46 mm in summer, very similar to the range of 42 mm and 47 mm previously reported by Hunter and Naylor (1993) in the Menai Strait during winter and summer, respectively. Naylor (1962) and Rewitz *et al.* (2004) found larger crabs in Swansea and the Looe Estuary than were found in the current study.

Table 2.2. Mean carapace widths (mm) over the study period and maximum and minimum mean carapace width in any one sample together with ranges of the percentage of female *C. maenas* and percentage of green crabs. Similar data from other studies are also presented.

Author	Location	Mean CW	Max CW	Min CW	% male	% green	Season
This study (Dredging)	Menai Strait	43	51	39	13-53	21-94	autumn/ winter
This study (Baited traps)	Menai Strait	46	49	41	26-46	19-86	spring/ summer
This study (Video)	Menai Strait	44	49	39	-	-	annual
Naylor (1962)	Mumbles Point, Swansea, UK	55	63	50	41-71	-	annual
Hunter & Naylor (1993)	Ynys Faelog, Menai Strait, UK	47	55	39	61-96	51-96	summer
		42	49	37	71-100	58-100	winter
Aagaard *et al.* (1995a)	Kerteminde Fjord, Denmark	43	45	40	80	74-89	summer
		39	39	38	62-78	85-87	winter
Abello *et al.* (1997)	Kerteminde Fjord, Denmark	52	61	41	13-87	21-89	spring
Rewitz *et al.* (2004)	Looe Estuary, Cornwall, UK	50	61	45	16-82	50-89	summer
Baeta *et al.* (2005)	Mondego Estuary, Portugal	~40	-	-	0-80	58-98	annual

Although temperature may have a major influence on the number of *C. maenas* present in intertidal and shallow subtidal waters, in addition to the number caught in traps (Naylor, 1962; Crothers, 1968), visible numbers also vary due to other factors, including moulting, copulation and the availability of food. No live crabs >30 mm were observed on the intertidal mussel beds when exposed (pers. obs.), though *C. maenas* was regularly observed in the intertidal zone when submerged in the video surveys. This is in contrast to rocky shores, where *C. maenas* is common in the exposed intertidal zone, particularly during the spring and summer (Seed, 1969b). The level of tidal migration shown by adult crabs over the commercial mussel beds is almost certainly due to the absence of suitable refuges for larger crabs when exposed to the air and potential predation by birds.

An annual decline and increase in *C. maenas* abundance is apparent in both the intertidal and subtidal zones, as was observed intertidally in the Menai Strait by Gascoigne *et al.* (2005), but this trend is clearest in the total abundance data, with a peak in numbers during winter and a decline in abundance from August to December. Even accounting for the losses of crabs to the fishery, this annual cycle of increasing and decreasing abundance is apparent. However, many crabs are also removed in the mussel dredging process, which contributes to the low numbers recorded on the mussel beds during the winter. Given the high variability in crab numbers intertidally and subtidally, and the seasonal variation in numbers between sites, *C. maenas* undoubtedly migrates extensively within and around the mussel beds. It is possible that some of the crabs observed on the intertidal mussel beds feed on the subtidal mussels when the intertidal mussels are exposed. However, given that the intertidal mussel beds are immersed on average for 79 % of the time, and that crabs will spend some of the time migrating and will have fed on the smaller intertidal mussels, it is assumed that these crabs will not generally consume the subtidal mussels. Dare and Edwards (1981) recorded widespread tidal migration by *C. maenas* with over twice as many crabs migrating between the lower and upper shore in June as in July, and low levels of tidal migration in May. Moulting occurred in most female crabs during June 2007 (Figure 2.15) thus the number of crabs migrating into the intertidal will be greatest during this period, when mating occurs.

The change in *C. maenas* abundance before the change in temperature suggests that crabs are either responding to changes in temperature, rather than absolute temperature, or to some other cue. A response to temperature change may have evolved as the crabs which responded most to temperature changes would have avoided being exposed to temperature at the extremes of, or beyond, their range of tolerance. However, there is a strong correlation between day length and *C. maenas* abundance. Day length has been known to influence bird activity for many years (Rowan, 1929). Many animals have been shown to respond in various ways to changing photoperiodism. Day length is a cue to initiate gonad growth in great tits *Parus major* (Silverin *et al.*, 1993) and endogenous circannual rhythms determine the start and end of migrations in birds (Gwinner, 1996). Kenagy (1981) showed that the reproductive and hibenatory functions in chipmunks *Eutamias minimus* and *E. amoenus* could be inhibited by increasing day length, while Last and Olive (2004) found that the errant polychaete *Nereis virens* exhibited an endogenous clock, shifting from somatic to reproductive growth in response to decreasing photoperiod. The activity of the onion fly *Delia antiqua* has also been shown to increasing with increasing photoperiod (Watari and Arai, 1997).

Naylor (1960) and Williams and Naylor (1967) postulated the existence of multiple clocks in *C. maenas* including circatidal and circadian clocks; thus it would not be surprising if *C. maenas* also possessed a circannual clock. The annual offshore migration exhibited by the species could also be a response to the risk of predation from over-wintering birds which, as described earlier, use day length as a cue to migrate. In addition, as metabolism falls with temperature energy requirements decrease and the value of the additional food resources present in the intertidal zone are decreased accordingly. The intertidal and subtidal zones each offer associated risks and benefits; the value of these factors to crabs, or other species, will change with energy requirements throughout the year.

The relationship between metabolism and feeding rates is not straightforward. Elner (1980) and Robertson *et al.* (2002) found no significant difference in the meal size of *C. maenas* between high and low temperatures, despite metabolism

increasing at higher temperatures (Wallace, 1973; Robertson *et al.*, 2002). Katsanevakis *et al.* (2004) found standard metabolism in *Octopus vulgaris* to be 37% higher at 28°C than at 20°C, and suggested that the annual migration of this species into cooler water during the summer may be to lower metabolism and reduce energy requirements (Katsanevakis *et al.*, 2005). Thus, although crabs eat more prey with increasing temperature (Sanchez-Salazar *et al.*, 1987a), this increase in food intake may only occur up to a point (see Figure 3.6) beyond which crabs will migrate in order to attempt to reach areas with a temperature towards the middle of their range of tolerance. The risk of mortality in crabs stranded in the intertidal zone will also be much greater during the warmest and coldest months.

Seawater temperatures in the Menai Strait closely follow air temperatures, but the minimum air temperature occurred in February, while seawater was coldest during March (Appendix A8). Crabs began moving onshore when water temperatures were at a minimum (Figure 2.5) but when air temperatures were increasing and the risk of mortality was thus lessened. Significantly more crabs are caught in baited traps at night than during the day (Crothers, 1968; Aagaard *et al.*, 1995b) indicating that crabs are more active in darkness, which reduces the risk of predation without inhibiting feeding, as *C. maenas* is a non-visual predator (Jubb *et al.*, 1983). Furthermore, *C. maenas* continues to exhibit circadian rhythms in the laboratory when kept in darkness for several days (Aagaard *et al.*, 1995b).

Obtaining estimates on predator abundance presents the greatest difficultly in assessing their potential effects on cultivated bivalves. Mussel growers thus often rely on relative measures obtained using baited traps, which are somewhat ineffective for assessing abundance (see Chapter 7). The use of a sine-wave model to predict crab abundance is therefore extremely useful if only limited data on crab (or other predator) abundance are available. As long as data on the maximum and minimum abundance can be obtained, which would mean sampling during the summer and winter months, then abundance can be estimated throughout the rest of the year and up to two years or more if necessary. The strong correlation between day length and crab numbers also

allows abundance to be estimated based on few measures of abundance. Given this correlation, an estimate of maximum abundance will correlate broadly with crab numbers during the rest of the year, and the linear regression in Figure 2.7b can simply be shifted along the y-axis to provide an estimate of annual abundance based on the annual maximum abundance, or preferably maximum and minimum abundance.

Prey consumption rates may be reduced by two types of competition, interference and exploitative (Smallegange *et al.*, 2006). Exploitative competition, where prey abundance is reduced, could also limit the numbers of *C. maenas*. However, mussel cultivators must lay sufficient seed to allow for such losses; thus prey is always available for the crab population. Interference competition will also occur but, again, given the high abundance of prey on commercial mussel beds and the fact single crabs, not groups, were most often observed in the video footage, this type of competition is presumably much lower on cultivated mussel beds than in natural mussel populations. Jensen *et al.* (2002) showed that *C. maenas* would readily compete for prey with *Hemigrapsus sanguineus* and *H. oregonensis*. Such competition will at times also occur with native crab species in the Menai Strait. *Cancer pagurus* and *Necora puber*, for instance, were occasionally observed in dredged samples, but were not consistently present on the mussel beds (pers. obs.). Therefore, given the huge food resource and the predominance of *C. maenas* on the mussel beds competition for prey is unlikely to affect food consumption rates.

The percentage of male crabs found in the present study ranged from 13 to 53 % of the crabs collected from the mussel beds. Other studies have reported higher maximum proportions of males, with Hunter and Naylor (1993) finding 100 % males in some populations. The proportion of green crabs recorded varied widely, both spatially and temporally, in other studies (Table 2.2) and the range found in the present study was also large (19 – 94%). Of the other studies of *C. maenas* populations, only Rewitz *et al.* (2004) reported more females than males, as was the case in this study. Both Hunter and Naylor (1993) and Rewitz *et al.* (2004) reported more green than red crabs in the populations studied. In the present study, red crabs were predominant until moulting occurred, in June.

The higher green to red ratios reported by Hunter and Naylor (1993) are indicative of more regular moulting. Styrishave *et al.* (2004) suggest that the relative proportion of red crabs increases with increasing mean size, as crabs divert energy to reproduction rather than to growth, and consequently moult less frequently. However, only when the proportion of red crabs is at its lowest should comparisons be made with other sites, as the proportion of red crabs can quickly change when crabs moult (Figure 2.15). The percentage of red crabs on the commercial mussel beds fell to only 7 % in June, suggesting that most crabs have not shifted entirely to a 'reproduction strategy', as described by Styrishave *et al.* (2004). However, the predominance of red crabs throughout most of the year does indicate that moulting is occurring only once per year in most of the local *C. maenas* population.

C. maenas often exhibits a high level of spatial heterogeneity in terms of numbers, sex and colour. Baeta *et al.* (2005) found increasing proportions of red *C. maenas* downstream in the Mondego Estuary, Portugal. Conversely, Rewitz *et al.* (2004) found an increasing proportion of red crabs upstream in the Looe Estuary. Hunter and Naylor (1993) recorded a sex ratio of 3 male to every 2 female *C. maenas* on both the upper and lower shore at Ynys Faelog, 10 km south-west of the commercial mussel beds in the Menai Strait. Rewitz *et al.* (2004) recorded higher green to red ratios of both male and female *Carcinus maenas* in deeper water (83:17) than at shallower sites (50:50); females were also more abundant at the deeper water sites. Hunter and Naylor (1993) suggested that early and mid-intermoult stage crabs (green) were more attracted to bait than late-intermoult stage crabs (red); however, the baited and unbaited traps were located at different sites and therefore could not be compared with any degree of confidence. Given the high proportion of red crabs caught using baited traps in the present study (Figure 2.12 and 2.14), especially in the subtidal zone where almost 100 % of the crabs caught were in late-intermoult, it seems extremely unlikely that there is any bias in favour of the number of green crabs caught. Furthermore, Rewitz *et al.* (2004) found red crabs to be dominant at some sites, and green crabs at others.

Naylor (1962) found most mating *C. maenas* during August and September, and most ovigerous females during April at Mumbles Point, Swansea. In the present study, female moulting, and presumably mating, occurred predominantly in June and the number of ovigerous females peaked during January (Figure 2.15). Thus, in both studies, the period between copulation and the first egg hatchings is eight months, though mating occurred three months earlier in the current mussel bed crab population. It should be noted that the trend of decreasing numbers of ovigerous females was apparent in dredged samples collected from January to March, and the decline is continued in the samples collected using baited traps, as ovigerous females do continue feeding (see Figure 3.11, Chapter 3). Moulting by males occurred before the peak in female moulting. The proportion of green males in the population increased in May, with the proportion of red males falling to only 1% in this month. Styrishave and Andersen (2000) reported a peak in male moulting in June and July, after crabs moved onshore during May, whilst female moulting peaked in August. Van der Meeren (1994) found similar behaviour in all receptive female crabs in Hjeltefjorden, Norway, which gathered at mating hotspots shortly before moulting; similar behaviour is likely to occur in the Menai Strait.

There was no decline in the abundance of *C. maenas* during June suggesting that copulation occurred within the range of the study sites, and crabs were not migrating elsewhere to mate. The number of ovigerous females recorded in the present study was much higher than that reported by Cameron and Metaxas (2005) at any time during the year in Nova Scotia when a maximum of 41% of the females caught were egg-bearing, compared to a maximum of 77% of females in the current study. There appears to be one peak in the number of ovigerous females during the year over the mussel beds, corresponding to the one major period of moulting observed.

The effect of the crab fishery on *C. maenas* population size within any one month is small throughout most of the year, reducing abundance by around 2 % at the maximum abundance of crabs. However, in February 2006, just over 60 % of the population was removed, despite fishing effort being low during this month (Figure 2.10); this was due to the small population of crabs present on the

mussel beds during the winter months. In March 2006, only 0.8% of the population were removed; fishing effort was lowest during March and there was also an increased abundance of crabs due to movement of *C. maenas* onshore. However, the cumulative effect of the fishery is substantial. During 2006, a total of 162,250 kg of *C. maenas* were caught, amounting to ~3,328 000 crabs. The import of *C. maenas* with seed mussels contributed only ~890,000 crabs to the local population. The mussel beds, both intertidal and subtidal, cover an area of 510 hectares; thus the *C. maenas* population size over the mussel beds is estimated to range from 789,475 crabs during winter to 7,412,850 crabs in summer. The crab population studied over the mussel beds will clearly extend beyond the bounds of the mussel cultivation sites, but determining the geographical range of the population is difficult as *C. maenas* is known to migrate over large distances (Roman and Palumbi, 2004). However, in terms of assessing the success of the crab fishery at removing *C. maenas* from the mussel beds, the estimated abundance of crabs over the mussel beds and in the immediate area is useful.

In summary, *C. maenas* is present in high numbers on the mussel beds in the Menai Strait. Both intertidal and subtidal mussel beds will therefore be subject to heavy predation by *C. maenas*. Numbers of *C. maenas* are much greater on areas where mussel cultivation is occurring than on adjacent areas where no mussels are present. The percentage of ovigerous females in the local crab population is greatest during January, with female moulting and mating occurring predominantly in June. The peak in male moulting occurred in April, but the change from red to green crabs was less obvious in males. Large numbers of crabs are imported with seed mussels, but over three times as many were removed by the crab fishery.

C. maenas abundance follows an annual cycle, with migration off the mussel beds from July through to winter, followed by migration onto the mussel beds from March to July. Annual migration by *C. maenas* may serve to reduce the risk of temperature-induced mortality, as well as reducing metabolism and food requirements. As crabs are rarely stranded in the intertidal zone on the cultivated mussel beds and there is always an abundant food source, the annual migrations

conducted by *C. maenas* are almost certainly an evolved response that in natural environments would, overall, be beneficial, although this is not necessarily the case on cultivated mussel beds. Changes in abundance precede changes in temperature by around two months, indicating that crabs may be responding to changes in temperature as cues for migration rather than absolute temperatures or, more likely, day length. It is feasible that estimates of *C. maenas* abundance can be obtained throughout the year based on only one or two annual sampling occasions using the relationship between abundance and day length; this therefore provides a useful tool for shellfish growers, as obtaining crab population estimates is the main barrier to predicting the impacts of crabs on commercial shellfish beds.

In the next chapter mussel selection by *Carcinus maenas* is examined. The number of mussels and biomass consumed by crabs in response to varying prey presentation and crab physiology is determined to allow predictions of their potential impact on cultivated mussel beds to be ascertained by applying them to the results presented in this chapter.

CHAPTER 3

SELECTIVE PREDATION OF *MYTILUS EDULIS* BY *CARCINUS MAENAS*

ABSTRACT

Cultivated mussels are often subjected to heavy predation by several predators, including the shore crab *Carcinus maenas*. Predation by *C. maenas* may result in substantial losses of mussels during the cultivation process. In the present study methods were developed to quantify the effects of crab predation on mussel beds, with the aim of estimating losses of mussels to crabs in the mussel fishery located in the Menai Strait. Feeding rates decreased exponentially with time in the laboratory. There were significant linear relationships between crab carapace width and the number and size of mussels consumed. Increasing the mean length of mussels presented to crabs resulted in an exponential decline in the number of mussels consumed. Green female crabs consumed significantly smaller mussels than other *C. maenas* and red female crabs damaged significantly more mussels than other crabs. There was no significant difference in the number of mussels consumed by ovigerous female crabs and male crabs. The number of mussels consumed was greatest at 13°C, decreasing at higher and lower seawater temperatures. The coefficients and formulae presented in this chapter can be used, together with crab abundance data, to estimate the potential losses of mussels to crab predation.

3.1 INTRODUCTION

Of the 1.94 million tonnes of marine molluscs harvested worldwide in 2005, the blue mussel *Mytilus edulis* (Linnaeus) represented 50 % of the catch, accounting for 6 % of all aquaculture production (FAO, 2007). Seabed mussel cultivation involves growing mussels from seed of around 20 mm in length to a marketable size of around 50 mm, a process usually taking 2.5 to 3 years. During this time mussels may be subjected to heavy mortality, particularly from predators such as the common starfish *Asterias rubens* (Linnaeus), the shore crab *Carcinus maenas* (Linnaeus), the dogwhelk *Nucella lapillus* (Linnaeus) and many bird species including gulls, diving ducks and waders (see Seed and Suchanek, 1992 and references therein).

Major predators of mussels include *A. rubens* (Saier, 2001) and *C. maenas* (Davies *et al.*, 1980). As an invasive species in many parts of the world, *C. maenas* is considered detrimental to both molluscan (Walton *et al.*, 2002; Miron *et al.*, 2005) and crustacean (Rossong, 2006; Williams *et al.*, 2006) fisheries. *C. maenas* migrates with the tide during the spring and summer months (Hunter and Naylor, 1993) and is thus found in both the intertidal and subtidal zones, and has a preferred salinity range of around 20 to 40 (Thomas *et al.*, 1981; Ameyaw-Akumfi and Naylor, 1987; McGaw and Naylor, 1992). The diet of *C. maenas* is dependent on the availability of prey. Ropes (1968) and Elner (1981) found bivalves to be the predominant items in the diet of *C. maenas*, whilst Brousseau and Baglivo (2005) found that mussels were always the preferred prey of the Asian shore crab *Hemigrapsus sanguineus* . Furthermore, both juvenile and adult *Cancer pagurus* and *C. maenas* select *M. edulis* more frequently than the oysters *Crassostrea gigas* and *Ostrea edulis*, whilst cockles *Cerastoderma edule* are selected in similar numbers to *M. edulis* (Mascaro and Seed, 2000; 2001). Although cultivated mussel assemblages may be rich in associated species, mussels themselves far exceed any other organism in abundance and biomass (Murray *et al.*, 2007) and are thus likely to be the main food source for *C. maenas* on commercial beds (see Chapter 5).

Prey selection by predators may vary as a result of preference for a particular prey item (Jackson and Underwood, 2007), the way prey items are presented (Burch and Seed, 2000), the physiology of the predator (Kaiser *et al.* 1990; Reid *et al.* 1997) or prey (Arnold, 1984; Côté, 1995; Leonard *et al.*, 1999), and different environmental conditions, including temperature. Acclimatization to different temperatures can cause food consumption rates to increase by 2.4 times in *C. maenas* acclimated at 24 °C compared to crabs acclimated at 10 °C (Wallace, 1973). However, Elner (1980) did not find any significant effects of temperature, between 10°C and 17°C, on feeding rates or prey size selection in *C. maenas* feeding on *M. edulis*.

In the present study, several experiments were conducted to determine the effects of varying prey presentation, and predator and prey size using a single predator species, *Carcinus maenas*, and prey species, *Mytilus edulis*. Field observations together with the commercial catch of *C. maenas* indicate that shore crabs are abundant on commercial mussel beds in the Menai Strait (Chapter 2), North Wales. It is currently unknown what the annual losses of mussels to *C. maenas* are and how losses vary with the growth of mussels. The current study aimed to determine the relationship between mussel size and crab size in terms of feeding rates and to elucidate the potential of *C. maenas* as a predator of commercially cultivated mussels. It was hypothesised that crabs would select prey above their preferred size where the mean prey size was increased, up to a maximum critical value. The relationships between mussel and crab size and the number of *M. edulis* consumed by *C. maenas* of contrasting sex and colour, and at different temperatures were determined. In doing so, constants were derived which could be used to predict the effects of *C. maenas* on the commercial mussel beds in the Menai Strait throughout the year, and furthermore, which could be applied to other mussel cultivation areas.

3.2 MATERIALS AND METHODS

General methodology

All *Carcinus maenas* used in the current study were collected from the cultivated mussel beds in the Menai Strait, either by dredging or using baited traps, and only undamaged crabs were used in the feeding experiments. Crabs were fed to satiation on mussel flesh; food was then withheld for 48 hours before feeding trials began in order to standardize hunger levels (Elner and Hughes, 1978; Jubb *et al.*, 1983) and allow a period for crabs to acclimatize to laboratory conditions. Crabs were kept individually in running seawater at 12 ±1 °C unless otherwise stated. In each experiment mussels were presented in sufficient quantities, based on pilot experiments, to prevent any one size class being eaten out during a feeding trial. All mussels were collected from the commercial mussel beds in the Menai Strait having undergone the same cultivation process. Any fouling organisms were removed from the mussels, although numbers of fouling organisms were low. Crabs were kept in complete darkness while feeding to prevent disturbance; *C. maenas* is a non-visual predator (Crothers, 1968; Ameyaw-Akumfi and Hughes, 1987) and, moreover, circadian (and circatidal) rhythms in heart rate and locomotory activity are maintained in the laboratory for at least four days when *C. maenas* is kept in constant darkness (Aagaard *et al.*, 1995b) or constant dim light (Naylor, 1958). One hundred mussels covering a size range of 15 to 60 mm were collected from the cultivated beds in the Menai Strait and were used to estimate the dry flesh biomass consumed (C_b) in the feeding experiments based on the regression of length against dry flesh weight (Appendix B1). Mussels were dried at 60°C until constant weight was reached (~48 hours). All mussels were measured to 0.1 mm using dial callipers.

Feeding rates, size and prey selection

Feeding rates of *C. maenas* were measured after 2, 4, 8, 12, 16 and 20 hours, and, thereafter, every day for 6 days. A total of 12 crabs of 60 – 75 mm carapace width (CW) were each presented with 45 mussels, with 9 mussels in each of five length

classes, which were: 20 – 22.4, 22.5 – 24.9, 25 – 27.4, 27.5 – 29.9, and 30 – 32.5 mm. The number of mussels in each size class eaten (C_e) or damaged was recorded and mussels were replaced every 24 hours.

To determine the difference in prey size selection and consumption rates by crabs of different CW, 21 crabs ranging from 22 mm to 68 mm CW were each presented with 42 mussels, consisting of seven mussels in each of six size classes which were: 17.5 – 19.9, 20 – 22.4, 22.5 – 24.9, 25 – 27.4, 27.5 – 29.9, and 30 – 32.4 mm. The number of mussels eaten from each size class was recorded after 8 hours. All eaten or damaged mussels were then replaced. An additional 21 crabs were presented with mussels in an identical manner to the first crabs. These crabs ranged in size from 22 mm to 69 mm CW. After 24 hours the number of mussels eaten from each size class was recorded; 17 crabs consumed mussels. To determine the effect of varying prey presentation, ten crabs ranging from 58 to 60 mm CW were presented with 42 mussels in seven length classes. Mussels were always presented in the proportions 3, 5, 8, 10, 8, 5 and 3 (approximating normal distribution), while the modal mussel length class presented to each crab was different, with length class mid-points ranging from 21.25 mm to 43.75 mm. The length distributions of mussels presented approximated the distributions of mussels on cultivated beds in the Menai Strait and covered the size range of mussels found on the intertidal mussel beds. The number of mussels consumed from each size class was noted after 24 hours.

To assess whether the number of mussels eaten and prey size selection varied between male and female, and between green and red *C. maenas*, mussels covering a wide size range were fed to crabs. A total of 32 crabs, eight crabs of each sex and red or green colour form (50 – 70 mm CW), were fed equal numbers of mussels in six length categories (20 – 24.9, 25 – 29.9, 30 – 39.9, 40 – 49.9, 50 – 59.9 and >60 mm). The number of mussels consumed or damaged in each size class was noted after 24 hours. Due to the limited number of available tanks and difficulty in obtaining enough green female crabs of sufficient size during any one sampling trip, the experiment was conducted using a randomised block design over two weeks. Where a crab did not eat during a particular feeding trial the trial was repeated using new crabs. In a separate experiment to establish whether

female *C. maenas* continued to feed normally when bearing eggs, six male and six ovigerous female crabs of 45 – 55 mm CW were fed with 10 mussels (20 – 25 mm) over three days. Eaten or damaged mussels were replaced every 24 hours. Few non-ovigerous females were found at the time of the study and thus ovigerous female feeding rates were compared to those of males.

To determine the effects of temperature on feeding rates, a total of 18 male *C. maenas* of ~60 mm CW were maintained individually at 6, 8, 10, 13, 16 and 18°C, with three crabs at each temperature. To each crab, 35 mussels of 20-30 mm length were presented. The number of mussels consumed by each crab was recorded after 24 hours. To ascertain the combined effects of changing temperature and prey presentation, mussels were presented in six size classes (25 – 29.9, 30 – 34.9, 35 – 39.9, 40 – 44.9, 45 – 49.9, and 50 – 59.9 mm) in equal proportions, with a distribution of 3, 16, 20, 8, 2, 1, based on the length frequency distribution of mussels on intertidal mussel beds in the Menai Strait, or exclusively with large mussels (40 – 60 mm). Mussels were presented to groups of three crabs; six groups of crabs were used for each treatment at 10, 13 or 16 °C. A total of 47 groups, each of three crabs, fed successfully. Temperature was controlled to ±1°C. Due to the limited number of temperature controlled tanks available, a randomised block design was used to run the experiment over several days.

3.3 RESULTS

Feeding rates, size and prey selection

There was a significant relationship between time and the feeding rate of *C. maenas* ($F_{1,10} = 8860.13$, $R^2 = 0.999$, $p<0.0001$). There was a sharp decline in feeding rates during the first 24 hours after crabs were presented with prey; following which, feeding rates levelled out (Figure 3.1). Feeding rates during the first 2 hours after crabs were presented with mussels were almost 8 times greater than after 6 days. The mean number of mussels eaten per hour during the first 24 hours of feeding was ~2 compared to ~1 after 48 hours and <1 beyond 48 hours.

The mean length of mussels consumed increased linearly with CW, which was responsible for 55% of the variation in mean length of mussels selected (Figure 3.2). Residuals were normally distributed (K-S = 0.103, p = 0.994) and variances were equal (p = 0.174). There was a weaker, but significant, correlation between CW and modal length consumed ($y = 0.346x + 3.272$, $R^2 = 0.418$). The smallest crab to consume any mussels had a CW of 44 mm. Crabs as small as 22 mm were presented with mussels as small as 17.5 mm in length but failed to eat. There was a general preference among all crabs for the smaller mussels (Figure 3.3). Crabs over a range of sizes from ~44 – 69 mm CW consumed, on average, most mussels from the smallest length class of mussels and fewest from the largest length class of mussels.

Residuals of CW against C_e regressions were normally distributed (K-S<0.143, p>0.848) and variances were equal (p>0.207) There was a significant linear relationship between CW and C_e (Figure 3.4a) and a significant exponential relationship between CW and C_b after 8 and 24 hours (Figure 3.4b). Only an average of four mussels extra were consumed over 24 hours compared to 8 hours (Figure 3.4a) reflecting the decline in feeding rates over time (Figure 3.1). The slope of CW versus C_e did not differ significantly between 8 and 24 hours (ANCOVA, $F_{1,27} = 0.15$, p = 0.706). The biomass consumed increased linearly with the number of mussels eaten (Appendix B2).

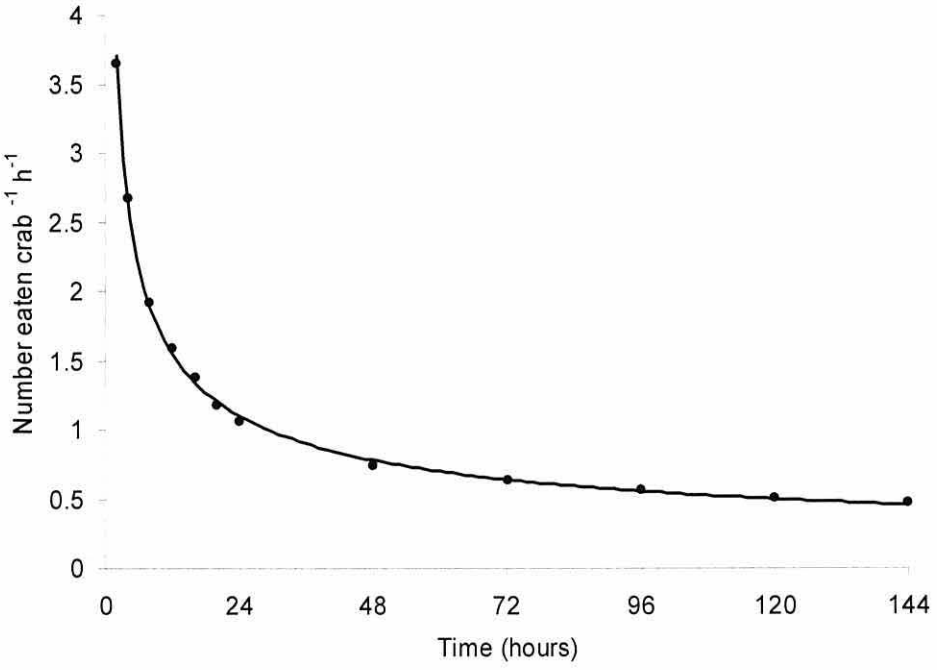


Figure 3.1. Mean number of mussels eaten per hour by *Carcinus maenas* individuals of 55 – 70 mm carapace width. Power function regression line is shown ($y = 5.161x^{-0.485}$).

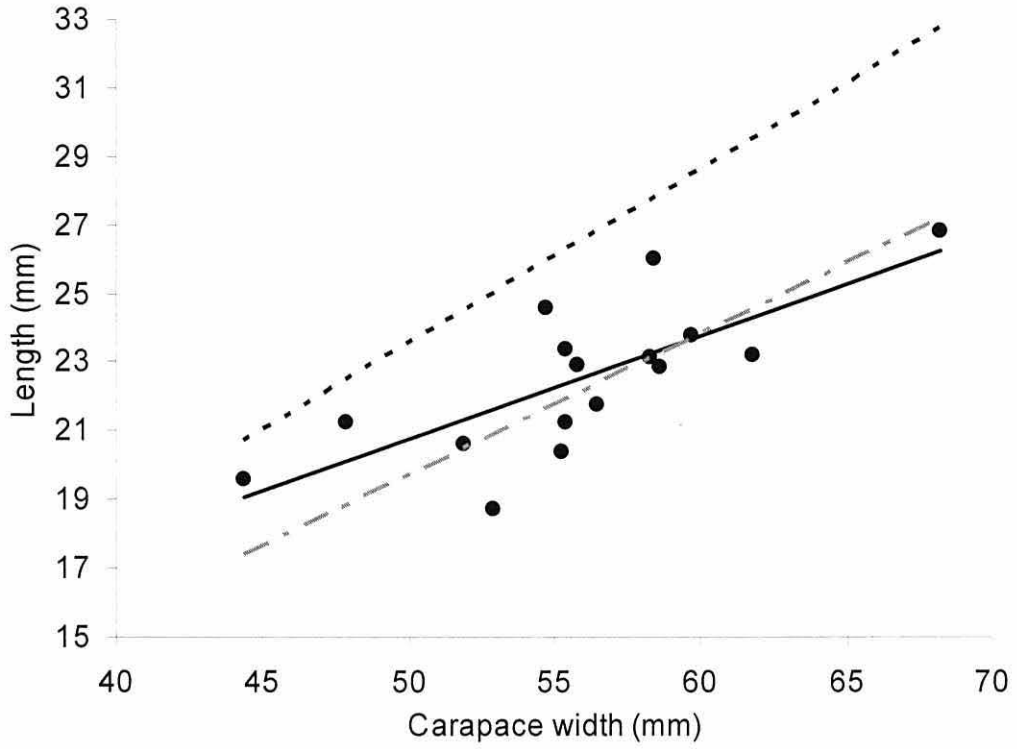


Figure 3.2. Relationship between carapace width of *Carcinus maenas* and mean length of *Mytilus edulis* consumed during 8 hours. Seven mussels in each of six size classes (17.5 – 19.9, 20 – 22.4, 22.5 – 24.9, 25 – 27.4, 27.5 – 29.9, and 30 – 32.5 mm) were presented to each of sixteen crabs. Solid circles/solid line: mean length consumed ($y = 0.301x + 5.699$, $R^2 = 0.554$; $F_{1,16} = 17.37$, $p = 0.001$); Dotted line: regression fitted to maximum length consumed data ($y = 0.504x - 1.634$, $R^2 = 0.506$; $F_{1,16} = 14.34$, $p = 0.002$). The regression fitted to mean mussel length eaten based on experiments conducted by Elner (1980) is also shown (dotted/dashed line).

There was a highly significant negative exponential relationship between the mean length of mussels (MML) presented to crabs and C_e (Figure 3.5a). Residuals were normally distributed (K-S = 0.313, p = 0.233) and variances were not significantly different (p = 0.127). C_e decreased from a maximum of 29 at a MML of 21.25 mm to 1 at a MML of 36.75 – 43.75 mm. MML and C_b were related by a cubic function (Figure 3.5b). Residuals were normally distributed (K-S = 0.253, p = 0.481) and variances were not significantly different (p = 0.089). C_b was greatest when crabs were presented with mussels with a mean length of 21.25 mm. For mussels between 23.75 mm and 36.25 mm C_b was lowest, while for those >36.25 mm C_b increased as larger mussels were consumed.

Mussels from the most abundant size class presented to the crabs were consumed in the greatest numbers when MML was <28 mm (Figure 3.6). Both the mean and modal length of mussels predicted to be consumed (Figure 3.2) was 24 mm. When the MML of presented mussels was only slightly greater (26.25 mm; Figure 3.6c) mussels were still consumed predominantly from the most abundant size class. Once MML was increased beyond this value, to 28.75 mm, more mussels were consumed from the 25 – 27.5 mm size class, rather than the most abundant size class (Figure 3.6d). As MML was increased further mussels were still selected from the smaller size classes until only a single mussel was consumed from the largest mussel sizes presented (Figure 3.5a).

There was a significant linear correlation between the modal length of mussels presented to crabs and the modal length eaten over the four smallest size distributions of mussels presented (Figure 3.7). The modal length of mussels consumed deviated most from a directly proportional relationship at the larger mussel size and least at the smallest mussel size, indicating the effect of increasing mussel size beyond the preferred size. At 21.25 mm length, the modal length consumed was 97 % of the modal length presented to crabs, decreasing to 92 % at 28.75 mm. The lower modal size selected than presented reflects the tendency of crabs to consume mussels from the most abundant size class and those in the smaller size classes.

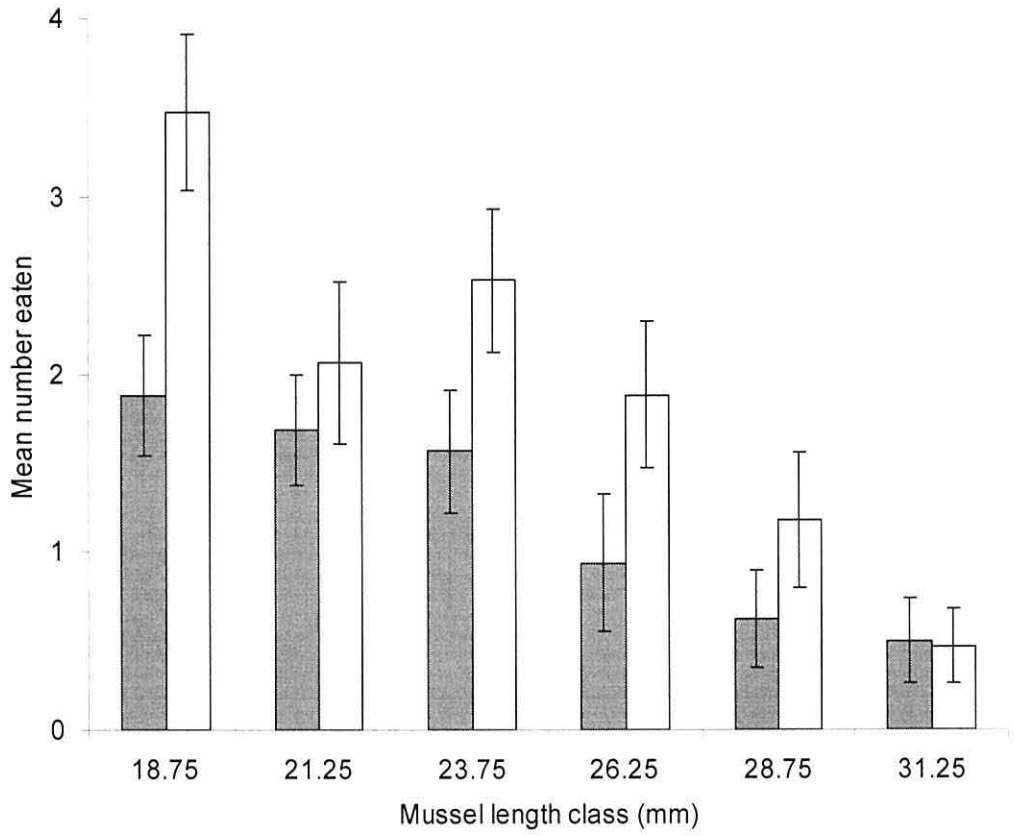


Figure 3.3. Mean number ±1 S.E. of mussels eaten by *Carcinus maenas* from each 5 mm length class during 8 hours (solid bars) and 24 hours (open bars). During the 8 hour feeding trials, 16 crabs ranging from 44 mm to 68 mm carapace width (CW) were presented with mussels. During the 24 hour feeding trials 17 crabs from 45 mm to 69 mm CW were presented with mussels. Seven mussels were presented in each length class.

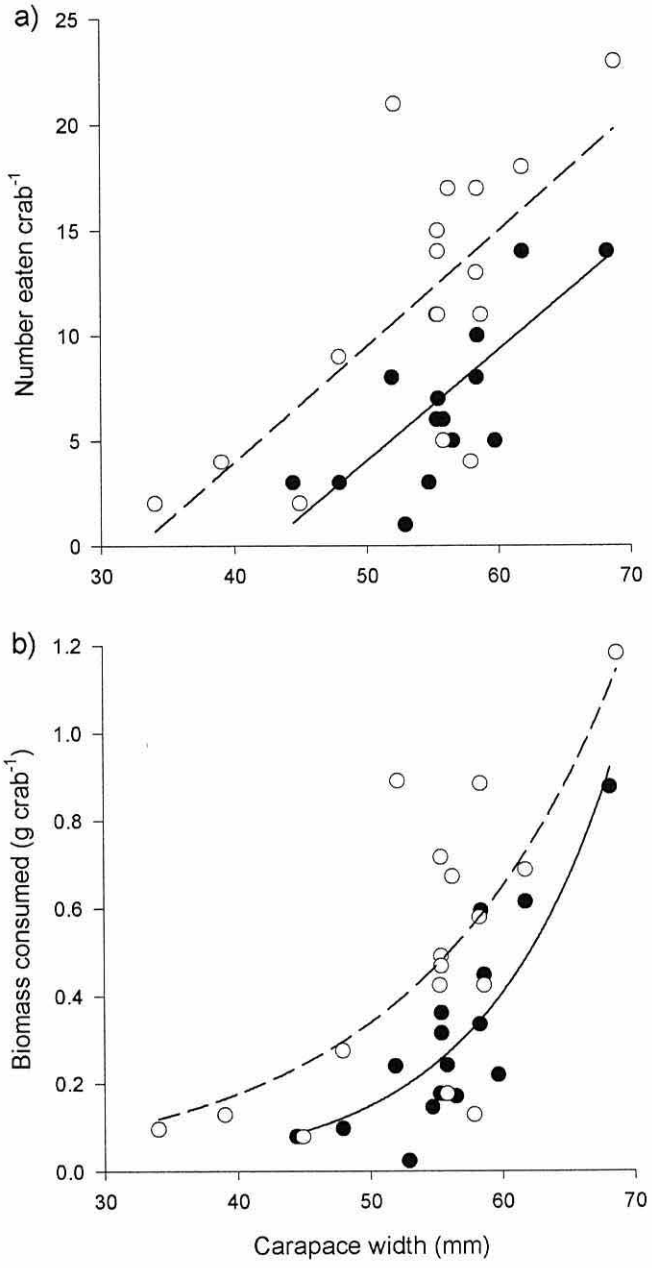


Figure 3.4. a) Number of mussels eaten and b) estimated biomass (dry flesh weight) consumed by *Carcinus maenas* after 8 hours (solid circles) and 24 hours (open circles). After 8 hours: number eaten: $y = 0.528x - 22.371$, $R^2 = 0.53$, $F_{1,14} = 15.78$, $p = 0.001$; biomass: $y = 0.0011e^{0.0993x}$, $R^2 = 0.746$, $F_{1,14} = 41.149$, $p<0.0001$). And after 24 hours: number eaten: $y = 0.55x - 18.02$, $R^2 = 0.492$, $F_{1,15} = 14.50$, $p = 0.002$. biomass: $y = 0.013e^{0.065x}$, $R^2 = 0.532$, $F_{1,15} = 17.077$, $p<0.001$).

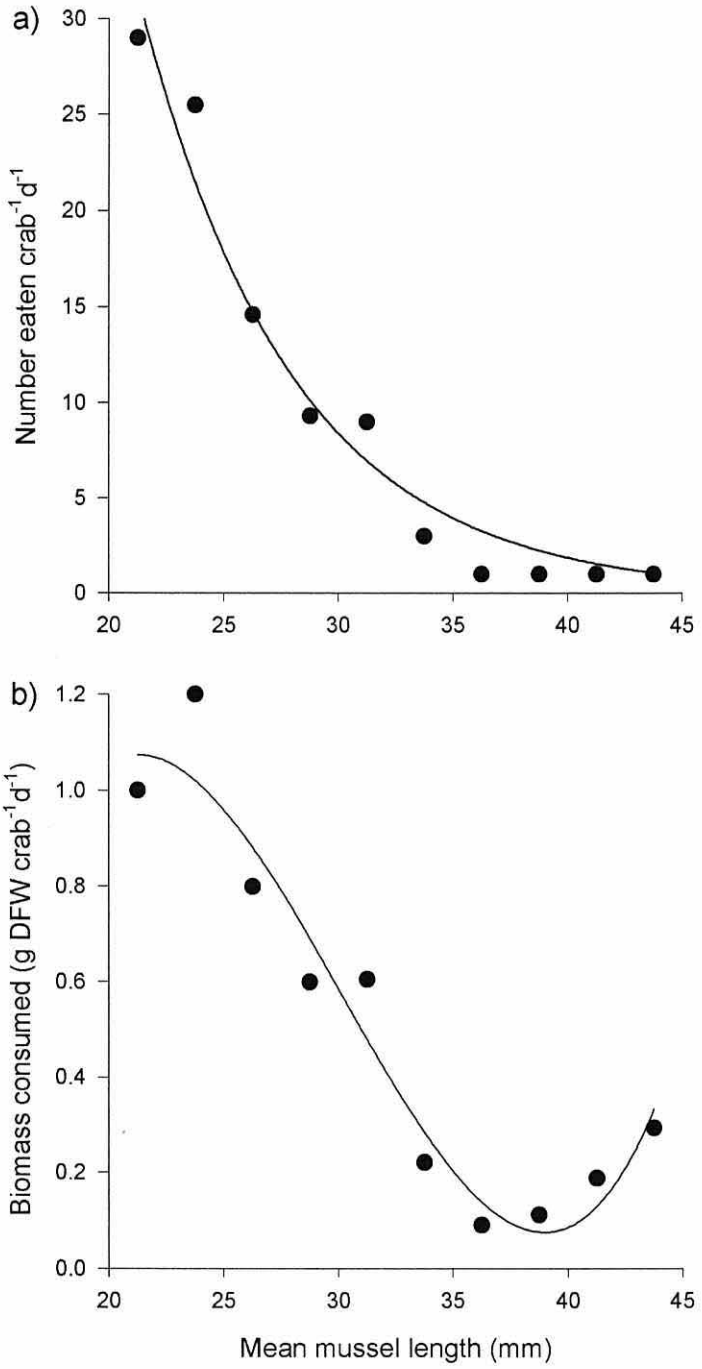


Figure 3.5. a) Number of mussels eaten per *Carcinus maenas* of ~60 mm carapace width during 24 hours when fed mussels in seven 2.5 mm length classes in the proportions 3, 5, 8, 10, 8, 5 and 3, at ten different mean lengths. Exponential regression: $y = 1517.8e^{0.18x}$, $R^2 = 0.963$, $F_{1,8} = 209.974$, $p<0.0001$, SE = 2.1352. b) Dry flesh weight biomass of mussels consumed. Cubic regression: $y = -8.1142+0.9299x-0.0349x^2+0.0004x^3$, $R^2 = 0.93$, $F_{2,7} = 26.565$, $p<0.001$, SE = 0.1007).

The mean length of mussels eaten equalled the mean length presented at 21.25 mm (Figure 3.8). The mean length eaten increased as the mean length presented was increased but at a lower rate as crabs selected smaller mussels rather than the most abundant. The length of mussels consumed at 41.25 and 43.75 mm were larger than would be predicted by the correlation at smaller sizes (21.25 – 28.75 mm); however, the crabs presented with the largest mussels only consumed a single mussel each over the study period.

Predicting prey consumption

The number of mussels predicted to be eaten (z_e; Figure 3.9a) based on the relationships between CW and C_e, and MML and C_e was calculated using the following equation:

$$z_e = (y_0 + ae^{(-by)}) + a_c x$$

where x = CW, and y = MML. The constant a_c (0.539) is the slope of the regression line describing the relationship between CW and C_e (averaged for the 8 and 24 hour feeding periods). The number of mussels consumed by crabs from 35 – 70 mm was predicted based on the curve ($y = ae^{-bx}$) describing the relationship between MML and C_e, obtained from crabs of 60 mm CW (Figure 3.5a). These values were adjusted by (CW-60)a_c to account for differences in the CW of crabs, giving constants: y_0 = -32.3459, a (MML v. CW constant) = 1517.8 and b = 0.18, which represent the theoretical relationship between MML and C_e at CW = 0.

Over 24 hours, z_e ranged from 0 to 37 (Figure 3.9a). The estimated number of mussels consumed by a crab of 70 mm CW was ~37 when presented with a MML of 21.25 mm, decreasing to ~6 when presented with a MML of 43.75 mm; for a crab of 35 mm the estimated number of mussels consumed ranged from 0 when presented with a MML >26.25 mm to ~16 when presented with a MML of 21.25 mm.

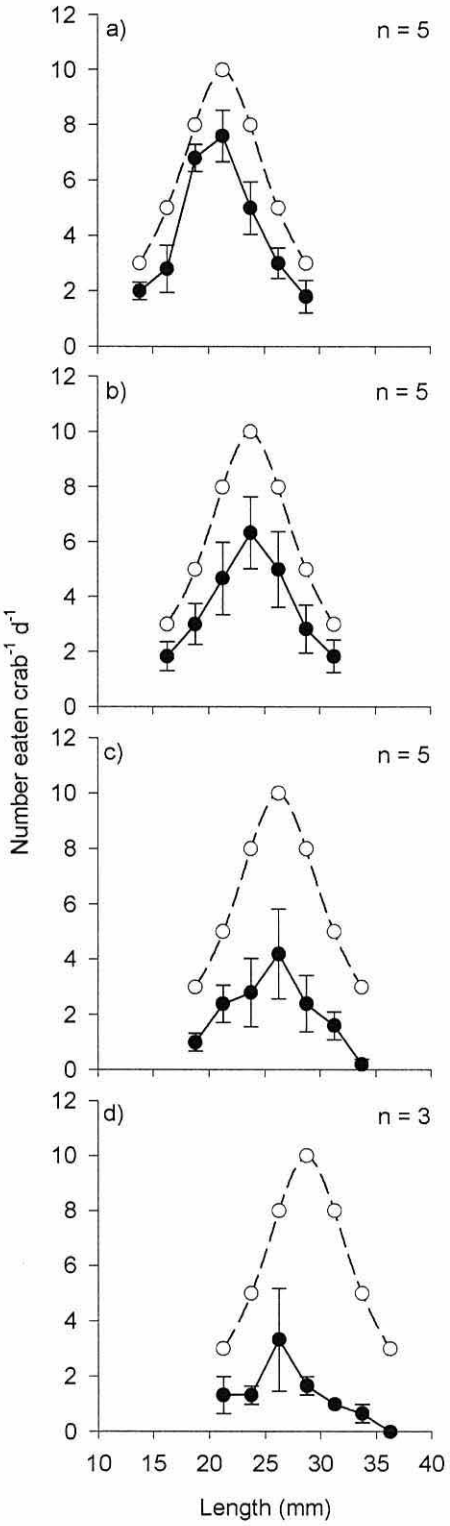


Figure 3.6. Mean number of mussels eaten by *Carcinus maenas* of ~60 mm carapace width during 24 hours (closed circles) when mussels were presented in seven length classes across differing size ranges (open circles). Mean mussel lengths were a) 21.25, b) 23.75, c) 26.25, d) 28.75 mm. Error bars show ±1 S.E.

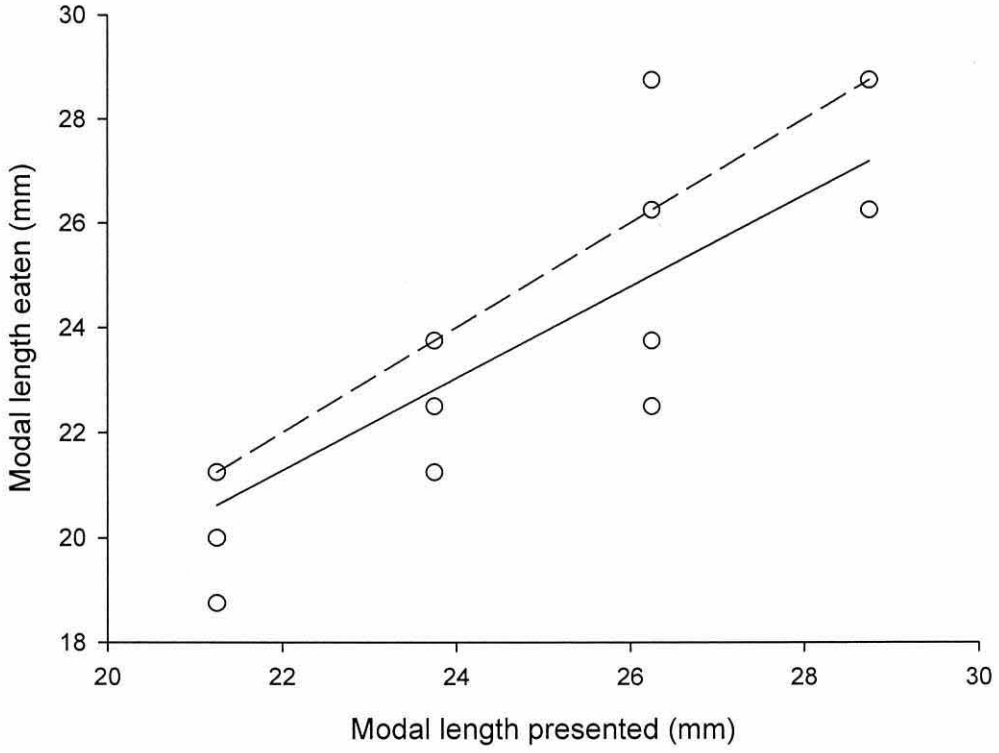


Figure 3.7. Modal length class mid-point of mussels presented to *Carcinus maenas* and those eaten. Dashed line indicates the modal length of mussels which would be consumed where prey presentation is the sole determinant of mussels selected. Solid line shows the correlation between modal length of mussels presented and modal length of mussels eaten ($y = 0.875x + 2.031$, $R^2 = 0.708$, $F_{1,16} = 38.812$, $p<0.0001$).

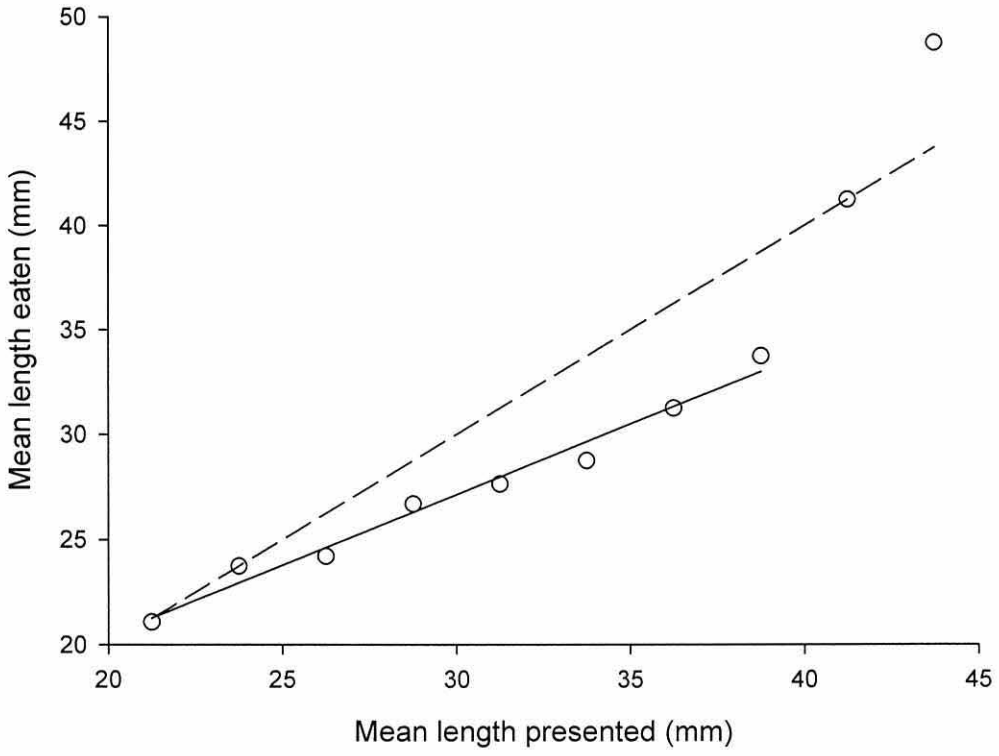


Figure 3.8. Correlation between mean lengths of mussels presented to *Carcinus maenas* and mean lengths of mussels eaten from 21.25 to 38.75 mm (solid line). Numbers eaten are shown from 21.25 to 43.75 mm, together with dashed line indicating the directly proportional ratio of mussel size eaten to mussel size presented ($y = 0.67x + 7.032$, $R^2 = 0.979$, $F_{1,6} = 283.35$, $p<0.0001$).

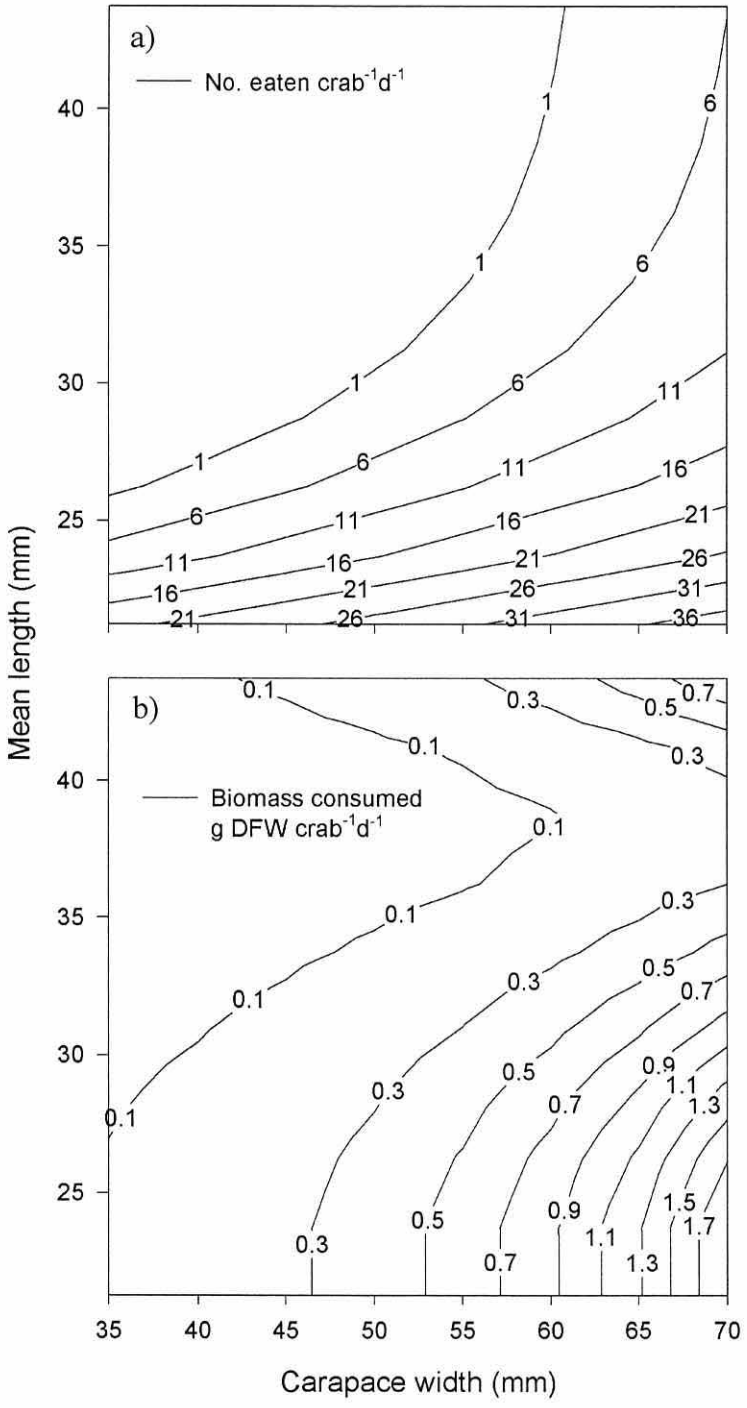


Figure 3.9. a) Predicted mean number of mussels (z_e) and b) predicted dry flesh biomass consumed (z_b) by *Carcinus maenas* during 24 hours when presented with mussels over a range of sizes approximating normal distribution.

The predicted biomass consumed (z_b) was calculated in a similar manner to z_e, using the exponential and three-parameter polynomial functions relating CW and C_b, and MML and C_b, respectively. Thus:

$$z_b = (y_0 + ay^3 - by^2 + cy)e^{a_c x}$$

Where, x = CW; y = MML; a_c = CW v. C_b constant (0.0791); a = 3.31204 x 10^{-6}; b = 3.03206 x 10^{-4}; c = 8.61571 x 10^{-3}; and y_0 = -0.07048.

The estimated biomass consumed by *C. maenas* individuals of 70 mm CW ranged from 0.88 to 1.90 g DFW d^{-1} (Figure 3.9b). For individuals of 35 mm CW, the biomass consumed ranged from 0 to 0.12 g DFW d^{-1}. The biomass consumed by the largest crabs (70 mm CW) was greatest for small mussels (21.25 – 36.25 mm MML) and larger mussels (41.25 – 43.75 mm MML). Mussels between 36.25 and 41.25 mm MML yielded the least biomass for large crabs. Small crabs (35 mm) were only able to eat mussels <26.25 mm in length, consuming 0.1 g DFW d^{-1}.

Sex and colour

There were no significant differences between the length of mussels selected by red and green, and male and female, *C. maenas* other than between green males and red females consuming 30 – 40 mm long mussels (Mann-Whitney, W = 133.0, p = 0.028; Figure 3.10), with green males consuming over twice as many mussels as red females. Ovigerous female crabs did not consume a significantly different number of mussels to male crabs (t = -0.46, p = 0.657; Figure 3.11) when presented with small mussels (20 – 25 mm).

There was no significant difference in the mean number of mussels selected by green male, red male, green female and red female crabs (ANOVA, $F_{3,28}$ = 0.84, p = 0.485; Table 3.1). However, there was a significant difference in the mean length of mussels selected by crabs of different sex and colour (ANOVA, $F_{3,28}$ = 6.76, p = 0.001). Tukey's pair-wise comparisons revealed that there were significant differences between the lengths of mussels selected by green female

crabs and all other crabs, with green females consuming smaller mussels. There was a significant difference in the number of mussels damaged between crab types (ANOVA, $F_{3,28} = 3.30$, $p = 0.035$). Tukey's pair-wise comparisons revealed that significantly more mussels were damaged by red female crabs then red male crabs.

Table 3.1. Mean number of mussels eaten or damaged during 24 hours, and mean length eaten by green (G) or red (R), and male (M) or female (F) *Carcinus maenas*.

Crab sex/colour	Mean no. eaten ±1SE	Mean no. damaged ±1SE	Mean length eaten ±1SE (mm)
GM	7.3 ±0.7	0.1 ±0.1	27.7 ±0.6
RM	6.1 ±0.8	0 -	26.5 ±0.9
GF	5.5 ±0.4	0.1 ±0.1	23.9 ±0.4
RF	6.3 ±1.2	1.1 ±0.6	27.4 ±0.6

Temperature and prey presentation

A significant correlation was found between seawater temperature and the number of mussels eaten ($R^2 = 0.66$, $F_{2,15} = 14.683$, $p<0.001$; Figure 3.12). Residuals were normally distributed (K-S statistic = 0.151, $p = 0.771$) and variances were equal ($p = 0.85$). The number of mussels eaten was 6 times greater at 13°C than at 6°C. There was a decrease in the number of mussels eaten above 13°C, falling to a mean level around the feeding rate exhibited at 9°C.

When exclusively large mussels (40 – 50 mm) were presented to crabs, values of C_e were 0.7 ±0.3, 0.4 ±0.2 and 0.5 ±0.3 mussels per three crabs per 24 hours at 10, 13 and 16 °C respectively (Table 3.2). No effect of temperature on C_e was detected when exclusively large mussels were fed to *C. maenas* (Kruskal-Wallis, $H = 0.49$, $p = 0.783$). More crabs ate larger mussels at 13 °C (5 crabs) than at 10 °C (3 crabs) or 16 °C (4 crabs). Data on feeding rates when mussels were fed in equal size proportions were approximately normally distributed and variances were equal (Levene's test = 0.22, $p = 0.806$). A one-way ANOVA revealed no significant difference in C_e at different temperatures ($F_{2,15} = 0.79$, $p = 0.455$; Table

3.2). In the experiment examining feeding rates over a wide range of temperatures (Figure 3.12), the rates of mussel consumption at 10°C and 16°C were 85 % and 86 %, respectively, of those found at 13°C.

C_e increased with temperature when mussels were fed to crabs in proportions approximating normal distribution (Table 3.2). However, within the temperature range studied (10 – 16 °C) there was no significant effect of temperature on C_e ($F_{2,15} = 0.42$, $p = 0.665$). Data were normally distributed (K-S = 0.130, $p>0.150$) and variances were equal (Bartlett's test = 0.98, $p = 0.612$). When mussels were presented in equal proportions, there was also no significant effect of temperature (Table 3.2). C_e was 98 % lower at 10 °C, 85 % lower at 13 °C and 90 % lower at 16 °C when mussels were fed in equal size proportions as opposed to the size proportions approximating the natural population structure.

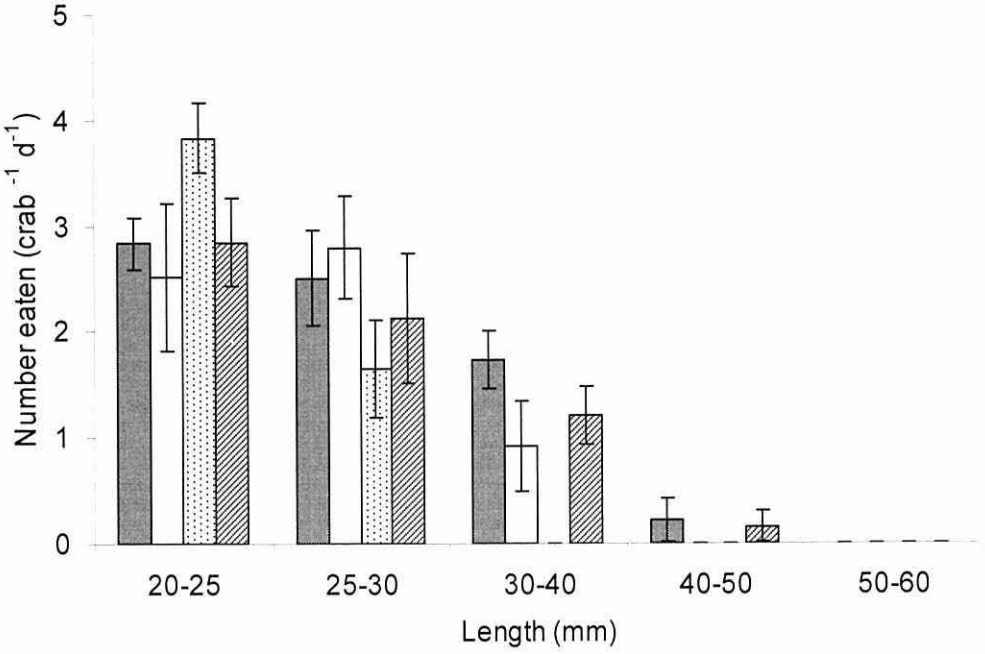


Figure 3.10. Number of *Mytilus edulis* consumed in each of six size classes presented to green males (solid bars), red males (open), green females (dotted) and red females (hatched) *Carcinus maenas* (53 – 70 mm carapace width; n = 8) in equal proportions. Error bars show ±1 S.E.

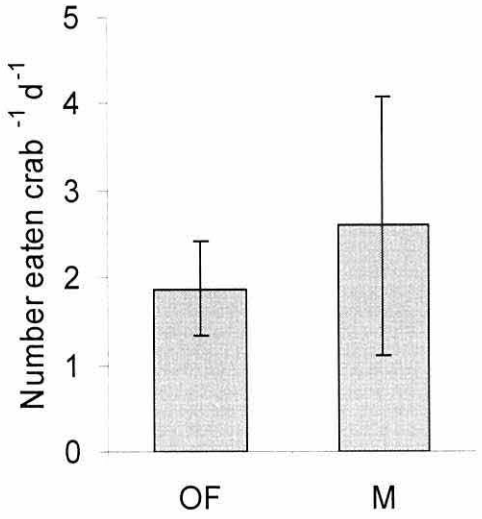


Figure 3.11. Mean number of mussels eaten by ovigerous female (OF) and male (M) *Carcinus maenas* at 12°C. Error bars show ±1 S.E.

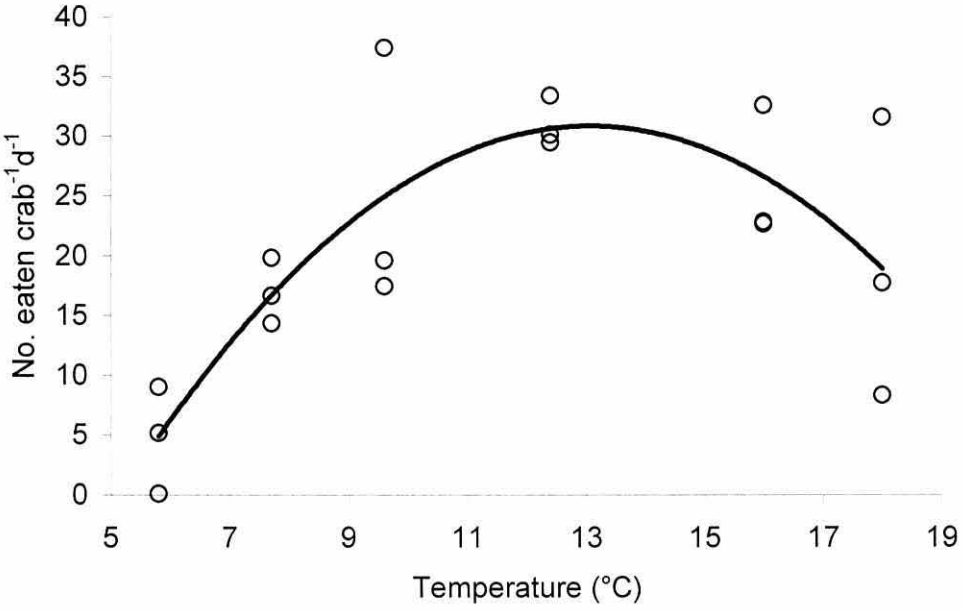


Figure 3.12. Number of mussels eaten during 24 hours by 18 crabs maintained at 6 temperatures and presented with 40 mussels (20-30 mm length) each. Numbers eaten are standardized to a crab CW of 65 mm. Quadratic regression line is shown ($y = -0.492x^2 + 12.856x - 53.12$).

Table 3.2. Number of *Mytilus edulis* consumed by groups of three *Carcinus maenas* (50 – 75 mm carapace width) during 24 hours at three temperatures. Mussels were presented in six size classes in the proportions found on commercial mussel beds in the Menai Strait and in equal numbers. Mean crab carapace widths at 10, 13 and 16 °C were 64.8 ±8.7 mm, 64.1 ±6.8 mm and 65.6 ±6.3 mm, respectively, when mussels were presented in field proportions. Mean crab carapace widths at 10, 13 and 16 °C were 70.4 ±4.2 mm, 70.3 ±3.7 mm and 70.6 ±3.3 mm, respectively, when mussels were presented in equal numbers.

	Length (mm)	25-30	30-35	35-40	40-45	45-50	50-60	Total
		Mean (n = 6)						
	Presented	*3*	*16*	*20*	*8*	*2*	*1*	*50*
	10	2.3 ±0.3	7.7 ±1.6	2.7 ±1.0	0.5 ±0.2	0	0	13.2
°C	13	2.8 ±0.2	7.9 ±1.3	4.1 ±0.8	0.6 ±0.2	0.1 ±0.1	0	15.4
	16	2.2 ±0.5	8.7 ±2.0	4.7 ±1.5	1.5 ±0.6	0	0.2 ±0.2	17.2
		Total						
	Presented	*18*	*96*	*120*	*48*	*12*	*6*	*300*
	10	14	46	16	3	0	0	79
°C	13	17	47	25	3	1	0	93
	16	13	52	28	9	0	1	103
		Mean (n = 4)						
	Presented	*10*	*10*	*10*	*10*	*10*	*0*	*50*
	10	2.6 ±1.3	0.6 ±0.5	0	0	0	-	3.2
°C	13	3.8 ±1.5	2.6 ±0.7	0.8 ±0.3	0	0	-	7.2
	16	3.0 ±0.4	1.3 ±0.9	1.3 ±0.8	0	0	-	5.6
		Total						
	Presented	*40*	*40*	*40*	*40*	*40*	*0*	*200*
	10	13	3	0	0	0	-	16
°C	13	15	5	1	0	0	-	21
	16	12	5	5	0	0	-	20

3.4 DISCUSSION

C. maenas generally selects smaller sized prey items (<25 mm) in preference to larger prey items (Seed, 1980; Sanchez-Salazar *et al.*, 1987a; Walton *et al.*, 2002; Floyd and Williams, 2004), but will eat larger prey, and will also select mussels in preference to other molluscan prey (Miron *et al.*, 2005). Mussels are therefore vulnerable to crab predation at all stages of the cultivation process. However, mussels may attain refuge on the upper shore, where predator numbers are lower, or in the lower shore and subtidal zones by way of more rapid growth rates to a larger size (Seed, 1980). Seasonal migration of *C. maenas* into deeper water means that intertidal prey species may also attain refuge from crab predation for several months of the year (Sanchez-Salazar *et al.*, 1987b).

C. maenas is almost absent from the intertidal zone in the Menai Strait during winter (Gascoigne *et al.*, 2005). Consequently, the impact of predation on intertidal mussel beds is likely to be small from January to March, when temperatures fall as low as 6 °C and the metabolic rate of crabs will be lower (Robertson *et al.*, 2002). Furthermore, commercial catches of *C. maenas* subtidally in the Menai Strait are up to 10 times lower in the winter months (Chapter 2) suggesting that *C. maenas* moves into much deeper waters than are present over the mussel beds (<22 m). In addition, it is during the spring and summer months in the Menai Strait that new seed mussels are laid and partially on-grown mussels are moved into the subtidal zone where they are more vulnerable to predation by virtue of their continuous immersion.

Mussels of 25 – 30 mm length provide the maximum profitability for *C. maenas* of 60 mm CW (Figure 3.5b). Based on profitability, Elner and Hughes (1978) predicted a preferred mussel length of 22.5 – 25 mm for *C. maenas* of 60-65 mm CW, but observed 17.5 mm as the most frequently selected length of mussels. Similarly, Smallegange and van der Meer (2003) predicted a preferred mussel length range of 20 – 22.5 mm but most mussels were selected from the 16 – 18 mm length class. In the current study, the smallest mussels presented to *C. maenas* were 17.5 – 20 mm in length yet the mean and modal mussel length selected was ~24 mm for crabs of 60 mm CW (Figure 3.2). The mean mussel length selected

was equal to the mean length presented at 21.25 mm, slightly lower than that shown in Figure 3.5, but still higher than estimates in other studies. In the studies by Elner and Hughes (1978) and Smallegange and van der Meer (2003) the smallest mussels presented to crabs were 3 mm in length. Therefore, the presence of smaller mussels may have resulted in an apparent preference for smaller mussels due to encounters made by the crabs and experience gained by feeding on smaller mussels. The increases in MML selected with increasing MML presented observed in the current study (Figure 3.6a) verify this suggestion. From Figure 3.2 it is apparent that despite the difference in regression equations between the current study and for the data presented by Elner (1980), the difference in predicted mean mussel length selected is very small, with the largest predicted difference in mean mussel size selected for the smallest and largest crabs, at 1.4 mm and 0.4 mm, respectively.

Rovero *et al.* (2000) showed that the energy cost for *C. maenas* consuming mussels increased from 1.6 % of the energy gained from small mussels (13 – 16 mm) to 3.3 % of the energy gained from larger mussels (27 – 30 mm). Therefore, even when consuming larger mussels *C. maenas* can make substantial energy gains. *C. maenas* switches from crushing mussels to using a more time-consuming cutting technique when the mussel width to major chela length ratio is ≥0.24 (Smallegange and van der Meer, 2003). Thus, crabs more frequently select smaller mussels due to the greater time required to open larger mussels combined with the greater risk of chelal damage. The effect of varying chelal size (Appendix B3) also accounts for some of the variability in the size and number of mussels consumed by crabs in the present study. However, carapace width is a more convenient measure that can be used to rapidly assess the potential levels of predation in the field. Furthermore, Elner (1980) found strong positive correlations between carapace width and master chelal height in both male ($y = 0.48x - 1.11$, $R^2 = 0.93$) and female ($y = 0.23x - 0.02$, $R^2 = 0.86$) *C. maenas* (also see Appendix B3).

It is important to note that in many studies (Elner and Hughes, 1978; Smallegange and van der Meer, 2003; Mistri, 2004) preference for a particular prey size is assumed where the proportion of prey consumed from a given size class is greater

than the proportion presented. Jackson and Underwood (2007) challenge this assumption, defining preference as a difference in the prey selected when choice is available compared to when no choice is available, thereby distinguishing preference from electivity. Thus the larger mussels selected by *C. maenas* in the current study should not be considered indicative of a difference in preference but of electivity, which in terms of assessing the effects of predators on a population of bivalves is the more useful measure.

The time over which experiments are conducted is also important, as mean feeding rates during the first 24 hours were three times greater than after 48 hours or four times greater than after 6 days. During the first few hours of feeding trials commencing crabs will feed more rapidly due to the fact that food was previously withheld for 48 hours to standardize hunger levels. After the initial period of feeding the continued decline in feeding rates may be due to decreased metabolic rates in the laboratory (Wallace, 1973); energy requirements and metabolic rate will be greater in the wild as a result of tidal migration, foraging, breeding, and encounters with other crabs and predators. Feeding rates of crabs in the wild will presumably vary between the extremes recorded over time in the current study, and will be dependent on food availability, season and environmental conditions.

The critical mussel length over which size preference became more important than prey abundance in terms of the mussel size selected was 26 mm, around 2 mm above the size most selected by 60 mm CW crabs when mussels were presented with equal numbers in each size class (Figure 3.2). In the current study, the mussel size selected most often by *C. maenas* of 60 mm CW was also the MML that was most profitable to the crabs (Figure 3.5b). When making their selection crabs investigate the prey sizes available, handling several mussels before selecting one to eat (Elner and Hughes, 1978; Ameyaw-Akumfi and Hughes, 1987). Furthermore, Jubb *et al.* (1983) suggests a relative-stimulus hypothesis in which the size of prey sensed by the crabs' pereiopods influences the prey selected or rejected by the crab. Consequently, foraging time, along with handling time, will be greatly increased by increasing the numbers of mussels above the preferred size causing an exponential decline in numbers eaten.

In the present study, the number of mussels consumed by *C. maenas* was greatest at 13°C (Figure 3.12). No significant difference in feeding rates between 10 and 17°C was reported by Elner (1980). By conducting feeding trials at a slightly lower maximum temperature, of 15.5°C, Sanchez-Salazar *et al.* (1987a) recorded much higher energy consumption at 15.5 °C compared to 9.5°C, but found no significant effect of temperature on the size of *C. edule* selected by *C. maenas*. In addition, feeding rates in *C. maenas* are not entirely dependent on metabolic rate, which changes by a factor 1.4 between crabs acclimatized at 10°C and 24°C, compared to feeding rates, which changed by a factor of 2.4 (Wallace, 1973). Robertson (2002) showed that the postprandial rise in oxygen consumption in *C. maenas* was three times greater than in starved crabs kept at 15°C, while oxygen consumption increased only two-fold in crabs kept at 7°C and 22°C. This supports the finding in the present study of higher feeding rates at ~11-14 °C compared to those found at higher or lower temperatures. However, Robertson *et al.* (2002) did not find ant significant difference in meal size between 7, 15 and 22°C. The effects of short-term temperature changes experienced by *C. maenas* due to weather conditions and tidal migration are also unclear. Temperatures in the Menai Strait range from approximately 6 to 17°C and *C. maenas* will feed within this range, although feeding rates are reduced at lower temperatures. Furthermore, Aagaard (1996) showed that the relationship between abiotic factors and *C. maenas* heart rate are extremely complex in the natural environment.

When larger mussels were presented to *C. maenas*, there were no significant differences between the length of mussels selected by red and green forms, or between males and females, other than between green males and red females consuming mussels 30 – 40 mm in length (Figure 3.10), with green males consuming over twice as many mussels as red females of comparable size. Green female crabs did not consume any mussels >30 mm in length. The more rapid chelal movements in green *C. maenas* compared to the stronger but slower chelal muscle contractions in red forms may be advantageous in opening larger mussels where crushing is not possible (Kaiser *et al.*, 1990), allowing green *C. maenas* to consume more large mussels than red forms. The combined effect of weaker chelal muscular contractions and smaller chelae in green female crabs (Berrill and Arsenault, 1982; Appendix B3) may therefore result in fewer mussels being eaten.

Red female crabs damaged significantly more mussels without eating them than the other crabs, presumably as they were unable to open the mussels. The number of mussels damaged but not eaten by all other crabs did not differ significantly from zero (Table 3.1), which is indicative of the shore crabs ability to select suitably sized prey when presented with a range of prey items of varying sizes.

When female *C. maenas* are egg-bearing they often remain buried in the sediment, feeding only occasionally (Cameron and Metaxas, 2005). However, feeding rates of ovigerous females are not significantly lower than those of males in the laboratory when feeding on small mussels; therefore, ovigerous females cannot be ignored as potential predators of mussels. Differences in the diet of male and female *C. maenas* (Scherer and Reise, 1981) and *H. sanguineus* (Brousseau and Baglivo, 2005) have been reported; however, Ropes (1968), Elner (1981) and Raffaelli *et al.* (1989) did not find any differences in the diet composition of male and female *C. maenas*. Brousseau *et al.* (2001) attributed differences in prey consumption rates and size preference between male and female *H. sanguineus* to larger chelal size in males. Several studies have found that male *C. maenas* are more migratory than females (Crothers, 1968; McGaw and Naylor, 1992; Aagaard *et al.*, 1995a) though Rewitz *et al.* (2004) found no differences in the levels of migration exhibited by male and female *C. maenas*. Moreover, green colour forms of *C. maenas* exhibit greater changes in behaviour due to circatidal and circadian rhythms than red forms (McGaw and Naylor, 1992; Hunter and Naylor, 1993; Warman *et al.*, 1993; Aagaard *et al.*, 1995b; Styrishave *et al.*, 1999).

Partitioning of the *C. maenas* population by sex or colour has been attributed to mating tactics (van der Meeren, 1994) or differences in salinity tolerance between red and green colour forms (Rewitz *et al.*, 2004). Although salinity may be an important influence on *C. maenas* population partitioning in an estuary, salinity in the Menai Strait is generally consistent, varying between only 31 and 33.7 from May 1962 to May 1963 at Menai Bridge Pier (Buchan *et al.*, 1967). Furthermore, the water-column in the Menai Strait is vertically well-mixed, and salinity varies only from 31.5 to 33 over a tidal cycle (Tweddle *et al.*, 2005). Consequently, seasonal variations in temperature (see Chapter 2), prey distribution and mating tactics are most likely to influence crab distribution in the Menai Strait. Mating

occurs predominantly during June (see Chapter 2) and it is during this time of the year that mating tactics will most influence population partitioning. In particular, crabs will move into the intertidal zone and predation of the smaller mussels present in the intertidal zone may be intensified by foraging male crabs at this time, although not by the moulting female crabs.

Several studies have shown circatidal and circadian rhythms to persist in *Carcinus maenas* in the laboratory when crabs are kept in continuous light (Naylor, 1958) and continuous dark (Aagaard *et al.*, 1995b). In addition, circadian and circatidal rhythms are exhibited by intertidal shore crabs *in situ*, with temperature exerting the greatest effect on heart rate and locomotor activity (Aagaard, 1996; Styrishave *et al.*, 1999). In contrast, subtidal *C. maenas* do not exhibit circadian rhythms (Lynch and Rochette, 2007). Green *C. maenas* exhibit significantly higher heart rates than red crabs (Aagaard, 1996) which, together with differences in feeding techniques (Kaiser *et al.*, 1990), explains the higher feeding rates in green crabs (Figure 3.10). Light intensity, salinity and depth also influence heart rate in *C. maenas* (Aagaard, 1996; Styrishave *et al.*, 1999) but to a lesser extent than temperature.

In summary, the results presented in this chapter describe the relationship, in terms of feeding rates and prey selection, between *C. maenas* and *M. edulis*. *C. maenas* is capable of consuming >30 mussels per day and when present at abundances of several thousand per hectare (see Chapter 2) clearly represents a potential major source of mussel losses. The formulae presented can be applied to the *C. maenas* abundance data presented in Chapter 2 to make estimates of the numbers of mussels lost to crab predation. The constants derived could also be applied to other mussel cultivation sites and the methods used to predict predator effects on bivalve populations in general. In the following chapter the ability of *Carcinus maenas* to select the most profitable areas in which to forage for mussels is examined. In addition, the effect on prey consumption of interaction with conspecifics is also assessed.

CHAPTER 4

THE FORAGING ABILITY OF *CARCINUS MAENAS*: EFFICIENT PATCH SELECTION FOR OPTIMAL FEEDING

ABSTRACT

The shore crab *Carcinus maenas* consumes a wide variety of prey, but often selects molluscs in preference to other phyla. Although shore crabs can feed on a wide size range of prey they usually exhibit a preference for smaller prey items. To date no study has shown whether crabs are able to identify the most suitable areas in which to forage. In the present study several hypotheses were tested that related to the foraging ability of shore crabs. Firstly, that *C. maenas* would spend more time searching on patches of smaller mussels. Secondly, that *C. maenas* would spend more time handling and feeding on patches of exclusively small mussels. Thirdly, that searching and feeding by *C. maenas* would be more efficient (crabs would search and feed predominantly where only smaller mussels were present) in crabs kept individually compared to individuals in the presence of other crabs. Crab activity in a tank divided into quadrants containing either small mussels, large mussels, small and large mussels, or no mussels was recorded for three hours. Crabs were observed in darkness under infrared light and were kept individually or in groups of three. The results showed that *C. maenas* clearly possesses the ability to identify the most profitable areas in which to forage and handle prey. Crabs responded to interference by increasing searching efficiency, with important implications for how populations might be distributed in the wild. Foraging and feeding in *C. maenas* is subtly affected by interactions between crabs of different sizes. Mean handling and feeding time is greater where there is a greater disparity in crab sizes within groups. Mixing larger mussels with smaller mussels could help to reduce losses from crab predation on cultivation sites. It would be of interest to determine whether the behaviour observed in the present study occurs over larger spatial scales.

4.1 INTRODUCTION

Mussel beds may consist of a single or several year classes of mussels (Seed, 1969b). Cultivated mussel beds in particular may consist of mussels across a wide range of sizes, from seed <10 mm in length up to mussels >60 mm (Chapter 2) and like naturally occurring beds may consist of several year classes of mussels (Murray *et al.* 2007). *C. maenas* is commonly found on mussel beds (Chapter 3; Saier, 2002; Beadman *et al.*, 2004) and crabs often consume molluscs in preference to other prey species (Crothers, 1968).

C. maenas selects prey using touch receptors on the pereiopods (Jubb *et al.*, 1983). The vulnerability of a particular prey size is increased when it comprises a greater proportion of the mussel population (Burch and Seed, 2000; Chapter 5). Sight is not used by *C. maenas* to identify suitable prey (Elner and Hughes, 1978) but this species does exhibit preference for different chemical signals (Shelton and Mackie, 1971). Although *C. maenas* can feed on large mussels (Ameyaw-Akumfi and Hughes, 1987) it must do so using a more time-consuming cutting technique, as opposed to crushing smaller mussels (Smallegange and van der Meer, 2003); this technique has also been reported in other decapod crustaceans (Seed, 1990).

Jackson and Underwood (2007) highlighted the difference between preference, electivity and acceptability in feeding, each of which influences the prey consumed by a predator. Several studies have shown that *C. maenas* frequently selects prey items below the maximum size that can be opened (Hughes and Seed, 1981; Seed, 1982; Sanchez-Salazar *et al.*, 1987a; Mascaro and Seed, 2000b), although it does not necessarily select the most profitable size of mussels (Elner and Hughes, 1978; Smallegange and van der Meer, 2003). Jubb *et al.* (1983) found that the frequency at which mussels were rejected increased during the first 30 minutes of feeding, when chelal stimuli were more important but thereafter remained level when pereiopod stimuli were more influential.

Ideal free distribution (IFD) theory (Fretwell, 1972) predicts that an organism will occupy the most suitable habitat, that is, the area that provides the highest gain (food, refuge, mating opportunities), assuming the animal has information on the

resource distribution and can move freely between patches. Several studies have shown that the distribution of animals, including pea aphids *Acyrthosiphon pisum* (Flaxman *et al.*, 2007), oystercatchers *Haematopus ostralegus* (Sutherland, 1982; Goss-Custard *et al.*, 1984) and herring gulls *Larus argentatus* (Monaghan, 1980), conform to various IFD models. Both interference and exploitative competition may influence a predator's choice of habitat, and thus influence its distribution. Griffen and Byers (2006) showed that feeding rates of *C. maenas* were reduced in the presence of *Hemigrapsus sanguineus* due to interference competition. Male *C. maenas* will engage in contests with one another to gain access to female crabs, with a 40% incidence of injury (Sneddon *et al.*, 2003), thus increasing energy demand and reducing the time available for feeding. Ramsay *et al.* (1997) observed that the encounter rate between the hermit crab *Pagarus bernhardus* individuals increased when food resources were limited. The suitability of food (or host species in the case of parasites) and refuges within a habitat will also be a major influence on the distribution of populations (Spataro and Bernstein, 2007).

Rovero *et al.* (2000) demonstrated that the energy costs of *C. maenas* feeding on *M. edulis* were minimal (≤3.3 % of energy gains) and that the time required to handle and consume prey most influenced prey selection. Similarly, foraging time is increased where prey is above the preferred size of a predator (Burch and Seed, 2000; Chapter 3). Therefore, in order to maximize profit from foraging and feeding crabs should move from areas with mussels above the optimal size. To do so, however, requires some ability of crabs to remember the potential gains that can be obtained from foraging in certain arrays of prey based on previous experience. Elner and Hughes (1978) suggest that *C. maenas* has only a very short-term memory that limits optimal foraging ability to small areas.

Any inability to distinguish between the most profitable areas in which to forage would be disadvantageous to *C. maenas*, but would allow commercial mussel growers to reduce the losses of smaller sized mussels by mixing them with larger sub-optimal mussels. Conversely, an ability of *C. maenas* to identify the most profitable areas in which to forage would reduce the time crabs spent searching for appropriately sized prey and handling overly large mussels. The aim of the current study was to determine whether *C. maenas* was able to select the most

profitable mussel patches in which to forage and handle prey. The effect of several crabs feeding together was also examined to assess whether encounters with other conspecific individuals reduces feeding rates compared with crabs feeding when maintained individually. Several hypotheses were made regarding the foraging ability of *C. maenas*. Firstly, that crabs would spend more time searching on patches of smaller mussels. Secondly, that *C. maenas* would spend more time handling and feeding on patches of exclusively small mussels. And thirdly, that searching and feeding by *C. maenas* would be more efficient (crabs would search and feed predominantly where only smaller mussels were present) amongst crabs kept individually.

4.2 MATERIALS AND METHODS

Mussels were collected from intertidal cultivated mussel beds in the Menai Strait, southeast of Bangor Pier, during May 2007. Mussels were removed from five cores (10 cm diameter) collected at each of four locations on the mussel beds; these were: year-one mussels, lower (L1) and upper (U1) shore, and year-two mussels, lower (L2) and upper (U2) shore. A third year class was also evident at L2. The year-one mussels had been laid 9 months prior to sampling, while the year-two mussels were laid 21 months prior to sampling. The length of all mussels collected was measured along the maximum antero-posterior axis to 0.1 mm, and the number of mussels per core recorded. Mussels ranged from around 15 mm to 40 mm in length at sites L1 and U1, and from approximately 20 mm to 65 mm in length at L2 and U2.

A total of 40 feeding trials were conducted using 80 male *C. maenas* of 55 – 80 mm carapace width (CW). All crabs used were collected from the commercial mussel beds using baited traps. Crabs were fed to satiation; food was then withheld for 48 hours prior to commencing each feeding trial. Crab CW was measured to 0.1 mm across the widest section of the carapace using dial callipers. The maximum height of the propus was also measured (chelal height). Each feeding trial was run for 190 minutes, and the entire experiment was conducted over three weeks using a randomized block design. Crabs were recorded either

individually (n = 20) or in groups of three (n = 20). The mean CW (±S.D.) of crabs recorded individually was 65.0 ±4.2 mm and those kept in groups was 64.3 ±5.6 mm. Mussels were presented in three combinations of sizes, which were: small mussels only (S), large mussels only (L), and a mixture of small and large mussels (SL). The mussel sizes presented represented two year classes of mussels found on commercial intertidal mussel beds in the Menai Strait, where mussel cohorts can occur both separately and as a mixture of both year classes. A rectangular tray (40 cm long x 30 cm wide x 5 cm deep) constructed from plastic mesh was divided into equally sized quadrants. Three of the quadrants were filled with mussels at densities approximating those found on the mussel beds; the fourth quadrant was covered with sand in solid shallow plastic tray (NM). Thus to each quadrant was added either 191 small mussels (1,276 g total wet weight), 58 large mussels (1,517 g total wet weight), or 80 small and 29 large mussels (1,397 g total wet weight) so that crabs had a choice of four different patches in which to search and feed during each trial. The mesh tray was placed in a solid plastic container filled with seawater (24 L), which was aerated gently at both ends of the container. Crabs were gently introduced into the water at the centre of the container and allowed to sink to the bottom.

The aquarium was filmed using a Sony DCR-TRV250E digital camcorder. Images from the camcorder were transmitted to computer via a FireWire 400 (IEEE 1394) cable. Time-lapsed images were captured directly to hard drive using Scenealyzer software, with one second of recording equivalent to one minute real-time footage. Both the camcorder and aquarium were covered with thick black plastic sheeting to ensure complete darkness and images were recorded under infrared light. After 190 minutes of recording, all eaten mussels were replaced. The S, L, SL, or NM treatments were moved at random between each quadrant and seawater was replaced for each of the 40 feeding trials. Water temperature ranged from 13 to 15 °C during the course of the entire experiment.

Recorded footage was analysed using Window Movie Maker software. After allowing ten minutes for crabs to settle, crab activity was recorded continuously to the nearest 0.08 of a second, time-lapsed duration, which amounted to one image every 4.8 seconds real-time. The time spent by each crab undertaking any particular

activity in each quadrant was noted during the course of each 180 minute trial. Five different activities were distinguished, namely: Searching – crabs moving about the aquarium and sometimes probing with their pereiopods as they investigated their surroundings and the available prey; Handling – handling and breaking mussels or digging into sand with the chelae; Feeding – consuming mussel flesh once the shell had been broken open; Resting – no discernible activity; and Encounters: interactions between crabs including fighting, stealing prey or any change in the activity of one crab due to the activity of another crab. The experiment was conducted and analysed using a Chi-squared design assuming that the time spent conducting each activity in each quadrant would be equal if *C. maenas* did not distinguish between the most profitable patches in which to search, rest, interact with other crabs, or handle prey and feed.

4.3 RESULTS

Mussels in the first year of growth during cultivation had a mean length of 27.0 mm, while those in the second year of growth had a mean length of 41.7 mm (Figure 4.1). First year mussels were present at a density of 6,366 ±676 mussels m^{-2}, while the predominantly second year mussels were present at a density of 1,948 ±317 mussels m^{-2}. There were no significant correlations between crab CW (or chelal height), or the standard deviation of crab CW (or chelal height) within groups, and the time involved in encounters or any other activity ($p>0.05$). Mean CW did not differ significantly between crabs recorded individually or in groups (ANOVA, $F_{1,78} = 0.30$. $p = 0.583$); variances were equal (Levene's test = 1.21, $p = 0.274$).

The most frequent number of feeding events observed amongst individual crabs was three, with a maximum of 17 handling events (Figure 4.2a). Almost twice as many crabs in groups rather than individuals did not feed (Figure 4.2b). However, groups of crabs also showed the highest number of handling events, with a maximum of 26. Over 40% of crabs in groups spent no time feeding, compared to 30% of individual crabs which did not feed (Figure 4.3a and b). Of the crabs observed individually, 50% spent 0-20 minutes exhibiting handling behaviour, while 40 % spent 10-20 minutes feeding. Of the crabs observed in groups, 45% spent only 0-20 minutes

feeding. The maximum time spent feeding was 130-140 minutes by individual crabs, while the maximum time spent feeding by crabs in groups was 100-110 minutes. Chi-squared tests revealed that the number of crabs which spent most time searching each quadrant differed significantly from equal proportions when groups of crabs were observed (Table 4.1). However, the quadrants in which most crabs spent the maximum time searching did not differ significantly from equal proportions for individual crabs. The numbers of crabs which spent the maximum time handling and feeding differed significantly from equal proportions for both individual crabs and groups of crabs, with crabs spending the most time in the quadrant with small mussels only. The numbers of crabs spending the maximum time resting in each quadrant did not differ significantly from equal proportions for either individual crabs or groups of crabs. Chi-squared tests were also conducted and were based on group and individual trials together. Expected values were calculated from two-way contingency tables. The results indicated that the time spent searching differed significantly from expected counts for individuals and groups, with the time spent in the quadrant with small mussels only contributing most (2.0) to the chi-squared value of 9.683 (Table 4.2) and more crabs in groups spending most time searching in the small mussel quadrant.

The time spent by individual crabs searching each quadrant was similar, at around 8 minutes per three hours (Figure 4.4a). Crabs in groups spent less time searching each quadrant, investigating each of them for around 5 minutes (Figure 4.4b). Crabs were only involved in encounters for an average of ~3 minutes in each quadrant. Both individual crabs and groups of crabs spent most time in the quadrant containing small mussels only, with individual crabs spending 70 minutes in this quadrant (Figure 4.4c) compared to 60 minutes for groups of crabs (Figure 4.4d). The time spent by individual crabs handling prey was greatest in the quadrants with small, and small and large mussels, and the time spent feeding in these quadrants was also greatest (Figure 4.5a). Groups of crabs also fed in the quadrant containing only large mussels (Figure 4.5b). There were no significant differences between individual and groups of crabs in the total time spent searching (Kruskal-Wallis, $H_{1,18} = 1.90$, $p = 0.168$), handling (ANOVA, $F_{1,18} = 0.66$, $p = 0.423$), feeding (ANOVA, $F_{1,18} = 0.05$, $p = 0.819$) or

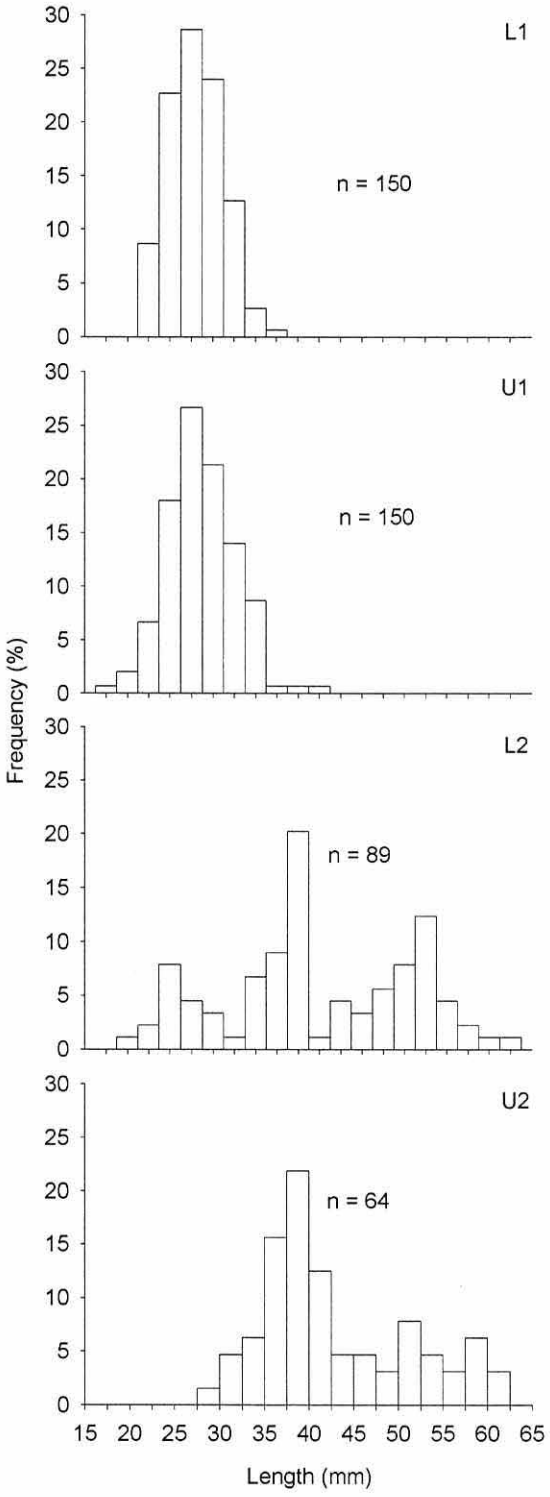
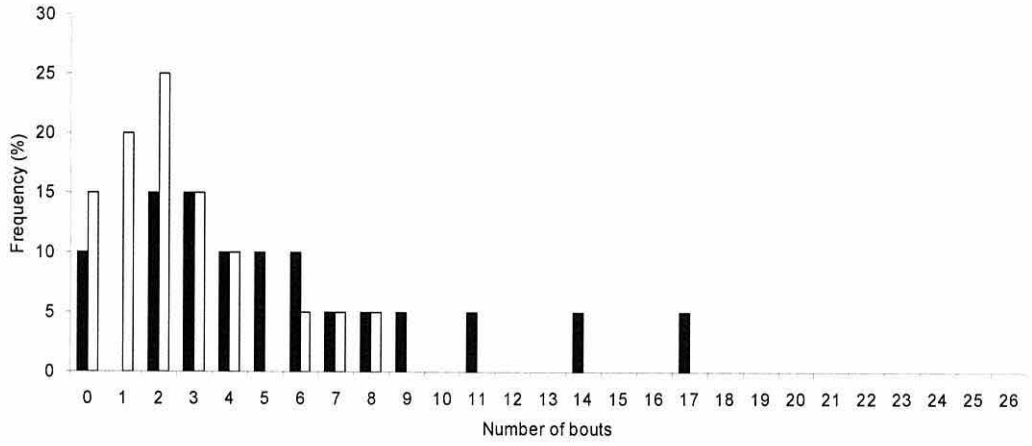


Figure 4.1. Size-frequency distributions of mussels collected from four sites on intertidal mussel beds in the Menai Strait. Sites were located in either the lower (L) or upper (U) reaches of the mussel beds and contained mussels predominately in the first (1) or second (2) year of growth after being re-laid as seed.

a)



b)

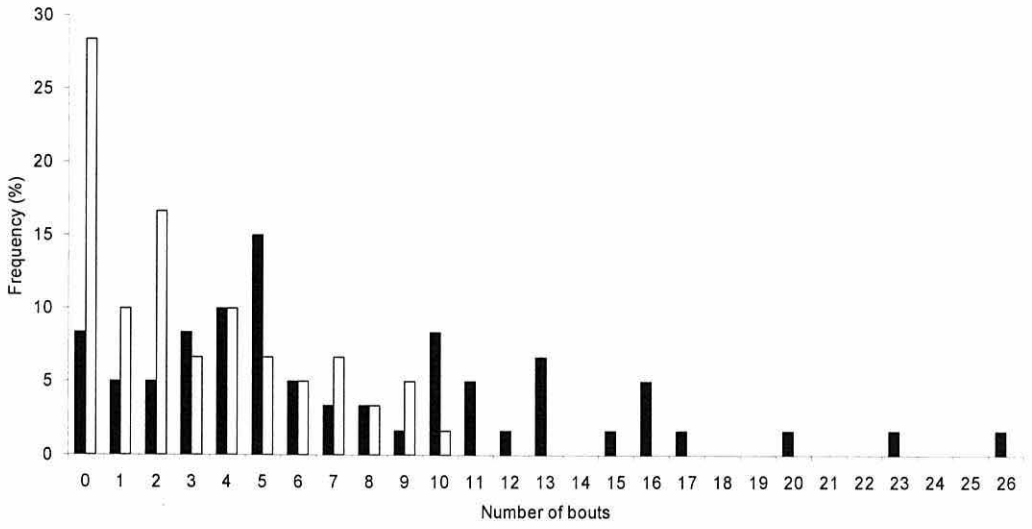
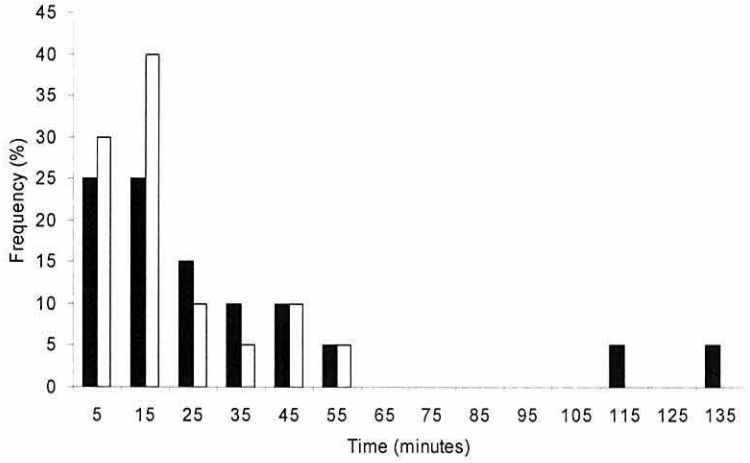


Figure 4.2. Percentage frequency of the number handling (solid bars) and feeding (open bars) bouts exhibited by *Carcinus maenas* kept individually (a; n = 20) or in groups of three (b; n = 20) over a period of three hours.

a)



b)

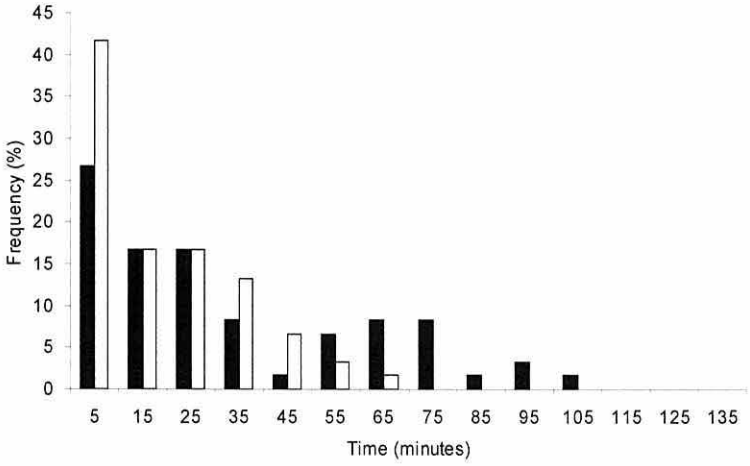


Figure 4.3. Frequency distributions of the time spent by *Carcinus maenas* handling prey (solid bars) and feeding (open bars) over a period of three hours. Crabs were kept individually (a) or in groups of three (b).

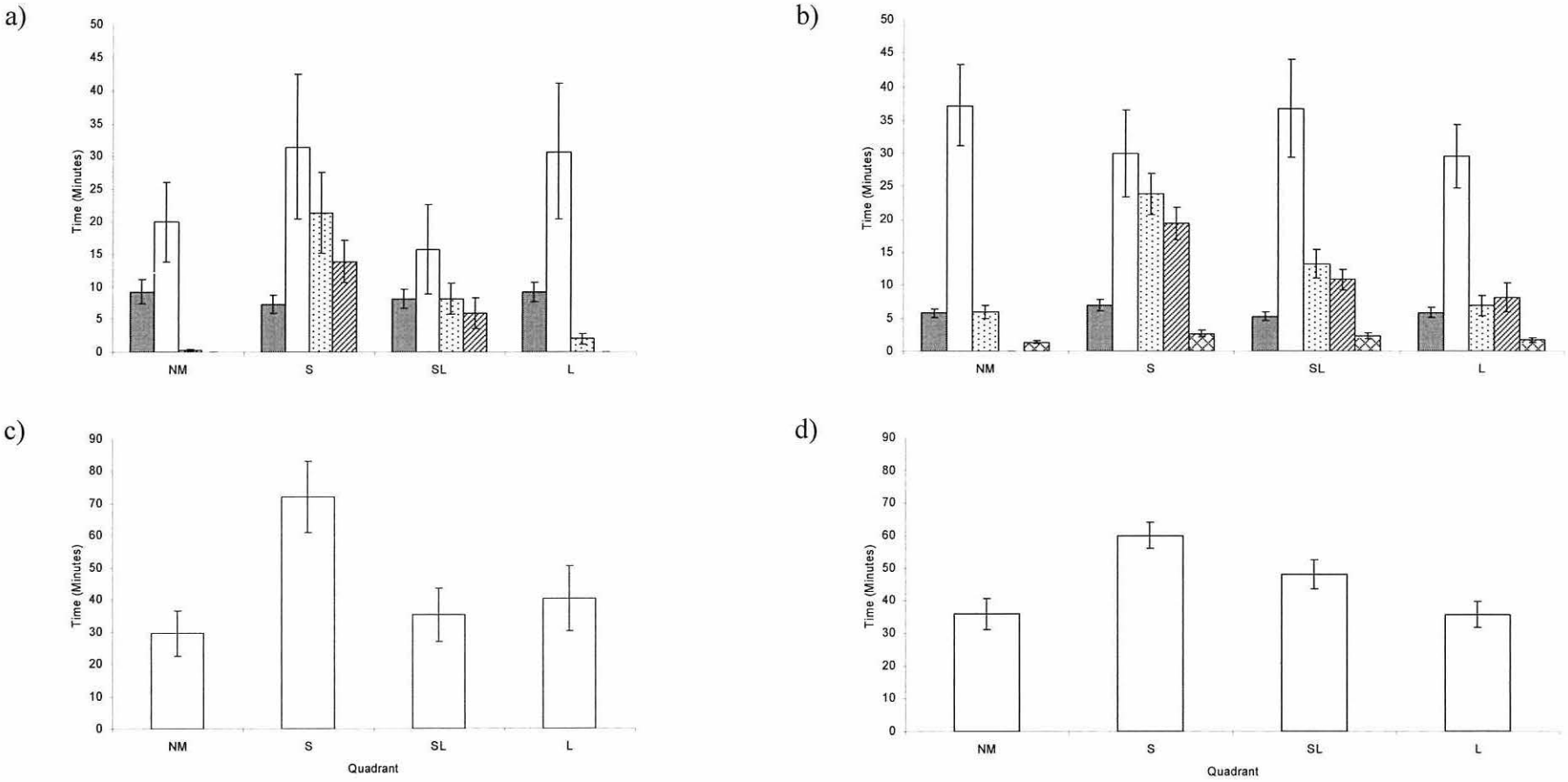


Figure 4.4. Mean time (±1 S.E.) spent by *Carcinus maenas* searching (solid), resting (open), handling (dotted), feeding (hatched), or engaged in encounters with other crabs (cross-hatched) when kept individually (a) or in groups of three (b) in each quadrant containing no mussels (NM), small mussels (S), small and large mussels (SL) or large mussels only (L). The total time spent in each quadrant is also shown for crabs observed individually (c) and in groups (d).

resting (ANOVA, $F_{1,18} = 0.18$, $p = 0.672$). The mean time ±S.E. crabs spent involved in encounters with other crabs was only 6.5 ±1.3 minutes out of each three hour period. The frequency with which mussels were handled by either individual crabs (Figure 4.4a) or crabs in a groups (Figure 4.4b) did not differ significantly (ANOVA, $F_{1,18} = 1.61$, $p = 0.212$), and variances were equal (Levene's test = 0.02, $p = 0.880$).

Likewise, the frequency with which crabs fed on mussels did not differ significantly between individuals and crabs in groups (ANOVA, $F_{1,18} = 0.43$, $p = 0.517$), and variances were also equal (F-test = 1.68, $p = 0.268$). Both individual crabs and groups of crabs handled more mussels and fed more in the quadrant containing small mussels only.

Table 4.1. Chi-squared test results based on the maximum time spent by *Carcinus maenas* exhibiting several forms of behaviour in each quadrant containing either no prey (1), small mussels (2), both small and large mussels (3), or large mussels only (4). Crabs were kept either individually or in groups of three. Expected counts were assumed to be equal for each quadrant in all cases. Observed counts are shown for quadrants 1:2:3:4, and 2:3:4 only for feeding. Significant differences from expected counts in bold.

Activity	*n*	*Obs.*	*DF*	χ^2	*p*
Groups					
Searching	20	2:12:5:1	3	14.8	**0.002**
Handling	20	0:17:3:0	3	39.6	**<0.001**
Feeding	20	14:5:1	2	13.3	**0.001**
Encounters	20	3:12:5:0	3	15.6	**0.001**
Resting	20	10:4:2:4	3	7.2	0.066
Total	20	3:9:5:3	3	4.8	0.187
Individuals					
Searching	20	6:4:4:6	3	0.8	0.849
Handling	18	0:12:6:0	3	22	**<0.001**
Feeding	17	11:6:0	2	10.7	**0.005**
Resting	19	5:6:2:6	3	2.3	0.520
Total	20	3:10:3:4	3	6.8	0.079

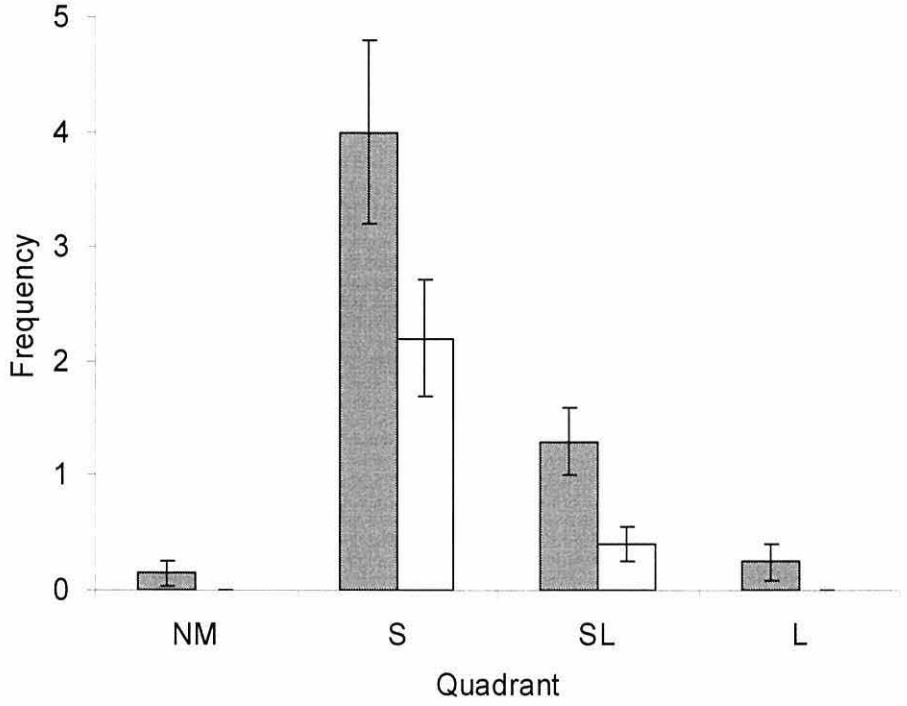
Table 4.2. Results of Chi-squared tests on all feeding trials, groups and individuals. Significant difference from expected counts (based on a two-way contingency table) in bold. Counts for handling and feeding were based only on the two quadrants containing small mussels.

Activity	*n*	*DF*	χ^2	*p*
Searching	40	3	9.683	**0.021**
Handling	38	1	1.762	0.184
Feeding	37	1	0.341	0.559
Resting	39	3	2.443	0.486

Although this study did not aim to assess the effects of crab size on foraging, there were small differences in the sizes of crabs within each group of three, as crab carapace width (CW) ranged from 55 – 80 mm overall. It was therefore considered worthwhile to determine whether variation in the size of crabs *within* groups influenced foraging behaviour. There were significant correlations between CW standard deviation (SD) within groups of three crabs and feeding+handling time SD ($R^2 = 0.371$, $F_{1,18} = 10.619$, $p = 0.004$; Figure 4.6), and resting time SD ($R^2 = 0.299$, $F_{1,18} = 7.682$, $p = 0.013$; Figure 4.6). There were no significant correlations between mean CW and either feeding+handling time SD ($R^2 = 0.062$, $p = 0.230$) or resting time SD ($R^2 = 0.024$, $p = 0.514$). Furthermore, no significant correlations between mean CW and mean feeding+handling time ($F_{1,18} = 0.100$, $p = 0.756$), or mean resting time ($F_{1,18} = 0.140$, $p = 0.713$) were apparent. Therefore, there is a real positive relationship between the variation in crab size within groups and the time spent feeding and handling prey, or resting. No significant correlations between CW SD and searching time SD ($R^2 = 0.063$, $p = 0.288$) or encounter time SD ($R^2 = 0.172$, $p = 0.069$) were observed. The CW SD was not correlated with the number of handling+feeding events ($R^2 = 0.008$, $p = 0.713$), or with handling ($R^2 = 0.124$, $p = 0.127$) or feeding ($R^2 = 0.151$, $p = 0.090$).

Overall these results show that *C. maenas* searches more efficiently when in the presence of conspecifics. Crabs spend more time handling and feeding on small mussels which are not mixed with larger mussels. The time spent handling prey and feeding is greater where there is a greater range of crab sizes within a group.

a)



b)

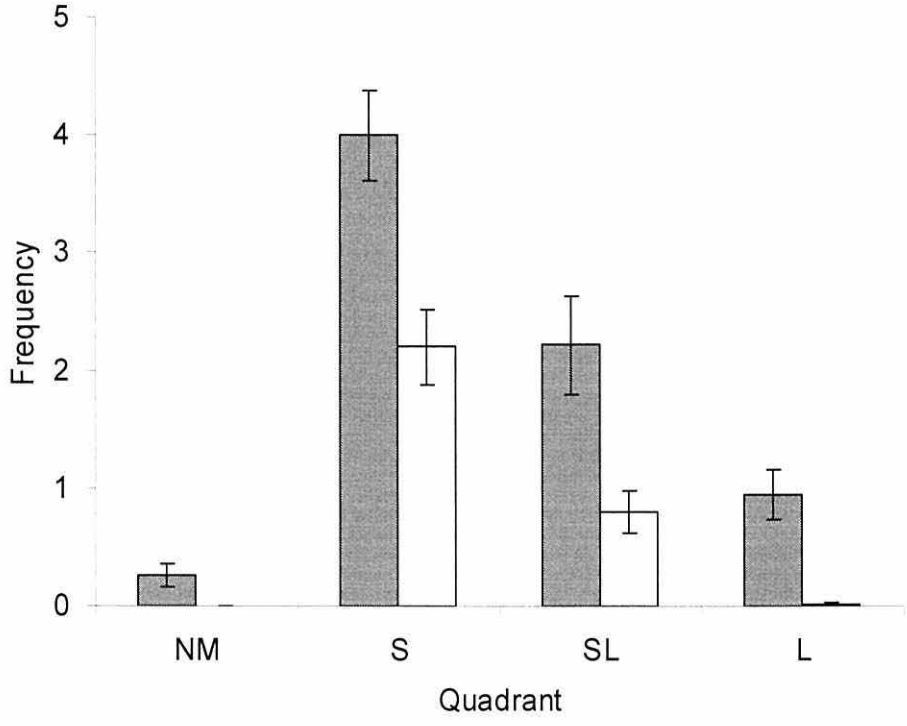


Figure 4.5. Mean number of handling (open bars) and feeding (solid bars) (±1 .S.E.) bouts undertaken by *Carcinus maenas* in each quadrant containing either no mussels (NM) small mussels (S), small and large mussels (SL) or large mussels (L). Crabs were kept individually (a) or in groups of three (b).

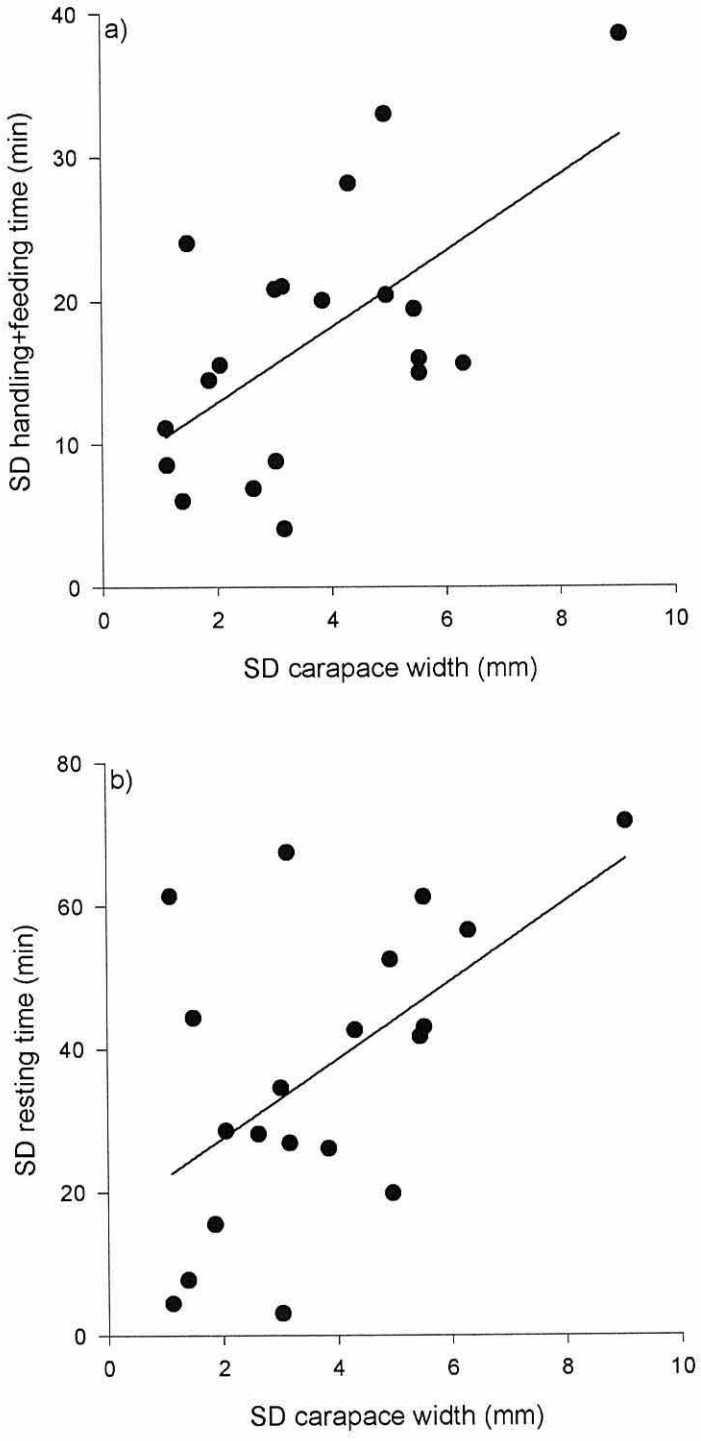


Figure 4.6. Correlations (regression lines are shown) between one standard deviation (SD) of carapace width (CW; n = 3) and (a) one SD of handling+feeding time (y = 2.641x + 7.636) and (b) one SD of resting time (y = 5.518x +16.482). NB. There were no significant correlations between mean CW and either mean (or SD) feeding+handling time or mean (or SD) resting time.

4.4 DISCUSSION

The ideal free distribution of *Carcinus maenas* populations on cultivated mussel beds could be expected to result in the majority of the population feeding in the intertidal zone where mussels are more accessible due to their smaller size (see Chapter 3). Schatz and McCauley (2007) suggest that population dynamics may be significantly altered by the ability of consumers to assess spatial variation in food quality. The tidal and annual migrations exhibited by *C. maenas* (see Chapter 2) show that the most suitable habitat for the species – in terms of food, environmental conditions, reproduction and refuge – varies widely with time. Consequently, crabs must continually assess their environment and the available resources. *C. maenas* is capable of feeding on a wide range of prey (Ropes, 1968; Elner, 1981) and prey sizes (see Chapter 3), but it is also highly selective when given a choice of prey sizes (Elner and Hughes, 1978) and is influenced by the available prey size only up to a critical size (see Figure 3.6). Therefore, the ability to recognise not only the most profitable prey to consume but also the most profitable areas in which to forage would be a distinct advantage to any selective predator involved in regular migrations.

Ameyaw-Akumfi and Hughes (1987) suggested that optimally foraging crabs base the size selection of mussels on the size of mussels previously encountered in sequence. Jubb *et al.* (1983) suggested a relative-stimulus hypothesis under which it is asserted that foraging crabs receive stimuli from both the chelae and the pereiopods, with the influence of each stimulus varying depending on prey size and hunger levels. Therefore, it is clear that *C. maenas* is well equipped to select suitably sized prey. It has not yet been determined whether *C. maenas* can also identify the best areas in which to forage. Crabs presented with a mixture of small mussels (the optimal size) and large mussels (sub-optimal size) can clearly select the smaller prey items. Can crabs also identify the most profitable areas in which to forage? Or more specifically, when presented with a mixture of small and large mussels and a separate patch in which only small mussels are present, can *C. maenas* identify that patch of smaller mussels as the most suitable area in which to forage and feed? To do so requires that crabs possess the ability to remember the

surrounding prey; stimuli received through the chelae and pereiopods at any given moment can only allow the crab to select the best mussel to eat next.

It is clear from the results of this study that *C. maenas* does have the ability to assess the best areas in which to forage (Tables 4.1 and 4.2). However, this ability was only apparent when crabs were maintained in groups. Smallegange *et al.* (2006) postulated that crabs might increase their searching efficiency in the presence of other crabs, but found no evidence of such a response. However, it seems that the crabs observed in this study were indeed more efficient in their foraging behaviour when maintained in groups in the laboratory. Hines *et al.* (1997) observed a prey density threshold in *Macomona lilliana* above which there was a sharp increase in the feeding activity of eagle rays *Myliobatis tenuicaudatus*, which it was suggested were able to assess prey densities. Based on the results of the present study, Elner and Hughes (1978) probably underestimated the ability of *C. maenas* to assess its environment possibly because crabs forage less efficiently when they are not exposed to competition. Interference generally increases with predator density (Sutherland, 1983), thus foraging lower quality (with fewer or suboptimally sized prey items) resource patches becomes more favourable as predator density increases. For example, Ramsay *et al.* (1997) observed that numbers of *Pagurus bernhardus* foraging on large resource patches increased during 140 minutes, whilst on small patches numbers increased only during the first 20 minutes before remaining approximately level. The tendency for crabs to forage more effectively when exposed to competition will certainly not increase indefinitely, but does nevertheless allow crabs to maximise energy intake in the presence of competitors before it becomes more favourable to move to a lower quality resource patch.

Encounters between *C. maenas* individuals varied from accidental collisions which caused crabs to alter their behaviour, by ceasing to feed, through to grappling and fighting using the chelae. Crabs were clearly sensitive to the activities of other crabs, often evading approaching crabs before contact was made. Given that the experiment was conducted in complete darkness, chemo-reception and touch undoubtedly provide crabs with detailed information of their surroundings in terms of the position of competitors and the available food

resources. Most time involved in encounters was spent in the quadrant with small mussels only, where crabs were most frequently feeding (Table 4.1), and attempts to steal prey were often observed. However, there were few prolonged encounters as the attacked crab usually backed down and moved away from the attacker. Where prey is abundant, as in this experiment, engaging in prolonged encounters would not represent an evolutionarily stable strategy. Encounters between competitors are generally longer where resources are more limited (Maynard Smith, 1982). Those encounters which lasted several minutes in the present study tended to involve one aggressor and one defender attempting to evade the attack, which is in contrast to the prolonged and damaging contests *C. maenas* will engage in over potential mates (Sneddon *et al.*, 2003), or that *Uca burgersi* will undertake to gain access to a burrow (Jones, 1980).

Smallegange *et al.* (2006) observed that *C. maenas* spent more time interfering with larger or similarly sized conspecifics. In the present study there was a positive relationship between CW SD (used as a measure of the variability in crab size within groups) and the SD of the combined handling and feeding time. Increasing disparity in crab size within groups did not result in more mussels being eaten and crab size did not affect the time spent handling prey and feeding, or the time engaged in encounters. Therefore, rather than there being a greater propensity for crabs most dissimilar in size to engage in encounters, crabs appear to be more sensitive to interruptions from larger conspecifics. This causes some crabs to spend longer handling prey and feeding, while others spend less time involved in these activities. The greater number of crabs exhibiting no handling or feeding behaviour when in groups, as opposed to individually, supports this assertion.

Assuming small crabs are more sensitive to encounters with larger crabs, as shown by Smallegange *et al.* (2006), then encounters between crabs will have increased the time spent handling and feeding as the interruptions required crabs to re-familiarise themselves with the prey item after each interruption. The implications of this are that, where there are regular interruptions, these crabs must invest more energy in foraging and feeding, in addition to the energy demands of encounters. The positive relationship between CW SD and resting

time SD supports the assertion that the energy demands placed on certain crabs in groups are greater. The time spent resting by crabs in groups was not significantly related to crab size, thus again it is the variability in crab size that causes the increasing variability in activity. In the long term, interruptions to foraging and feeding, even non-aggressive encounters, must be detrimental to crabs. A crab must either rest more in order to balance increased energy demands, or consume more prey. By consuming more prey, however, crabs will be exposed to further interruptions and will suffer relative to competitors in terms of energy gains.

The present study has shown that foraging and feeding by *C. maenas* was not significantly impeded in the presence of other crabs, and that searching efficiency may actually have been improved where there was competition from other crabs. Were food to become limiting, more encounters would occur, requiring a greater investment of time and energy from crabs that would, at a critical point, make foraging in less profitable patches worthwhile. Tregenza (1994) highlighted that, at its simplest, the ideal free distribution model assumes a continuous supply of food that is consumed immediately, a situation which is probably rare in nature. The results of the present study further emphasise that the influence of predator density on food intake is complex. Where predators have the ability to compensate for interference, up to a certain threshold, then food intake rates will not reveal a decrease in resource value; however, there may be a more subtle decrease in resource value due to the increased energy demands created by interruptions to foraging and feeding.

The findings of this study also have potential practical applications in terms of mussel cultivation. Mussels at the sites LI and U1 consisted only of those mussels laid during August 2006, whilst sites L2 and U2 appeared to comprise mussels from three cohorts. Some of the seed mussels laid in the year-one cultivation area during August 2006 were also laid on to the existing mussels in the year-two cultivation area. There were also mussels remaining from the previous year's cultivation which were missed in the dredging process. Consequently, the mussel bed structure in the year-two cultivation area, although containing mussels available as prey to *C. maenas*, presents a much more complex array of prey in which crabs can forage. Foraging times within the year-two area should therefore

be substantially prolonged. If the behaviour observed in the current study occurs on a wider spatial scale then crabs in the wild should recognise the most profitable areas in which to forage and migrate to these areas when exposed to competition from conspecifics or other predators. Therefore, the distribution of crabs may be density dependent, and, perhaps counter-intuitively, crabs may be more likely to forage in less profitable areas when competition is reduced.

In summary, crabs seem to respond to interference by increasing searching efficiency. This has important implications for how populations will be distributed in the wild. Foraging and feeding in *C. maenas* is subtly affected by interactions between crabs of different sizes. Mean handling and feeding time is greater where there is a greater disparity in crab sizes within groups. This effect is not due to the increased time involved in encounters, and thus is indicative of increased sensitivity to encounters which results in more interruptions to handling and feeding. Encounters between *C. maenas* (excluding those over females) are unlikely to result in a major decrease in feeding activity but may increase the energy requirements of crabs due to interruptions to feeding. Mixing larger mussels with smaller mussels could help to reduce losses from crab predation on commercially cultivated mussel beds. It would be of interest to determine whether the behaviour observed in the present study occurs over large spatial scales, and how far *C. maenas* travels to achieve efficient foraging. A similar study conducted at higher predator densities and with more varied prey distributions would help to elucidate further the foraging ability of crabs or other predators, and how this might influence their distribution.

In the following chapter the macrofaunal communities associated with mussels in the Menai Strait are examined. The contribution of this fauna to the diet of *C. maenas* was determined, and mussel losses during the initial months of the cultivation process were ascertained in order to allow the relative impact of *C. maenas* to be considered.

CHAPTER 5

MUSSELS AND THEIR ASSOCIATED MACROFAUNA AS A FOOD SOURCE FOR *CARCINUS MAENAS*

ABSTRACT

Mussel beds harbour numerous species which, in addition to the mussels themselves, may be preyed upon by *Carcinus maenas*. Numerous studies have reported that mussel cultivation results in substantial changes in benthic communities. *C. maenas* can consume large quantities of mussels as well as molluscs, annelids and crustaceans. The aim of this study was to ascertain the effects of mussel cultivation on the benthic communities both within and beneath the mussel matrix, to determine which of the species within the community are consumed by *C. maenas* and to establish how mussel consumption rates might be affected. In addition, total mussel losses within the first few months of cultivation were determined so that the impact of *C. maenas* predation relative to losses from other sources could be assessed. More taxa (19) were found exclusively in the mussel layer than in the underlying sediments (4). There were no significant differences in the numbers of mussels consumed by *C. maenas* when these were presented alongside other macrofaunal species. The biomass of mussel associated macrofauna remaining in control microcosms after one week was greater than in microcosms with crabs, although not significantly so. There were also fewer cirratulid and tubificid worms in microcosms with crabs suggesting that shore crabs do consume these species. Losses of mussels within the first two months of the cultivation process were >50% but only some of these losses could be attributed to crab predation. Mussels easily form the greatest part of the diet of *C. maenas* and can effectively be considered the only prey species for adult crabs on the local commercial mussel beds.

5.1 INTRODUCTION

Carcinus maenas can consume substantial numbers of mussels over a wide range of sizes (see Chapter 3 and Murray *et al.*, in press). Predators of mussels, including *C. maenas* and *Hemigrapsus sanguineaus*, may reduce mussel density by >90% (Lohrer and Whitlatch, 2002). Cultivated mussel beds, in particular, provide a massive source of potential prey to *C. maenas*. Furthermore, mussel cultivation creates complex habitats, potentially increasing the amount of prey available to predators due to the macrofauna that inhabit the mussel matrix (Murray *et al.*, 2007); mussel-associated epifauna, in particular, constitute a major part of the diet of the portunid, *Necora puber* (Freire and Gonzalez-Gurriaran, 1995). Mussel beds form a habitat for organisms requiring a solid substratum, permanent water pools or organic matter (Dankers *et al.*, 2001). In addition, the number of species and number of individuals is greater in larger mussel patches, possibly due to the greater accumulation of organic matter which provides a food source for scavengers (Tsuchiya and Nishihira, 1985). Cultivated mussels are grown on-bottom in both the subtidal and intertidal zones and are laid in patches at an optimum density of between 300 and 600 mussels m^{-2} to achieve maximum growth rates and meat yield (Campbell and Newell, 1998).

Commercial mussel dredging can also have major environmental impacts; damage to *Zostera marina* beds has been detected up to seven years after disturbance (Neckles *et al.*, 2005). The effects of mussel dredging on epifaunal communities were observed by Dolmer (2002) four months after disturbance, with significantly fewer *Asterias rubens*, *Sagartia troglodytes*, *Macropodia rostrata* and *Crangon cragon* at the dredged sites. The communities remaining at dredged sites consisted of newly colonizing individuals, and organisms that had passed through the mussel dredge, as well as infauna below the effective depth of the dredge. A cutting edge is commonly added to the bottom of mussel dredges to increase the depth of dredging but in doing so the amount of sediment brought onboard the dredging vessel, and thus the amount of by-catch, is increased (pers. comm., Trevor Jones). Davies (2003) found by-catch to constitute between 5 and 13% by weight of the total catch on seed mussel dredgers in the Irish Sea. However, the

production of mussel beds is among the highest of all marine benthic ecosystems (Asmus, 1987), and the matrix of cultivated mussels may harbour as many species and individuals as that of the natural mussel beds (Murray *et al.*, 2007). Saier (2002) found that higher intertidal abundance of juvenile common periwinkles *Littorina littorea*, and *Carcinus maenas* together with higher numbers of subtidal species accounted for most of the difference between subtidal and intertidal mussel beds.

The epifauna associated with raft-grown mussels in the Ria de Arousa is the main source of food for demersal fishes, infauna constitutes only a small proportion of the diet as a result of impoverishment by raft based mussel cultivation (Lopez-Jamar *et al.*, 1984). Similarly, Dittmann (1990) recorded higher species richness on mussel beds (25) compared to adjoining sandflats (20) due to the beneficial effect of mussels on the epifauna, but found infauna to be more abundant on sandflats. *M. edulis* is generally the preferred prey of *C. maenas* (Brousseau and Baglivo, 2005). Mascaro and Seed (2000a) found that *M. edulis* was selected in preference to the oysters *Crassostrea gigas* and *Ostrea edulis*, while Tyrrell *et al.* (2006) showed that *Semibalanus balanoides*, *Spirorbis* sp. and *M. edulis* were consumed in similar numbers, although a greater mussel biomass was consumed. As an omnivorous scavenger, many other species may also be eaten by *C. maenas*. Elner (1981) recorded molluscs, crustaceans and algae in the diet of *C. maenas*, and this species is also known to eat echinoderms and annelids (Crothers, 1968). Given the huge ratio of mussel biomass to macrofaunal biomass in mussel assemblages, it is likely that mussels will form the major part of the diet of *C. maenas*.

The aim of the current study was to determine the fauna associated with commercial mussel beds. It was hypothesised that the mussel-associated fauna is not a significant source of food to *C. maenas* on commercial mussel beds due to the huge ratio of mussel biomass to biomass of the associated fauna. The total losses of mussel during the early stages of the cultivation process were also assessed in order to determine the impact of *C. maenas* relative to other predators (see Chapter 7).

5.2 MATERIALS AND METHODS

Biodiversity

To assess the biodiversity within and beneath mussel assemblages, samples were collected from intertidal mussel beds at Gallows Point (see Figure 2.1, site I2, Chapter 2) during November 2004. Mussels were either attached in clumps to the sediment surface or on and among *Fucus spiralis*. Four distinct habitats in the intertidal mussel beds were selected, these were: the mussel matrix (M), mussel and algal assemblages (MA), the sediment layer beneath mussels (SM) and the sediment layer in patches not covered by mussels (NM). Two habitat types were also identified adjacent to the mussel beds, these were: algae attached to a rocky substratum (A), and sediment not covered by mussels and outside of the mussel beds (SC). Cores were collected from two stations in each habitat. Stations were located in the lower and upper mid-shore region. From each station, five cores of 10 cm diameter were collected using a plastic corer. Mussel layer and algal assemblage samples were collected by pressing the corer to the bottom of the mussel assemblage or onto the underlying rock. All core contents were then removed and sealed in plastic bags. Sub-mussel layer samples were collected by pressing the corer into the sediment to a depth of 5 cm before removing all the contents. Additional cores were collected from two extra stations at the lower and upper reaches of the mussel beds for mussel and sub-mussel layer habitats to allow differences in communities with shore height to be included in the analyses.

Samples were returned to the laboratory within one hour, sieved through a 1 mm mesh and all species identified to the lowest taxon possible. Shell-free dry weight was measured by removing shells manually and drying samples at 60°C until constant weight was reached (~48 hours). If samples could not be processed immediately they were frozen prior to sorting and identification. Multivariate data analysis was conducted using PERMANOVA (Anderson, 2005) and PRIMER. Data were not transformed prior to analysis.

Benthic microcosms

A section of mussels and sediment (170 mm L x 130 mm W x 50 mm H) with a volume of 1.1 litres was extracted from the mussel beds in the mid-intertidal zone of mussel beds at Gallows Point using a box quadrat; samples were then carefully transferred to solid (but open on the top side) plastic boxes of the above dimensions. A further 15 sections were collected in the same manner over two sampling trips one week apart, as the experiment was conducted using a randomized block design. Each of the 16 cores contained within the plastic containers was encased in plastic mesh of 4 mm mesh size, enclosed on all sides. To each of eight cages ~172 mm L x 132 mm W x 100 mm H), three male *Carcinus maenas* (35 – 40 mm carapace width, CW) were added. The remaining eight cages were used as experimental controls and were positioned alternately with the treatment cages in an aerated running seawater tank kept at 12 ± 1 °C in darkness. These microcosms were left undisturbed for 7 days before analysis. Mussels and sediment from all mussel bed sections were washed through a 1 mm sieve in seawater. Taxa were identified and counted in each sample. Total ash-free dry weight (AFDW) biomass was measured after combusting samples at 500°C for 4 hours. The length of mussels was measured to 0.1 mm using dial callipers.

Effects of other prey species on mussel selection

To determine whether the presence of other prey species affected the number of mussels consumed by *C. maenas*, crabs were presented with six different combinations of prey. Experiments were conducted in individual aerated plastic aquaria measuring 35 x 20 cm. Sediment (~200 g) which had been sifted by hand to remove any fauna was added to each tank. Species commonly found on the mussel beds and that are known to be consumed by *C. maenas* were selected.The treatments were: small mussels (20 – 30 mm in length; SM); large mussels (35 – 45 mm; LM); small mussels with cirratulid worms (SW); large mussels with cirratulid worms (LW); small mussels with *Littorina littorea* and amphipods (SA); large mussels with *L. littorea* and amphipods (LA). Ten cirratulid worms were added to each of the 'worm' treatments. To the 'littorinid' treatment, eight *L. littorea* were added together with 10 g wet weight of *Fucus spiralis* and ten

amphipods. A total of 36 crabs were used, with six crabs of 50 to 70 mm CW used in each treatment. The experiment was conducted using a randomized block design over six days. Crabs were allowed to feed for 24 hours before the number of mussels eaten was recorded.

Predator exclosure experiments

To establish whether significant losses of mussels occurred on the cultivated beds in the Menai Strait cages were deployed in a pilot study run for one week during August 2006, shortly after seed mussels were laid and *C. maenas* was abundant (see Chapter 2) and when predation levels were therefore expected to be at their highest. Three cages measuring 35 cm in diameter and 20 cm in height were constructed from 4 mm plastic mesh and pinned firmly, via wooden frames, into the sediment of the seed mussel beds (see Figure 2.1, site I1). A further three cages identical in construction but without any top panel were also deployed, and an additional three plots were marked but not encaged. The partial enclosures were designed to restrict lateral water flow in a manner similar to the cages in order to assess whether increased mussel mortality resulted from the presence of the cages themselves. Caged, partially enclosed and open plots were distributed randomly and were each separated by a distance of ~50 m. All plots were located on the lower reaches of the mussel beds to ensure maximum immersion time. After one week the mussels contained within five cores of 10 cm diameter were removed from each plot. All the mussels from each core were counted and 30 were selected at random and measured along the antero-posterior axis to 0.1 mm.

Following the pilot study, a further exclosure experiment was conducted in the same area ensuring the original plots were not re-used. Four partial enclosures, together with four full cages, and four open plots were used. Cages were left in place for nine weeks. Any fouling organisms (predominantly macroalgae) were removed from the cages every three weeks. After nine weeks, all mussels were removed from within the plots and measured as in the pilot study. The total weight of entire samples was determined and the number of mussels estimated from the relationship between length and wet weight (Appendix B1).

Multivariate analysis was conducted using PERMANOVA (Anderson, 2005) and PRIMER; data were not transformed. Bray-Curtis similarity (PERMANOVA) and dissimilarity (PRIMER) measures were used to generate (dis-)similarity matrices. All univariate analyses were conducted using Minitab.

5.3 RESULTS

Biodiversity

The mean number of species found per core was greatest in the mussel layer, particularly where mussels and algae were present (Table 5.1). The sub-mussel layer contained an average of three species per core. Control sites for both the mussel layer and sub-mussel layer contained fewer than half the number of individuals present within or beneath the mussel assemblages. Mussels were present at a higher density where no algae were present and their mean length was also greater (Table 5.1). A total of nineteen species were found only within the mussel-layer, while eight species were present both within and beneath the mussel layer (Table 5.2). Four species were found in the sub-mussel layer only. The most abundant species in the mussel assemblage was the brittlestar *Amphipholis squamata* (Figure 5.1). The amphipods *Melita palmata* and *Ampithoe rubricata* were more abundant within the sites with mussels only, as were *Carcinus maenas* and *Semibalanus balanoides*. *Littorina* spp. (predominantly *L. littorea*) were found at the algae-only sites at over twice the abundance found at the algae and mussel sites, and at over 32-times the abundance found on the mussel-only sites. *C. maenas* was present in all three habitats but was most abundant at the mussel-only sites. Tubificid worms were most abundant at sites with both mussels and algae. PERMANOVA revealed a significant difference between mussel layer and sub-mussel layer samples at Gallows Point ($F_{1,48} = 5.057$, $p<0.001$). There was also a significant difference between sites within mussel layer or sub-mussel layer habitats ($F_{4,48} = 2.791$, $p=0.008$) and between stations within sites ($F_{6,48} = 1.799$, $p = 0.002$). However, no significant differences were detected, using *a posteriori* pair-wise comparisons, between any pair of sites ($t <1.994$, $p>0.3129$).

Table 5.1. Mean number (±1 S.E.) of individuals, species, and mean dry weight biomass (g) of mussel-associated fauna per core in each habitat together with mean length (±1 S.D.) and mean number (±1 S.D.) of mussels per core (10 cm diameter). Cores from the sub-mussel layer were taken to a depth of 5 cm while cores from the mussel layer were taken to the bottom of the mussel assemblage.

	Sub-mussel layer (5 cm deep)						*Mussel layer*					
	Mussels		No mussels		Control		Mussels and algae		Mussels		Control	
Individuals	11.5	±1.7	12.5	±7.8	5.6	±4.8	12.7	±1.8	12.3	±2.1	3.2	±1
Species	2.8	±0.3	3	±0.2	2.2	±0.4	5.8	±0.4	4.4	±0.3	2	±0.5
Biomass	0.1	±0.01	0.1	±0.01	0.52	±0.3	1.3	±0.7	0.13	±0.02	0.39	±0.08
Length (mm)	34.6	±4.9	-	-	-	-	34.6	±4.9	37	±5	-	-
No. mussels	27	±7	-	-	-	-	21	±7	27	±7	-	-

Table 5.2. Taxa found within cultivated mussel beds in the Menai Strait in either the mussel layer (ML), sub-mussel layer (SM) or both (B).

	Family	Taxa (Authority)	Location
Crustacea			
	Ampithoidae	*Ampithoe rubricata* (Montagu)	B
	Atylidae	*Atylus swammerdami* (Milne Edwards)	ML
	Balanidae	*Semibalanus balanoides* (Linnaeus)	ML
	Gammaridae	*Chaetogammarus marinus* (Leach)	ML
	Hyalidae	*Hyale nilssoni* (Rathke)	ML
	Janiridae	*Jaera nordmanni* (Rathke)	ML
	Melitidae	*Melita palmata* (Montagu)	ML
	Pinnotheridae	*Pinnotheres pisum* (Linnaeus)	ML
	Porcellanidae	*Pisidia longicornis* (Linnaeus)	ML
	Portunidae	*Carcinus maenas* (Linnaeus)	ML
Echinodermata			
	Amphiuridae	*Amphipholis squamata* (Chiaje)	B
	Asteriidae	*Asterias rubens* (Linnaeus)	ML
	Ophiolepidae	*Ophiura affinis* (Lutken)	ML
Mollusca			
	Littorinidae	*Littorina littorea* (Linnaeus)	ML
	Littorinidae	*Littorina obtusata* (Linnaeus)	ML
	Muricidae	*Nucella lapillus* (Linnaeus)	ML
	Mytilidae	*Mytilus edulis* (Linnaeus)	ML
Nemertea			
	Eurylepidae	-	ML
	Tetrastemmatidae	*Tetrastemma helvolum* (Burger)	ML
Oligochaeta			
	Tubificidae		B
Polychaeta			
	Ampharetidae	*Ampharete acutifrons* (Grube)	ML
	Aphroditidae	*Lepidonotus clava* (Montagu)	SM
	Capitellidae	*Capitella capitata* (Fabricius)	B
	Cirratulidae		B
	Eunicidae	*Marphyssa belli* (Audouin & Milne Edwards)	SM
	Nephtyidae	*Nephtys* sp.(Cuvier)	B
	Opheliidae	-	SM
	Orbiniidae	*Scoloplos armiger* (Muller)	SM
	Phyllodocidae	*Phyllodoce* sp.	ML
	Spionidae	*Polydora ciliate* (Johnston)	B
	Syllidae (Sub-family: Syllinae)	-	B

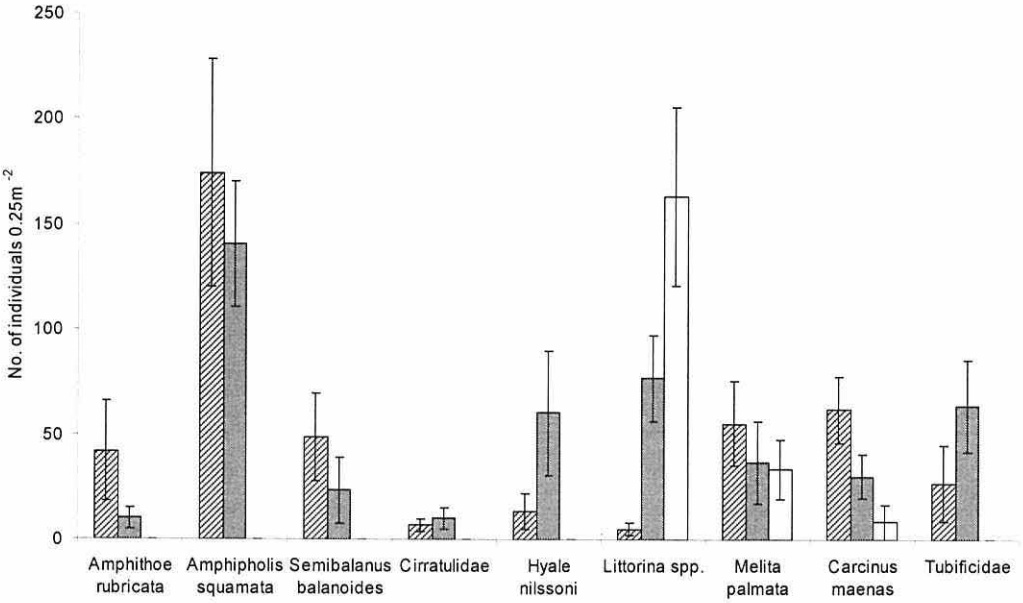


Figure 5.1. Mean abundance (±1 S.E.) 0.25 m^{-2} of species with the greatest difference in abundance between habitats (Bars: Hatched, mussels; Solid, mussels and algae; Open, algae).

Infaunal species inhabiting the sub-mussel layer showed similar levels of variance between cores within each habitat (Figure 5.2) and community composition was very similar between habitats. Variance of community composition data was greatest among the mussel-only cores (Figure 5.3). The algal assemblages were the most distinct of the three assemblages studied although there was substantial variation in community composition within the mussel assemblages.

Benthic microcosms

The mean length (±1 S.D.) of mussels presented to crabs in the microcosms was 44 ±4 mm, and all the mussels presented were above the size these crabs were able to open; consequently, the only source of prey available to these crabs was the macrofauna in the sediment and associated with the mussels. The mean number of individuals remaining in the microcosms after one week was greater in the control microcosms than in those with crabs (Table 5.3) and AFDW was also substantially greater. Twelve taxa were present in the microcosms; there were fewer tubificids and cirratulids in the control microcosms than in the treatment microcosms (Figure 5.4). Amphipod numbers were not included in analyses as individuals may not have been contained within the micrcosms. However, there were no significant differences between controls and treatments for the number of individuals (ANOVA, $F_{1,14} = 1.88$, $p = 0.192$) , the number of species (ANOVA, $F_{1,14} = 0.76$, $p = 0.398$), or AFDW (ANOVA, $F_{1,14} = 0.56$, $p = 0.465$). In all cases data were normally distributed (Anderson-Darling <0.654, $p>0.071$) and variances were equal (F-test <0.27, $p>0.109$). The lack of any significant differences was largely due to the high variance among both the controls and treatments (Figure 5.5). PERMANOVA revealed no significant differences between the macrofaunal community composition in control and treatment microcosms after one week ($F_{1,14} = 0.583$, $p = 0.604$).

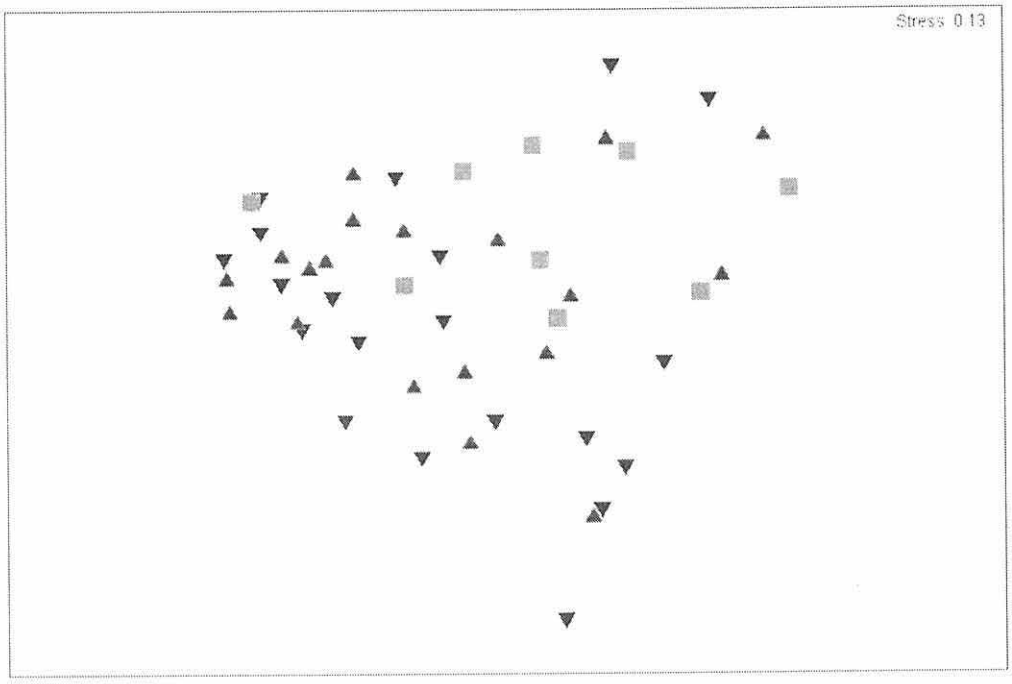


Figure 5.2. 2-D multi-dimensional scaling plot based on species abundance in the sub-mussel layer at Gallows Point beneath mussels (▲), in patches of sediment without mussel coverage but within the mussel bed (▼), and in sediment outside the mussel bed (■).

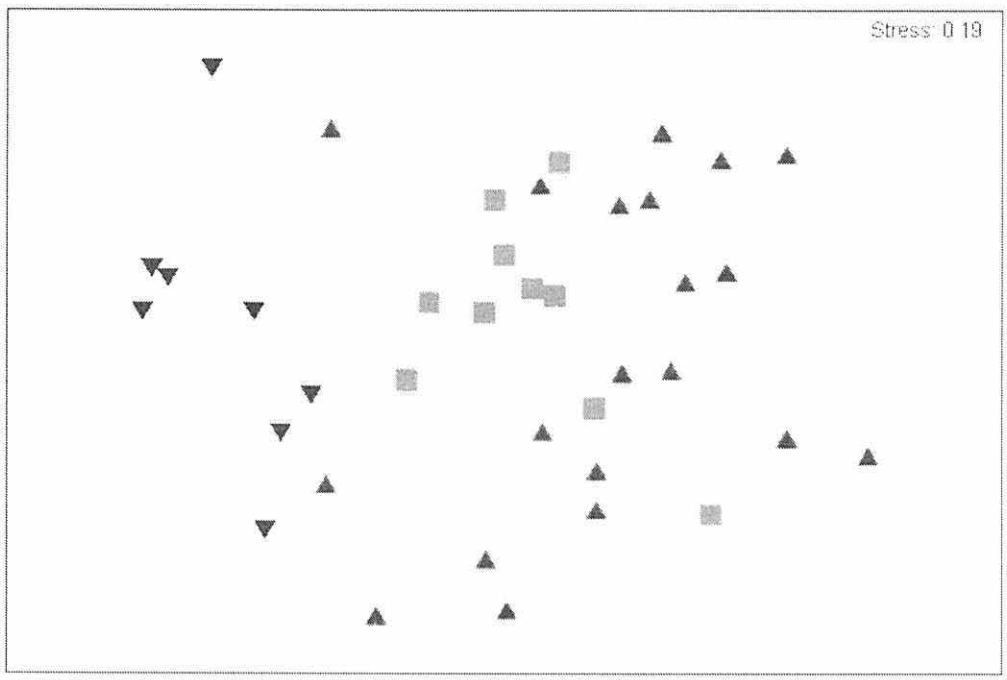


Figure 5.3. 2-D multi-dimensional scaling plot based on species abundance in the mussel or macroalgal layer at Gallows Point within mussel assemblages (▲), in macroalgal assemblages (▼), and in assemblages with both mussels and algae (■).

Table 5.3. Mean number (±1 S.E.) of individuals and species and ash-free dry weight (AFDW) biomass of the associated fauna after one week in control (n = 8) and treatments (n = 8) containing three *Carcinus maenas* of 30 – 40 mm CW.

	No. Ind.	No. Species	AFDW (g)
Control	21 ±3.9	4.4 ±0.8	0.26 ±0.13
Treatment	14 ±3.3	4.3 ±2.0	0.07 ±0.05

Effects of other prey species on mussel selection

The mean number of mussels consumed by *C. maenas* (50 – 70 mm carapace width) differed significantly when crabs were presented with large (35 – 45 mm shell length) mussels rather than small (20 – 30 mm shell length) mussels (ANOVA, $F_{1,30} = 39.2$, $p<0.001$; Figure 5.6); however, there was no significant effect on the number of mussels consumed (either large or small) due to the presence of other macrofauna ($F_{4,30} = 1.71$, $p = 0.174$). Tukey's pair-wise comparisons revealed that no pair of treatments differed significantly within the small or large mussel treatments. Data approximated normal distribution and variances were equal (Levene's test = 1.80, $p = 0.142$).

Predator exclosure experiments

At the end of the pilot exclosure experiment, the modal length class of mussels was 22.5 – 25 mm in caged, partially enclosed and open plots (Figure 5.7). The mean lengths of mussels in cages, partial enclosures and open plots were 23.1 ±3.7 mm, 24.0 ±3.6 mm and 22.6 ± 3.9 mm, respectively. There were more mussels of 15 – 22.5 mm length within the cages than in either the partially enclosed or open plots. A fully nested ANOVA revealed that the mean length of mussels differed significantly between treatments ($F_{2,1783} = 11.02$, $p<0.001$), between plots within treatments ($F_{6,1783} = 15.14$, $p<0.001$), and between cores within plots ($F_{37,1783} = 1.71$, $p = 0.005$) at the end of the experiment. No overall significant difference in the length frequency distributions of mussels from within full cages, partial enclosures or open plots were detected (PERMANOVA,

$F_{2,36} = 1.467$, $p = 0.215$). However, *a posteriori* pair-wise comparisons revealed significant differences between mussel length frequency distributions in partial cages and open plots ($t = 2.054$, $p = 0.045$). There were significant differences between the length frequency distributions of mussels in one pair of full cages ($t = 1.984$, $p = 0.03$) and between two pairs of open plots ($t = 2.336$, $p = 0.012$; and $t = 1.790$, $t = 0.049$). There were no significant differences between any pair of partial cages. There was a similar level of variation in length distributions of mussels in cores from caged, partially enclosed and open plots (Figure 5.8) and no clear differences are apparent between the different treatments.

The mean length of mussels immediately before cages were deployed for the second exclosure experiment was 22.7 ±0.3 mm; the mean length of mussels present in the plots after two months was 25.06 ±3.4 mm (open), 24.7 ±4.0 mm (caged), and 25.1 ±4.1 mm (partial). The number of mussels in control plots was around half that found in caged and partially enclosed plots. After the two months during which cages were deployed, the number of mussels was lower in every length class from 12.5 mm to 30 mm in the control plots than the caged plots (Figure 5.9). In the partially caged plots there were fewer mussels in the 22.5 – 25 mm length class than in either the next smaller or larger length class. The modal length was around 25 mm in the mussels from open plots, compared to around 23 mm in caged plots.

There was no significant difference in the mean length of mussels between treatments (ANOVA, $F_{2,520} = 0.56$, $p = 0.571$); however, there were significant differences in the mean lengths between plots ($F_{9,520} = 4.22$, $p<0.001$). No significant difference in the number of mussels per plot was detected (ANOVA, $F_{2,9} = 2.33$, $p = 0.153$), though the mean number of mussels was 525 ±112 per plot in the open plots, compared to 1,079 ±608 in the caged plots, and 1,000 ±284 in the partially caged plots. No significant differences were detected between length frequency distributions (PERMANOVA, $F_{2,9} = 1.463$, $p = 0.209$), most probably due to the high variance in the open and partially caged plots.

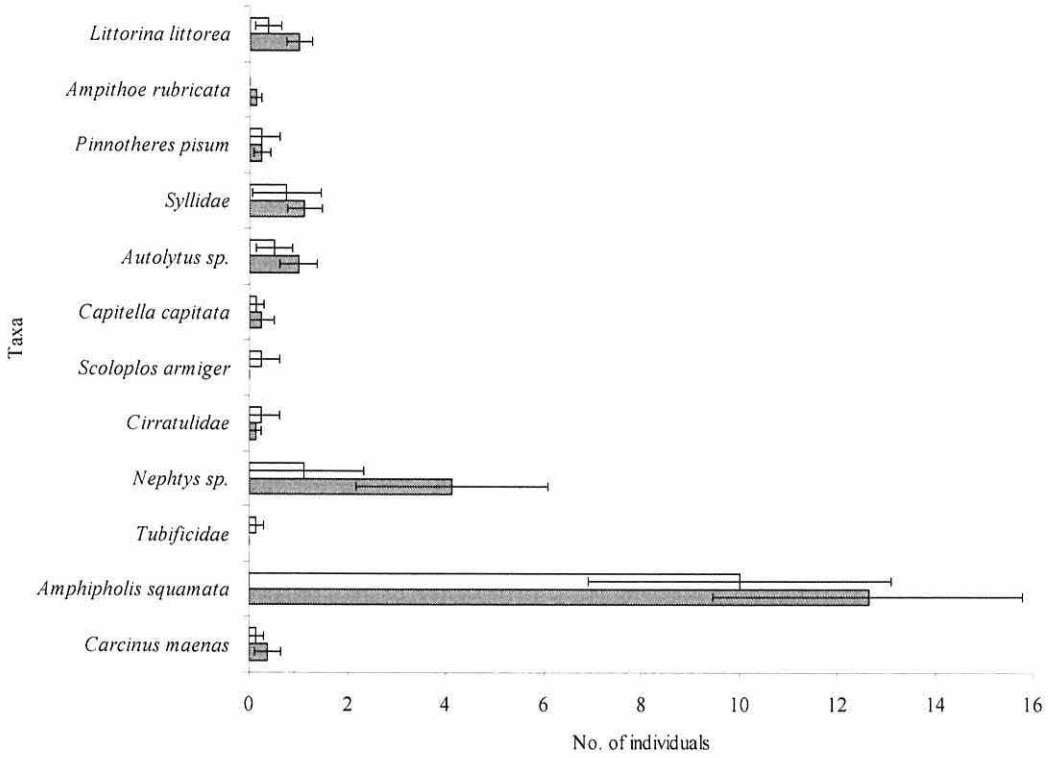


Figure 5.4. Mean number of individuals (±1 S.E.) in control microcosms (shaded bars, n = 8) and microcosms containing 3 *Carcinus maenas* of 30 – 40 mm CW (open bars, n = 8) after one week.

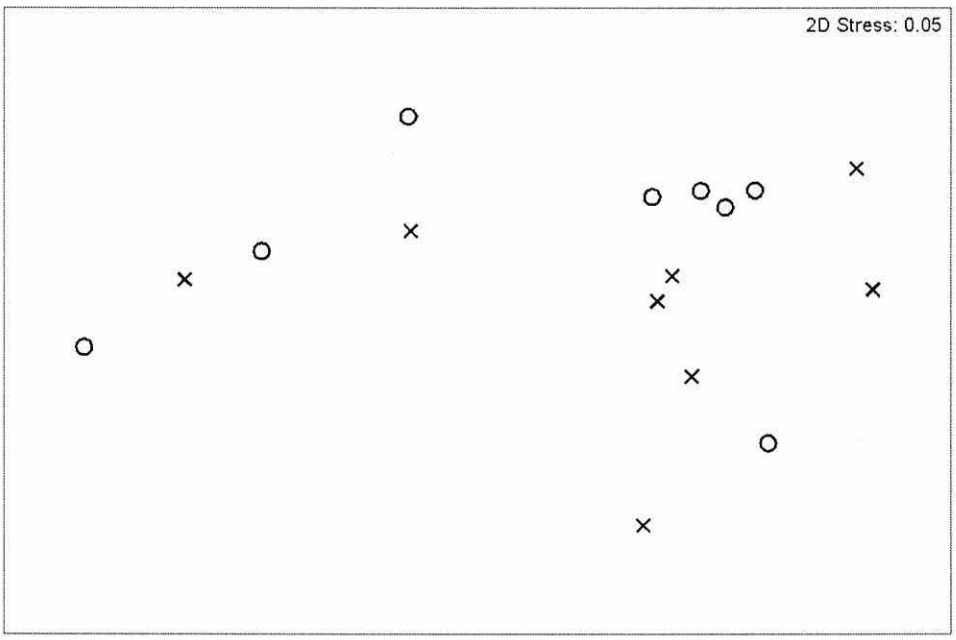


Figure 5.5. 2-D multi-dimensional scaling plot of number of individuals of mussel-associated macrofauna in control (×) and treatment (○) microcosms after one week. Treatment microcosms contained three *Carcinus maenas* of 30 – 40 mm CW.

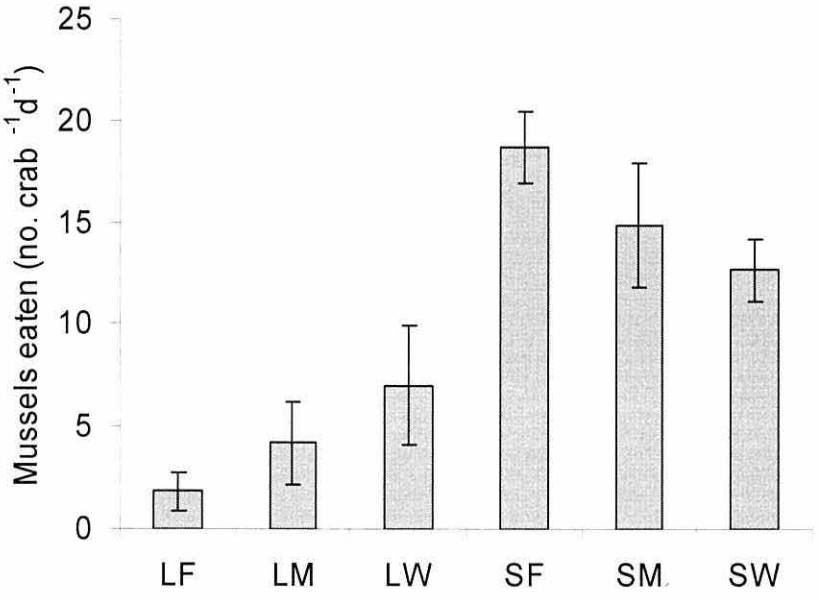


Figure 5.6. Mean number of mussels (±1 S.E.; n = 6) consumed by individual *Carcinus maenas*. Values are standardized to a crab carapace width of 65 mm (see Figure 3.4, Chapter 3). Crabs were presented with either small mussels (S; 20 – 30 mm length) or large mussels (L; 35 – 45 mm). Mussels were presented without any other fauna (M), with cirratulid worms (W), or with *Littorina littorea* and *Fucus spiralis* (F).

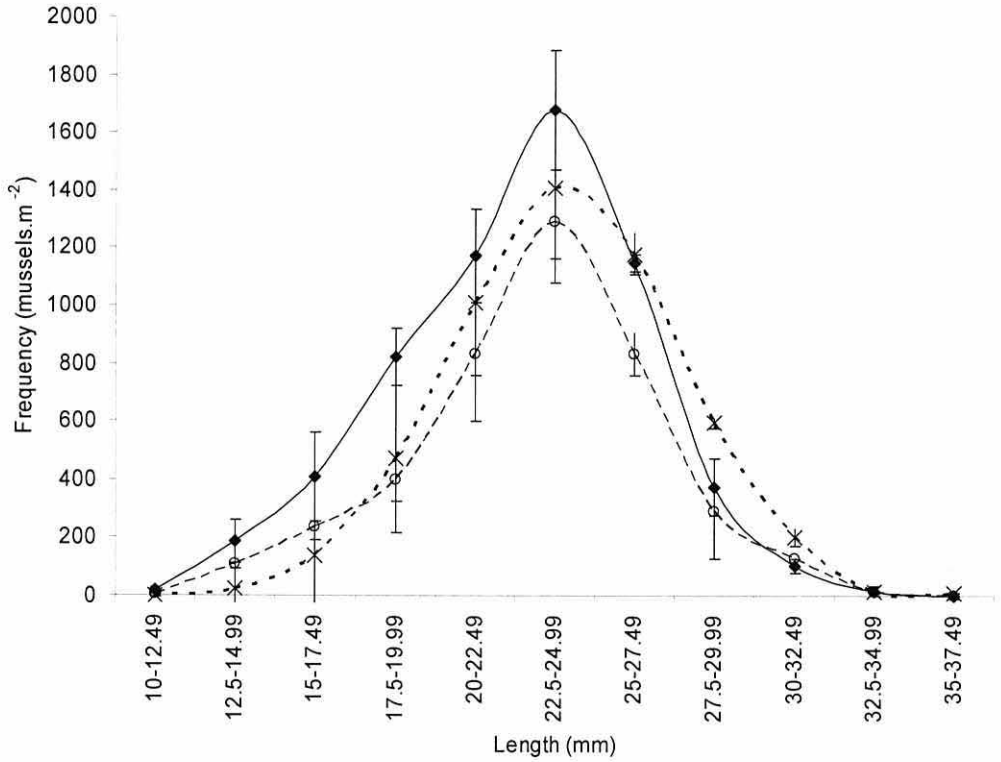


Figure 5.7. Mean number of mussels m^{-2} extrapolated from measurements of 150 mussels from each of nine sites, three each with either full cages (solid line/diamond), partial enclosures (dashed line/open circle) or no cages (dotted line/cross). Error bars show ±1 S.E.

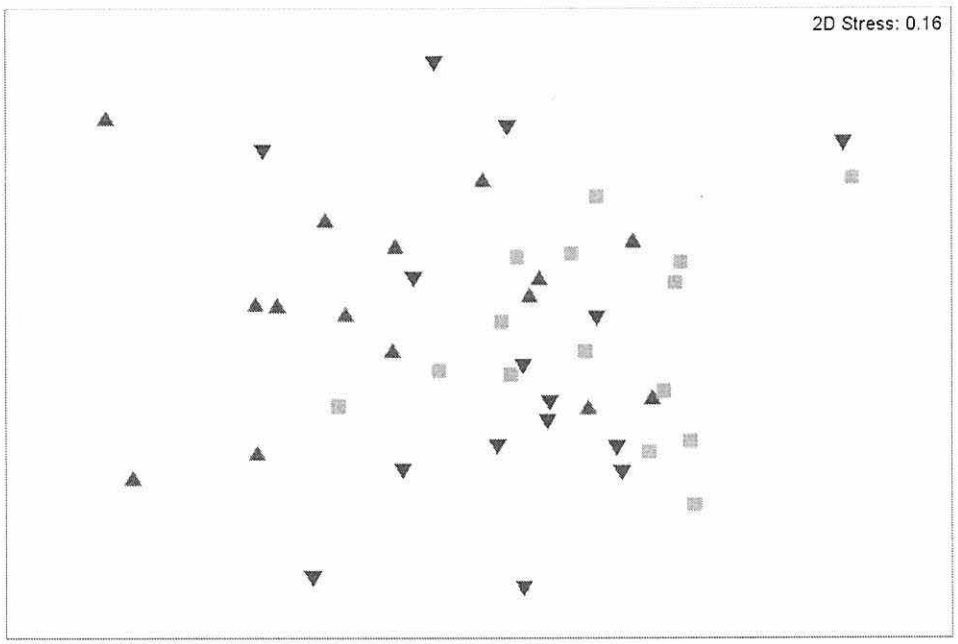


Figure 5.8. 2-D multi-dimensional scaling plot based on the frequency of mussels in each of 12 length classes in plots with full cages (▼), partial enclosures (■) or without cages (▲).

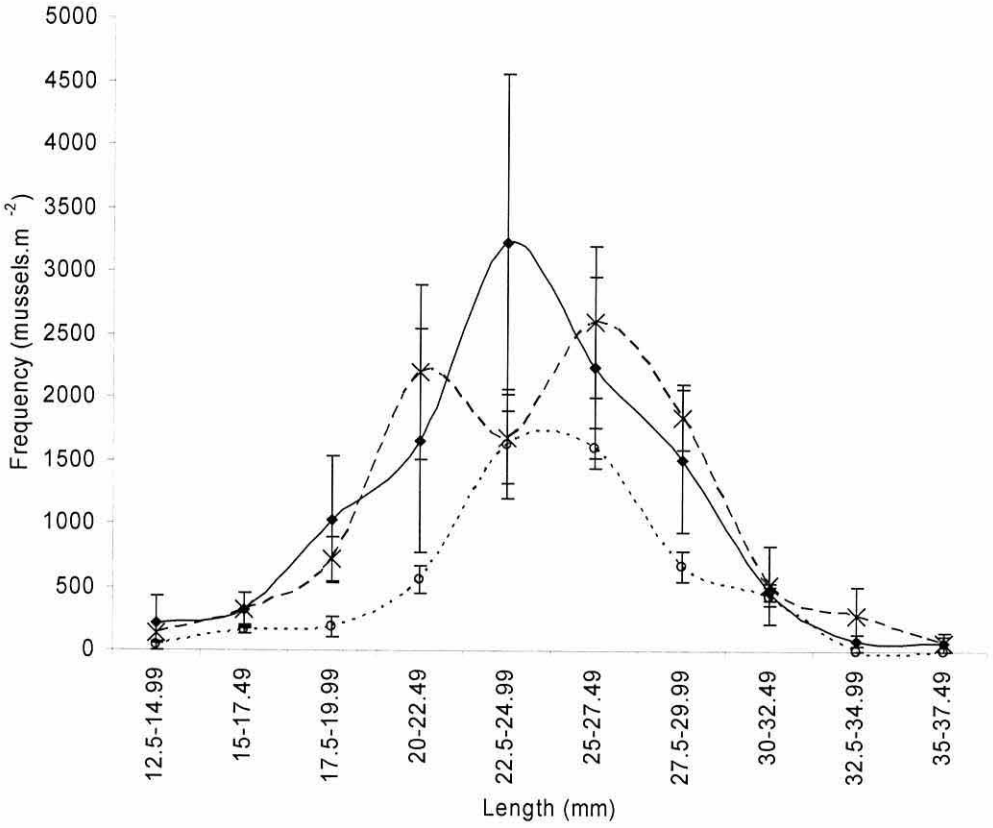


Figure 5.9. Mean number of mussels m^{-2} extrapolated from measurements of 150 mussels from each of 12 plots, four each with full cages (solid line/◆), partial enclosures (dashed line/×) or no cages (dotted line/○). Error bars show ±1 S.E.

Overall these results show that there were substantial losses of mussels during the two months after seed were laid. These losses may be due to both crab and bird predation. The mussel structure is richer in macrofaunal species than the underlying sediments or areas without mussels. However, there was no effect of mussel-associated macrofauna on the number of mussels consumed by crabs, suggesting that mussels are the main component of the shore crab diet on commercial mussel beds.

5.4 DISCUSSION

Studies of mussel beds have often considered the mussel layer and the underlying fauna as a single entity (Saier, 2002; Beadman *et al.*, 2004). In the current study the macrofaunal communities inhabiting the mussel matrix were significantly different from the macrofaunal communities inhabiting the sediment beneath the mussels. The presence of macroalgae along with mussels allowed additional species to inhabit the mussel layer, in particular *Littorina littorea*. The mussel layer can support many species, even when mussels are cultivated off-bottom (Murray *et al.*, 2007; Chapter 6) as sediment and pseudofaeces are trapped between the mussels providing a substratum which infaunal species can inhabit. The algal assemblages on the rocky substratum sampled adjacent to the mussel beds in the Menai Strait lacked a complex substratum and harboured fewer species and individuals than the mussel beds.

A total of 31 taxa were recorded on the cultivated mussel beds in the Menai Strait (Table 5.2), 19 of which were found only in the mussel layer. Four taxa were restricted to the sub-mussel layer of sediment, and eight taxa were present in both layers. Asmus (1987) recorded 41 species on mussel beds in the Wadden Sea, with the greatest biomass in the form of tubificid oligochaetes, *C. maenas*, barnacles, *L. littorea* and *Nereis diversicolor*. Beadman *et al.* (2004) recorded 35 taxa on mussel beds in the Menai Strait over two years. Barnacles, amphipods and tubificid oligochaetes were common on intertidal mussel beds in Maine (Chapter 6) and were also abundant on the mussel beds in the Menai Strait (Figure 5.1). Unlike the mussel beds in Maine, however, *C. maenas* was present

in all the habitats studied in the Menai Strait. Beadman *et al.* (2004) also found that numbers of *Melita palmata*, *C. maenas* and tubificids were greater on mussel beds than at sites without mussels. Natural mussel beds in Maine harboured only 15 species. Thus, cultivated mussel assemblages are clearly not impoverished of species compared to naturally occurring mussel beds. Tubificid oligochaetes, *C. maenas*, barnacles, amphipod crustaceans and various polychaete species appear to be ubiquitous to intertidal mussel beds worldwide. However, negative effects of mussel cultivation on macrofauna have been widely reported (Dittmann, 1990; Dolmer *et al.*, 2001; Smith and Shackley, 2004) either when comparing biodiversity before and after mussel cultivation, or by comparison between mussel and non-mussel sites.

Although *M. edulis* may form a major part of the diet of *C. maenas*, the prey consumed by *C. maenas* is varied and includes molluscs, polychaetes and crustaceans. Raffaelli *et al.* (1989), for example, found that of 326 *C. maenas* individuals, 23.6 % had *M. edulis* in their guts, compared to 30.1 % containing barnacles, and 6.4 % containing *Nereis* sp. Grosholz and Ruiz (1995) reported that *C. maenas* caused significant decreases in the abundance of bivalves (*Transennella confusa* and *T. tantilla*) and crustaceans (*Cumella vulgaris* and *Corophium* sp.) but not polychaetes. Ropes (1968) and Elner (1981) found bivalves to be predominant in the diet of *C. maenas*, and Brousseau and Baglivo (2005) found that mussels were always the preferred prey of the Asian shore crab *Hemigrapsus sanguineus*. Raffaelli *et al.* (1989) showed that *C. maenas* had a significant effect on the abundance of the mud snail *Hydrobia ulvae* but not polychaetes, oligochaetes, nematodes or crustaceans in enclosure experiments. The findings of this study, similarly, show that *C. maenas* selects mussels in preference to other prey, with no significant levels of predation on other species found within the commercial mussel beds. The presence of other prey species did not alter predation rates of crabs feeding on *M. edulis*, even when mussels were above the optimal size. Despite the absence of any significant difference in the numbers of individuals of any one species consumed, it is likely that *C. maenas* consumes at least small quantities of mussel-associated fauna. However, mussels comprise over 95 % of the biomass on both natural mussel beds (Asmus, 1987) and in cultivated mussel assemblages (Chapter 6). Consequently, regardless of

the quantity of macrofauna associated with mussel beds, predation by *C. maenas* is likely to occur principally on the mussels themselves.

The average depth of dredging has been reported as being <5 cm (Holmer *et al.*, 2003; de Groot, 1984) and Palanques *et al.* (2001) found that the effects of otter trawling on sediment particle size were restricted to the upper 2-3 cm of sediment. In addition, Riemann and Hoffmann (1991) showed that suspended particulate sediment concentrations were increased by up to seven times due to mussel dredging, indicating that a substantial quantity of sediment is disturbed during the dredging process. It is in the upper sediment layer that macrofauna will be most accessible to *C. maenas*, which was observed to readily burrow in the surface sediments of the microcosms used in the current study. The community composition recorded in the microcosms after one week was not significantly different between controls and treatments; however, this is due partly to high variance among the microcosms (Figure 5.5). There were fewer cirratulids, tubificids, and littorinids in the microcosms with crabs, and the macrofaunal biomass was almost fours times lower. It is highly probable that *C. maenas* does consume mussel-associated macrofauna, particularly when mussels are too large to be opened. However, it seems unlikely that mussel-associated macrofauna constitutes a major component of the diet of *C. maenas* on commercial mussel beds where mussels are of an accessible size.

Clear losses of mussels occurred on the intertidal beds during the two months that cages were deployed. There were fewer mussels from 12.5 mm to 30 mm in length in the open plots compare to caged and partially enclosed plots, excluding the 22.5 – 25 mm length class in which there was an apparent loss of mussels from the partially enclosed plots. The presence of cages does not appear to have induced any mortality in the mussels, as the density of mussels was similar in the full and partial enclosures at 1,079 ±608 and 1,000 ±284 mussels per plot, respectively. The reason for the decline in mussel numbers in the 22.5 to 25 mm length class in the partial enclosures is unclear. It may simply reflect an artefact of caging, whereby some mussels have grown at the expense of others, as may be evidenced by the peaks in the 20 – 22.5 mm and 25 – 27.5 mm length classes in the partial enclosures but not among those in the full cages. Alternatively,

predation by particular size classes of predator attracted to the partial enclosures could be responsible; crabs of around 60 mm CW would most frequently select mussels of 22.5 – 25 mm length (see Chapter 3). Furthermore, the greatest loss of mussels in open plots occurred in the 22.5 – 25 mm length class.

The mean abundance of *C. maenas* recorded at the caging site from July to September 2006 was 1.1 ±0.3 m^{-2} (see Chapter 2). The mean loss of mussels was 5758 mussels m^{-2} during the 62 days that the cages were deployed, or 93 mussels m^{-2} d^{-1} (230,000 $ha^{-1}d^{-1}$), which would thus amount to 85 mussels $crab^{-1}$ d^{-1} if *C. maenas* predation was the sole cause of mussel losses. However, this value is over twice as much as even the largest crabs ate in the laboratory. The mussel losses predicted based on laboratory feeding trials and abundance as recorded on video surveys during August and September across the intertidal mussel cultivation sites in the Menai Strait were 56,129 mussels $ha^{-1}d^{-1}$. Summer crab abundance at the caging sites was 1.9 times greater than the overall intertidal abundance, which would amount to 104,400 mussels $ha^{-1}d^{-1}$. Crab abundance and resultant mussel losses are discussed further in Chapters 7.

There are three possible reasons why losses were so high from the open plots. Firstly, other predators may have been consuming mussels from the intertidal beds. The predators most likely to have consumed mussels are *C. maenas*, oystercatchers *Haematopus ostralegus* (Ens and Goss-Custard, 1984; Goss-Custard and Durell, 1987) and herring gulls *Larus argentatus* (Vermeer, 1982; Sibly and MacCleery, 1983; Craeymeersch *et al.*, 1986). The common starfish *Asterias rubens* is abundant on mussel beds in the subtidal zone of the Menai Strait but has rarely been observed on intertidal mussel beds (pers. obs.). Adult oystercatchers eat mussels from a mean length of 23 mm up to 43 mm, eating smaller mussels at a rapid rate during spring and summer (Goss-Custard and Durell, 1987). Craeymeersch *et al.* (1986) estimated that nearly 70% of the number of mussels eaten by oystercatchers in the Eastern Scheldt, Nertherlands, were between 30 and 50 mm in length, but mussels from 10 to 60 mm were also consumed. Juvenile *H. ostralegus* will also readily eat smaller (~20 mm length) mussels (Goss-Custard *et al.*, 1987). Caldow *et al.* (2003) recorded *H. ostralegus* numbers of 5.6, 6.4 and 9.5 birds ha^{-1} from 1999/2000 – 2001/2002 on mussel

beds in the Menai Strait, and Goss-Custard and Durell (1987) recorded a mean mussel intake rate of around 1.2 per oystercatcher per 5 minutes in the Exe Estuary. Assuming a mean oystercatcher abundance of 7.2 birds ha^{-1}, and that birds fed continuously during the 2.5 hours that the caging sites were exposed during daylight hours, oystercatchers would only have consumed 259 mussels $ha^{-1}d^{-1}$. Herring gulls *Larus argentatus* may be an important predator, as the species is commonly observed on the mussel beds in the Menai Strait. Other studies have shown that birds are a major source of mussel losses in the intertidal zone; mean annual biomass consumption by birds in the Wadden Sea is estimated at 15-30 %, and is highest on intertidal mussel beds (Nehls *et al.*, 1997; Scheiffarth and Nehls, 1997). In addition, Meire *et al.* (1994) estimated that *H. ostralegus* and *L. argentatus* are responsible for 58 % and 15 % of total biomass consumption, respectively, in the Oosterschelde.

The second possible source of mussel losses is that mussels may have been carried away by the particularly strong tidal currents in the Menai Strait. Recently laid, mussels would have been especially vulnerable to detachment. Thirdly, estimates of crab abundance may be too low; however, smaller and inactive crabs (i.e. those not feeding on the mussels) were those least likely to be detected. Moreover, the estimates of *C. maenas* abundance presented in Chapter 2 are two orders of magnitude greater than previous estimates (Gascoigne, 2005). Overall mussel losses in the Menai Strait during the cultivation process are estimated at 92-4 %, and 75 % of crab predation occurs in the first two months of cultivation (Murray *et al.*, in press; Chapter 7). Thus, whilst the losses of 49% as reported for the open plots are certainly feasible, they are unlikely to be due wholly to *C. maenas* predation and a combination of the above factors is likely to have contributed to these losses.

The proportions of different size classes of prey presented to crabs in laboratory experiments has a greater influence on the size of prey selected than any preference for a particular size class up to a certain critical size limit beyond which size preference becomes the dominant factor in determining prey selection (see Chapter 3; and Burch and Seed, 2000). Consequently, predation may not result in obvious changes in the skewness or kurtosis of prey size frequency

distributions unless the predator is highly size selective. Therefore, it may be necessary to conduct enclosure or exclosure experiments over longer periods in order to detect predation effects, as was the case in the present study (cf. Figure 5.7 and Figure 5.9). Prey density is perhaps a more reliable indicator of predation than the effects of mortality on size frequency distributions, although sessile populations are subject to considerable patchiness (Svane and Ompi, 1993; Seed, 1996; Gascoigne, 2005) and thus high variability in density.

It is clear from this and many other studies that mussel beds harbour a diverse range of macrofauna and cultivated mussel beds may be at least as rich in fauna as naturally occurring mussel populations. Certain taxa are often found in commercial mussel beds; these include tubificid oligochaetes, *L. littorea*, and various polychaete and amphipod species depending on location. All of these organisms are potential prey species for *C. maenas*, which is also a common member of the mussel bed community. However, given that mussels are the preferred prey of the shore crab and that mussel biomass is so much greater than that of the associated macrofauna, mussels are mostly predominant in the diet of *C. maenas*. The results of the current study suggest that *C. maenas* consumes cirratulid polychaetes, tubificid oligochaetes and *L. littorea*. In spite of this, the presence of these organisms does not have a significant effect on the number of mussels consumed. Consequently, predictions on the impact of crab predation on cultivated mussel beds can effectively assume that mussels are the predominant prey species for adult crabs. However, mussel-associated fauna will help to sustain juvenile crabs and provide a food source for those crabs unable to open mussels due to chelal damage or when mussels are too large to be opened; for example, this may become more important immediately before seed mussels are imported each year. Substantial losses of mussels (>50%) occur during the first few months of cultivation, some of these losses are undoubtedly caused by *C. maenas* predation but losses also occur due to avian predation and probably detachment. Even where predation levels are high, experiments using size-cohort analysis to detect mortality should be conducted over several weeks to be effective due to the effects of prey size frequency on prey selection.

The following chapter examines the macrofaunal communities associated with natural and cultivated mussels in Maine, USA. Both mussel and associated macrofaunal biomass are also considered for natural and cultivated mussel beds, and rope-grown mussels, allowing the mussel beds in the Menai Strait to be considered in a wider geographical context.

CHAPTER 6

THE STRUCTURE AND BIODIVERSITY OF NATURAL AND CULTIVATED MUSSEL ASSEMBLAGES

ABSTRACT

Mussel cultivation involves collecting mussel spat or transplanting mussels, that typically harbour complex assemblages of associated species, into more favourable growing sites. The aim of the current study was to make a quantitative comparison of the macrofaunal communities associated with natural intertidal seed beds and with cultivated mussels grown either on the seabed or on ropes, particularly in relation to the structure of the mussel populations, and to determine the biomass of mussels and associated fauna the different mussel assemblages. The biomass of macrofauna associated with mussels was significantly greater within rope-grown mussel assemblages than on mussel beds. There were significantly fewer individuals among bottom-cultured mussels than either rope-grown or naturally occurring intertidal mussels. Positive correlations between mussel biomass and associated faunal biomass existed at certain sites but not others. There was a shift from oligochaete to polychaete dominated worm communities caused by mussel cultivation. Sessile polychaetes were most abundant among rope-grown mussels while highly motile polychaetes were most abundant at the bottom-culture sites. Fewer amphipod crustaceans were found under both types of cultivation. To maintain or increase the abundance and biomass of mussel-associated fauna relative to the intertidal beds, suspended culture is preferable to on-bottom cultivation. Positive mussel and associated-macrofaunal biomass correlations are species dependent; cultivation sites could thus be selected to minimise detrimental impacts of mussel farming or even increase the biomass of mussel-associated macrofauna. Tubificids and amphipods are common to both cultivated and natural intertidal mussel beds and the tidal height of mussel beds is likely to be a more important determinant of community composition than whether mussel assemblages are natural or cultivated.

6.1 INTRODUCTION

The potential ecological impacts of mussel cultivation as described in numerous studies (Romero *et al.*, 1982; Stenton-Dozey *et al.*, 1999; Beadman *et al.*, 2004; Smith and Shackley, 2004) are widespread and on a substantial scale; however, these studies have focused primarily on the differences in biodiversity between mussel and non-mussel covered areas. To date, no study has been made of the macrofauna associated with mussels in the habitats created by different methods of mussel cultivation relative to natural populations. It is essential that distinct methods of cultivation of the same organism are quantitatively compared if aquaculture sites are to be located and cultivation techniques selected to minimise ecological impacts.

Marine bivalve molluscs are cultivated using either off-bottom (ropes suspended in the water-column from rafts) or on-bottom techniques (Hickman, 1992; Garen, *et al.* 2004). Mussel seed beds, where spatfall has occurred, are often exploited by dredging the young seed mussels and moving them to areas where growing conditions are more favourable. Spat-collectors are also used to catch larvae from the water column which then grow into seed mussels that can be used to stock ropes. The structure formed by mussels, both natural and cultivated, provides an important habitat for numerous species (Tsuchiya and Nishihira, 1985; Seed and Suchanek, 1992; Seed, 1996; Saier, 2002; Smith and Shackley, 2004) including both infaunal and epifaunal organisms (Dittmann, 1990).

Romero *et al.* (1982) found significantly more of the crabs *Macropipus depurator* and *M. puber* throughout the year in areas of raft mussel cultivation compared to non-raft areas in northwest Spain, and suggested that they were feeding on epifauna associated with the mussels. Khalaman (2001) recorded 71 species associated with raft-grown mussels in the White Sea, Russia; the most abundant species after *Mytilus edulis* were the bivalve *Hiatella arctica*, the hydroid *Obelia longissima*, the polychaetes *Nereis pelagica* and *Harmothoe imbricata*, and the ascidians *Molgula* sp. and *Styela rustica*. Beadman *et al.* (2004) recorded 35 taxa in newly created intertidal mussel beds that resulted in more shore crabs *Carcinus maenas*, amphipods *Melita palmata*, and oligochaete worms *Tubificoides*

benedeni, but fewer of the polychaetes *Pygospio elegans* and *Notomastus latericeus*, and the eumalacostracan *Corophium* spp.

Dolmer (2002) suggested that the positive relationship between mussel density and the number of associated species may be due to the complex substratum provided by mussels which increase the area available for larval settlement. Furthermore, Thiel and Dernedde (1994) demonstrated that mussel clumps provide refuge for juvenile *C. maenas*, and that the fauna associated with mussel beds provide an important food source for both juvenile and adult crabs (Scherer and Reise, 1981) allowing crabs to thrive. However, Beadman *et al.* (2004) found that increasing the density of mussels decreased infaunal diversity and abundance. Likewise, Stenton-Dozey *et al.* (1999) found consistently fewer suspension feeders beneath rafts compared to control sites, but found both positive and negative effects on carnivores, deposit feeders and herbivores depending on site, although no quantification of fauna on the rafts was made. Dolmer (2002) observed reduced numbers of poriferans, echinoderms, anthozoans, molluscs, crustaceans and ascidians in dredged areas four months after dredging for mussels.

Predators can have major impacts on mussel beds (Davies *et al.*, 1980; Saier, 2001). Birds are usually prevented from consuming raft-grown mussels, and the fauna associated with them, by predator nets. Bottom-grown mussels may also be protected to some degree by fences or by using mops to remove crabs and starfish but are generally more vulnerable to predators (Hickman, 1992). Therefore, the use of off-bottom culture techniques alleviates the effect of predators, and yields of *M. edulis* per area are greatest from rope culture and lowest from bottom culture in terms of shell length total weight (Garen *et al.*, 2004).

Whenever ropes or beds are stocked with intertidal seed mussels much of the associated fauna is also transported, including species which prey on the mussels (Davies, 2003). By transplanting mussels or collecting spat to stock cultivation sites new habitats are created that will support some of the animals present on seed beds together with newly colonizing species. In terms of biodiversity, the

change in community composition between exploited seed beds and newly created habitats may be as important as the effects observed at the cultivation sites alone.

No studies to date have made comparisons between the community composition of natural and cultivated mussel assemblages. It was hypothesised that by increasing mussel biomass through cultivation, the species richness, abundance and biomass of the associated macrofauna would also increase. The aims of the current study were thus to determine the differences in mussel population structure between natural seed beds, rope-grown mussels and cultivated subtidal beds, and to quantitatively compare the macrofaunal communities associated with mussels in each type of habitat within a commercial mussel fishery in northeast Maine, United States. In doing so, the changes in mussel-associated macrofauna resulting from the creation of new habitats using mussels collected from wild populations could be identified. In addition, the potential impacts of *C. maenas* on commercial mussel beds outside the Menai Strait and on natural mussel beds, based on the findings presented in this thesis, could be considered.

6.2 MATERIALS AND METHODS

Sample collection

Six study sites were selected in Maine (Figure 6.1) in three types of habitat formed by the blue mussel. Sites R1 and R2 (Rafts) were located respectively in Belfast Bay, near Northport, and St. Helena Island near Stonington. Sites S1 and S2 (Subtidal) respectively were located at Old Point and Hadley's Point, both near Bar Harbor. Sites I1 and I2 (Intertidal) were located at Stave Island Bar and Burying Island. Whilst sites R1, R2, S1 and S2 consisted of cultivated mussels, sites I1 and I2 were wild populations typical of those from which seed mussels are collected for stocking on-bottom cultivation sites. The study was conducted using a nested design (see Underwood, 1997) with three factors, namely: habitat (raft, subtidal, and intertidal), site (S1, S2, R1, R2, I1, and I2) and station. At each site, five replicate cores (10 cm diameter) were collected (separated by ~2 m) from each of three stations (separated by ~40 m), giving a total of 90 cores. The number

of suitable sites was restricted by the mussel cultivation practices in the area, with intertidal sites furthest east and raft sites most westerly. Sites within treatments (Subtidal, Raft, Intertidal) were spaced as far apart as possible so that the variance within treatments would reflect any environmental gradients. Although S1 and S2 were much closer than either I1 and I2 or R1 and R2 (Figure 6.1) these sites were still separated by ~2 km.

Mussel samples together with the associated macrofauna were collected during May 2006; on subtidal beds this was achieved by SCUBA diving. On both subtidal and intertidal substrata, a plastic corer (10 cm diameter) was pressed into the mussel assemblage to the bottom of the mussel layer and all enclosed mussels and associated fauna removed. On the rafts, mussels were grown on ropes approximately 12 m long suspended from the rafts. To sample raft-grown mussel assemblages ropes were lifted on board the harvesting vessel, and the mussel structure along 30 cm lengths of rope was carefully peeled away and laid flat. A sub-sample was then collected using a 10 cm corer in a similar manner to that used for the intertidal and subtidal beds. Five samples were collected at approximately equidistant intervals from the top to the bottom of each rope in order to obtain a representative range of the mussels and associated macrofauna. Sub-sample and total sample weights were then measured to the nearest 5 g. Using the weight of the core samples as a proportion of the total weight of mussels removed over each 30 cm length of rope the actual area of mussels per length of rope could be calculated. Three ropes were sampled at random from a single raft at each site, each rope being analogous to a station on the mussel beds. All cores were sealed in plastic bags, chilled (~4 °C) and returned to the laboratory.

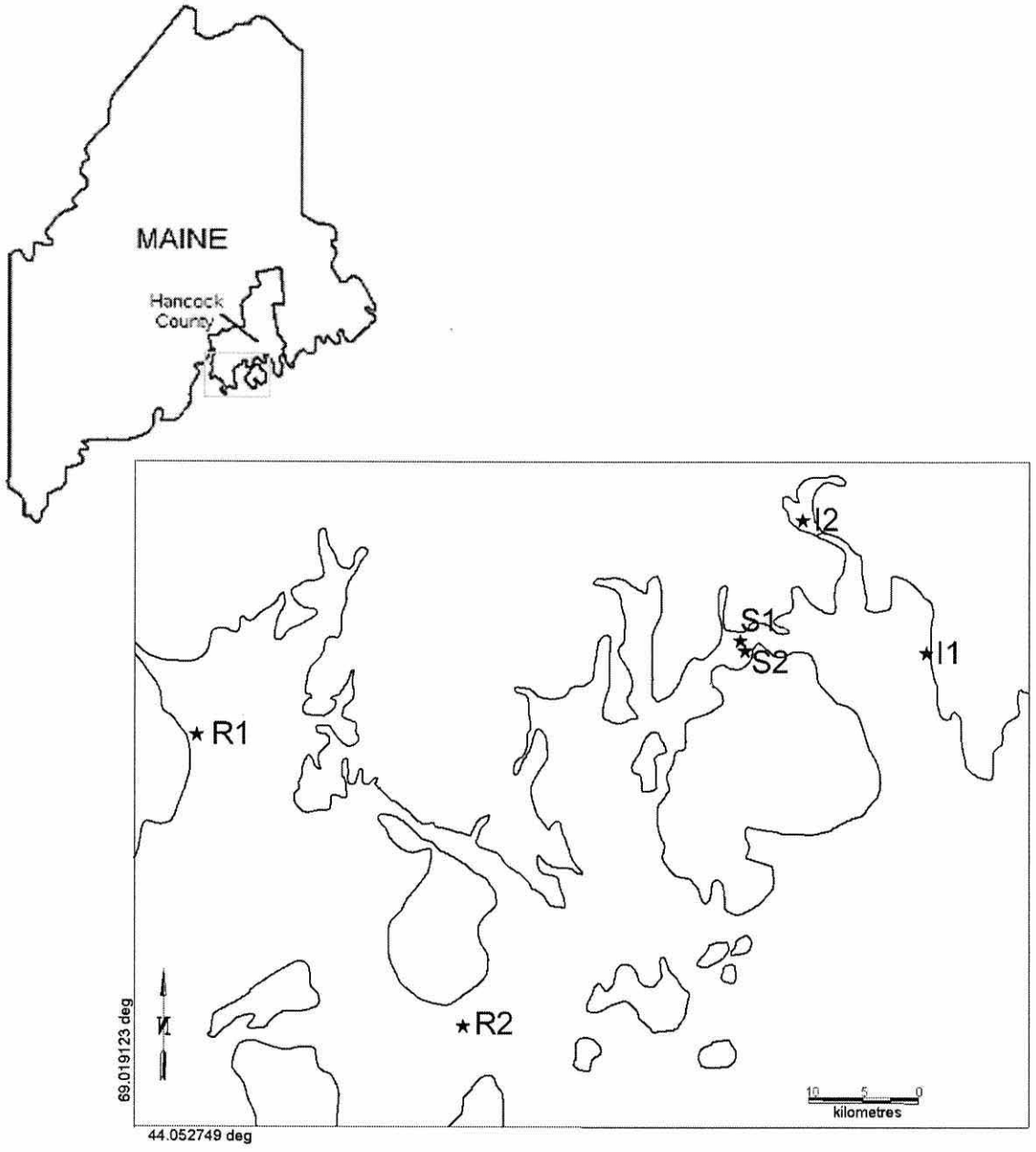


Figure 6.1. The six study sites in Maine: intertidal (I1 and I2); subtidal (S1 and S2); rafts (R1 and R2).

Sample processing

The maximum length (anteroposterior axis) of each mussel was measured (to 0.05 mm). Total dry weight (shell + flesh) was measured in a sub-sample of 50 mussels per station across the size range of mussels present; mussels were dried at 60 °C to constant weight measured to 0.001 g. Spatial density was recorded as the number of mussels per core. Average biomass in each size class of mussel was calculated from length versus total dry weight regressions; this value was then multiplied by the number of mussels in a given class to give the total biomass in each length class. After washing through a 1 mm mesh sieve with seawater all fauna were identified to the lowest taxa possible. If samples could not be processed immediately, they were frozen at –20 °C. Total dry weight biomass of the mussel-associated macrofauna was measured by drying samples at 60°C to constant weight (~24 hours).

All univariate ANOVA and Tukey's pair-wise comparisons were conducted using Minitab 14. Permutational multivariate ANOVA was conducted using PERMANOVA v1.6 (Anderson, 2005). Multi-dimensional scaling plots were produced from untransformed data using PRIMER.

6.3 RESULTS

Mussel populations

The density of mussels at the subtidal on-bottom sites (Table 6.1; Figure 6.2) was lower than on the rafts, in particular at R1 where the density of mussels was over three times that at either S1 or S2. Mussel density was greatest at sites I1 and I2. A 1.6 m length of mussel-covered rope was equivalent to an area of 0.25 m^2. Total mussel biomass was greatest on the rafts (Table 6.1; Figure 6.3), and similar at subtidal and intertidal sites. The sampling technique used on the rafts gave good repeatability, with an average sample weight of 696 ± 14 g (±1 S.E.). Sites S1 and S2 exhibited broadly unimodal length frequency distributions with similar mean

lengths (Table 6.1). The mean length of mussels was greater at R2 than R1 and mussels at R1 existed at over twice the density of those at R2 (Table 6.1). Mussels from R1 and R2 also showed polymodal distributions and mussels were present over a wider range of sizes than at the other sites (Figure 6.2). Mussels at the intertidal sites showed the smallest range of sizes. The greatest proportion of biomass occurred in the 30 – 50 mm length class at sites S1 and S2. Site R2 had a higher proportion of biomass in the larger length classes (>55 mm) than R1. Although most mussels at I1and I2 were less than 40 mm in length, larger mussels made a substantial contribution to total biomass (Figure 6.3).

Table 6.1. Means (± 1. S.E.) of: number of mussels, total dry weight mussel biomass (shell + flesh) and length of mussels at subtidal (S), raft (R) and intertidal (I) sites.

Site	Density (ind. $0.25m^{-2}$)	Total biomass (g $0.25m^{-2}$)	Length (mm)
S1	329.2 ± 41.2	1686.8 ± 126.4	48.2 ± 0.9
S2	297.6 ± 38.0	1496.8 ± 107.6	47.8 ± 0.8
R1	1493.6 ± 190.0	2322.8 ± 971.6	35.5 ± 0.6
R2	639.2 ± 79.2	2509.6 ± 737.2	53.8 ± 0.9
I1	1746.8 ± 221.6	2170.8 ± 354.4	25.9 ± 0.2
I2	1623.6 ± 205.6	1655.2 ± 129.6	23.4 ± 0.3

PERMANOVA revealed significant differences between the size frequency distributions of mussels at the habitat level ($F = 5.160$, $p = 0.004$) and site level ($F = 2.441$, $p = 0.012$). Pair-wise *a posteriori* comparisons showed significant differences between the size frequency distributions of mussels at the subtidal bottom habitat and the intertidal habitat ($t = 3.335$, $p = 0.033$) but no significant differences between any other pair of habitats. The size frequency distributions of mussels differed significantly between sites R1 and R2 ($t = 2.243$, $p = 0.033$). PERMANOVA also revealed that there were significant differences in the biomass distribution across length classes at the habitat level ($F = 3.990$, $p = 0.008$) and site level ($F = 2.071$, $p = 0.019$). Pair-wise *a posteriori* comparisons

revealed no significant differences in mussel biomass between any pair of habitats or sites. Thus, the range of mussel sizes and spread of biomass across size classes was greatest at the raft sites and lowest at the intertidal sites. Even a small proportion of larger mussels contributed greatly to total biomass.

Community composition

Thirty-two species from 29 genera were recorded across the six sites studied (Table 6.2). Twelve species of polychaete, eight species of mollusc and six species of crustacean were found. *Gammarus oceanicus*, *Jaera marina*, *Nucella lapillus* and tubificid oligochaetes were exclusive to the intertidal seed beds (I1 and I2). *Balanus crenatus*, *Arabella iricolor*, *Glycera dibranchiata* and *Nephtys* sp. were found only on the subtidal mussel beds (S1 and S2). The echinoderms *Asterias forbesi*, *Amphipholis squamata* and *Strongylocentrotus droebachiensis* were only present on the mussel rafts (R1 and R2) as were *Anomia aculeata*, *Clinocardium ciliata*, *Amphitrite* sp., *Marphysa sanguinea*, *Sabella* sp. and *Cliona* sp..

The most abundant species differed between sites both within and between habitats. Seven species contributed to the greatest difference in numbers of individuals between any pair of habitats (Figure 6.4). *Lepidonotus* spp. was common to both S1 and S2, and to R1. *Amphitrite* sp. was found only at R1 and R2. Tubificidae were found only at sites I1 and I2. At S1, 26% of all individuals were cirripedes but the most abundant class were the polychaetes (51%), which were also the most numerous class at S2 (84%) and R1 (94 %; Table 6.3). At R2, bivalves were most abundant (43%) although polychaetes still constituted 40% of the community. Crustaceans predominated at both intertidal sites; malacostracans were most abundant at I1 (44%) while cirripedes were most numerous at I2 (39%).

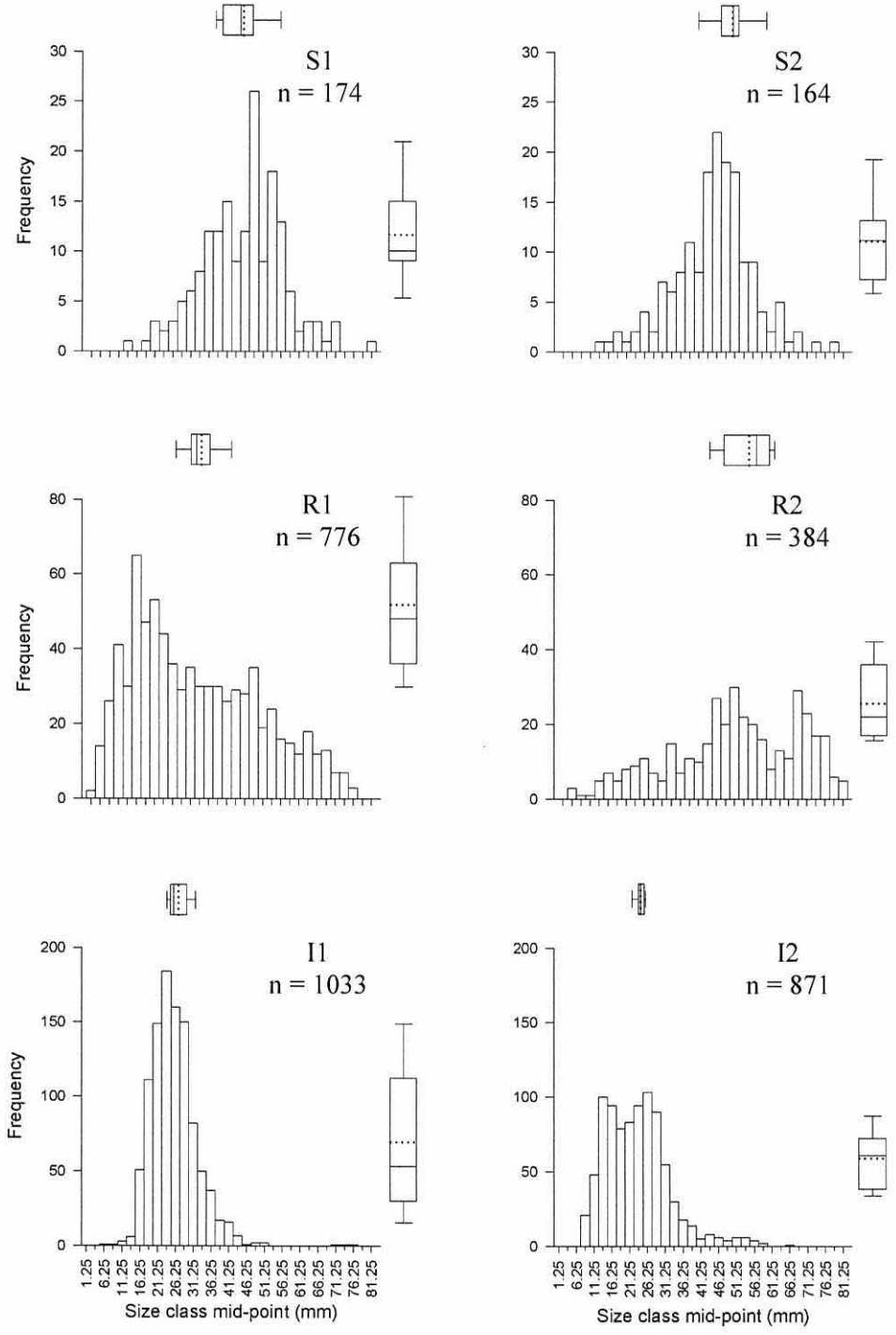


Figure 6.2. Length frequency distributions of *Mytilus edulis* at the subtidal (S1 and S2), raft (R1 and R2) and intertidal (I1 and I2) study sites in Maine. Box plots show median (solid line), mean (dotted line), 25th, 75th, 10th and 90th percentiles for mussel length (horizontal) and number of mussels per core (vertical).

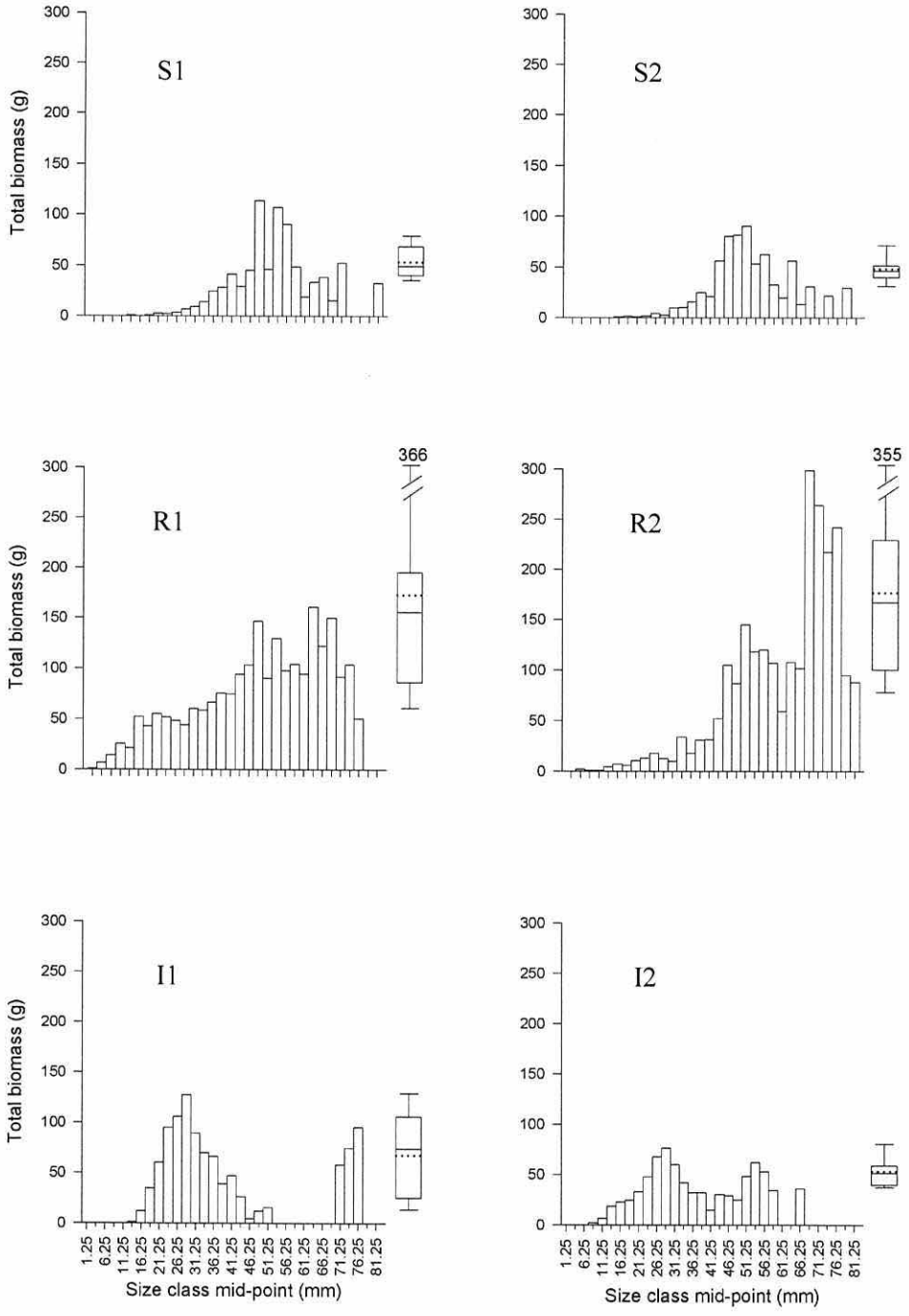


Figure 6.3. Total dry weight biomass (number of mussels x mean dry weight) of mussels in each length class at the subtidal (S1 and S2), raft (R1 and R2) and intertidal (I1 and I2) study sites in Maine. Box plots show median (solid), mean (dotted), 25th, 75th, 10th and 90th percentiles of total mussel biomass per core.

Table 6.2. Mean numbers of individuals 0.25 m^{-2} found at subtidal (S1 and S2), raft (R1 and R2) and intertidal (I1 and I2) sites.

Taxa (Authority)	Subtidal	Raft	Intertidal
Crustacea			
Semibalanus balanoides (Linnaeus)	3.2 ±2.3	22.2 ±13.9	74.9 ±24.4
Balanus crenatus (Bruguière)	4.2 ±2.5	-	-
Balanus eburneus (Gould)	12.7 ±4.9	19.0 ±9.6	2.1 ±2.1
Gammarus oceanicus	-	-	144.0 ±36.0
Jaera marina (Fabricius)	-	-	3.2 ±1.8
Leptocheirus pinguis (Stimpson)	1.1 ±1.1	-	1.1 ±1.1
Echinodermata			
Asterias forbesi (Desor)	-	8.4 ±4.4	-
Amphipholis squamata (Delle Chiaje)	3.2 ±1.8	-	-
Ophiopholis aculeata	-	2.1 ±1.5	-
Strongylocentrotus droebachiensis (Müller)	-	1.1 ±1.1	-
Mollusca			
Acmaea testudinalis (Müller)	10.5 ±3.5	-	5.3 ±3.4
Anomia aculeata (Müller)	-	24.3 ±12.4	-
Buccinum undatum (Linnaeus)	3.2 ±1.8	-	1.1 ±1.1
Clinocardium ciliatum (Fabricius)	-	1.1 ±1.1	-
Littorina littorea (Linnaeus)	4.2 ±2.0	-	23.2 ±6.2
Littorina saxatilis (Olivi)	4.2 ±2.5	-	-
Macoma calcarea (Gmelin)	1.1 ±1.1	97.0 ±28.5	1.1 ±1.1
Nucella lapillus (Linnaeus)	-	-	2.1 ±1.5
Oligochaeta			
Tubificidae	-	-	146.9 ±43.2
Polychaeta			
Amphitrite sp.	-	227.8 ±55.1	-
Arabella iricolor (Montagu)	1.1 ±1.1	-	-
Capitella capitata (Fabricius)	6.3 ±2.8	-	1.1 ±1.1
Cirratulidae (Ryckholdt)	3.2 ±2.3	7.4 ±6.6	-
Glycera dibranchiata	2.1 ±1.5	-	-
Lepidonotus squamatus (Linnaeus)	1.1 ±1.1	21.1 ±7.0	-
Lepidonotus variabilis (Webster)	48.5 ±8.1	24.3 ±9.2	2.1 ±1.5
Marphysa sanguinea (Montagu)	-	5.3 ±4.5	-
Nephtys sp. (Cuvier)	19.0 ±7.1	-	-
Nereis pelagica (Linnaeus)	5.3 ±3.4	48.5 ±12.6	11.3 ±3.9
Phyllodoce arenae (Webster)	3.2 ±1.8	14.8 ±8.8	1.1 ±1.1
Sabella sp. (Linnaeus)	-	1.1 ±1.1	-
Porifera			
Cliona sp.	-	2.1 ±2.2	-
Mean no. individuals	**4.3 ±0.5**	**16.8 ±2.5**	**12.7 ±2.2**
Mean no. taxa	**2.8 ±0.3**	**0.5 ±0.1**	**0.4 ±0.1**
Total no. individuals	**130**	**509**	**391**
Total no. taxa	**19**	**17**	**15**

Table 6.3. Mean number of individuals ± 1 S.E. 0.25 m^{-2} in all classes found, at each site.

Class	S1	S2	R1	R2	I1	I2	All
Malacostraca	-	2.1 ±2.1	-	-	175.1 ±68.2	109.7 ±23.9	47.8 ±13.8
Cirripedia	38.0 ±9.9	2.1 ±2.1	-	82.3 ±27.2	-	154.0 ±41.4	46.1 ±10.2
Asteroidea	-	-	16.9 ±8.1	-	-	-	2.8 ±1.5
Echinoidea	-	6.3 ±3.4	4.2 ±2.9	-	-	-	1.8 ±0.8
Gastropoda	31.6 ±6.9	12.7 ±5.2	-	2.1 ±2.1	23.2 ±6.5	54.9 ±12.5	20.7 ±3.4
Bivalvia	2.1 ±2.1	-	12.7 ±6.0	232.1 ±52.9	-	2.1 ±2.1	41.5 ±12.5
Polychaeta	73.8 ±15.9	105.5 ±19.5	497.9 ±102.4	221.5 ±50.4	16.9 ±5.2	12.7 ±6.0	154.7 ±26.0
Oligochaeta	-	-	-	-	2.1 ±2.1	4.2 ±2.9	1.1 ±0.6
Calcarea	-	-	-	4.2 ±4.2	-	-	0.7 ±0.7

PERMANOVA revealed significant differences in the community composition at the genus level between habitats ($F = 3.335$, $p = 0.003$), sites ($F = 2.910$, $p<0.001$) and stations ($F = 2.824$, $p<0.001$). Pair-wise *a posteriori* comparisons revealed significant differences between sites S1 and S2 ($t = 2.235$, $p = 0.025$), and R1 and R2 ($t = 2.161$, $p = 0.027$). There were significant differences between stations at S1, R1, R2, I1 and I2. At I2 each station differed significantly from each other station ($p<0.001$). No significant differences were found between any pair of habitats.

PERMANOVA showed significant differences between the classes of organisms found in the three habitats ($F = 3.439$, $p = 0.009$), sites ($F = 2.266$, $p = 0.010$) and stations ($F = 2.897$, $p<0.001$). Pair-wise *a posteriori* comparisons showed no significant differences between any pair of habitats. However, there were significant differences between S1 and S2. There were also significant differences between all stations at I1 and at I2.

Two-dimensional multi-dimensional scaling plots showed clear grouping of subtidal, intertidal and raft sites at genus (Figure 6.5a) and class (Figure 6.5b) level. The three habitats showed approximately equal similarity to one another but habitats were more similar at the class level. However, cores from sites S1 and, in particular, I2 showed least similarity, verifying the significant within-site differences found with PERMANOVA.

A fully-nested univariate ANOVA was conducted on number of individuals, number of species and dry weight macrofaunal biomass data. Variances were not significantly different for number of species data (Levene's test = 1.08, $p = 0.386$), square root transformed number of individuals data (Levene's test = 1.31, $p = 0.212$) and square root transformed dry weight biomass data (Levene's test = 0.143, $p = 0.150$). There were no significant differences in the number of species found between habitats or between stations. However, there were significant differences between sites ($F = 4.27$, $p = 0.029$). The number of individuals differed significantly between habitats ($F = 161.32$, $p<0.001$) and stations ($F = 3.660$, $p<0.001$) and showed very little variation at the site scale ($F = 0.040$, $p = 0.988$). Biomass differed significantly between habitats ($F = 0.033$, $p = 0.033$) but not between sites and stations.

The mean number of species recorded was greatest at R2 and lowest at S2 (Figure 6.6a) although more species were recorded at S1 and S2 (Table 6.2). Tukey's pair-wise comparisons revealed that there was only a within-site significant difference in the number of species at the intertidal sites but there was no significant difference in the number of species between habitat types. There were, however, significant differences in the total number of individuals between the subtidal on-bottom habitat and both the raft and intertidal habitats (Figure 6.6b), being highest on the rafts and lowest in the subtidal. Macrofaunal dry weight biomass was significantly higher at the raft sites than at either the intertidal or subtidal sites (Figure 6.6c). Given the univariate ANOVA results, the station scale variability found with PERMANOVA can be attributed to differing numbers of individuals, while the site scale variability is best attributed to the numbers of species.

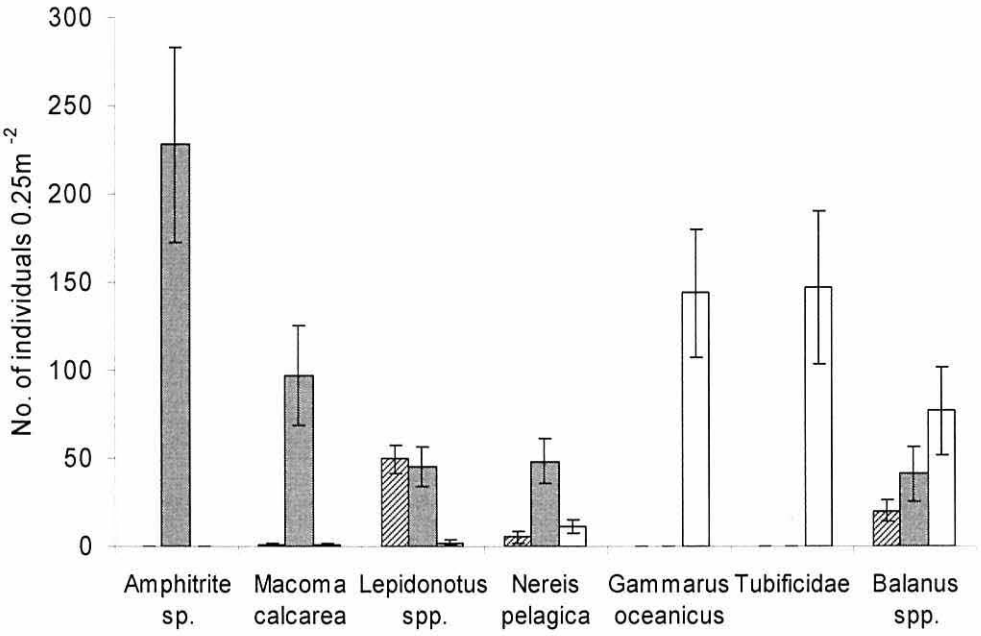


Figure 6.4. Mean abundance (± 1. S.E.) 0.25 m^{-2} of species with the greatest difference in abundance between habitats (Bars: Hatched, subtidal; Solid, rafts; Open, intertidal).

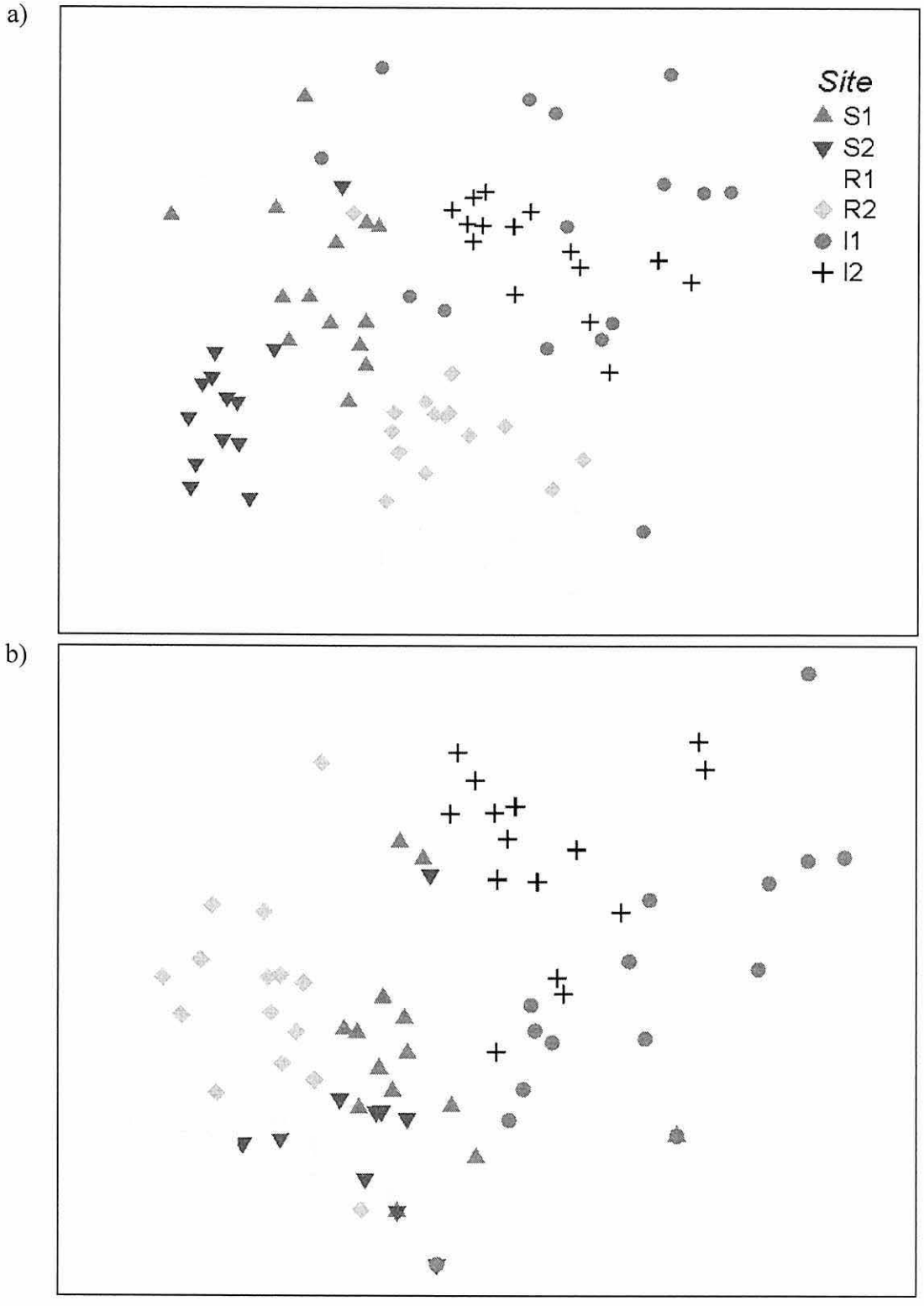


Figure 6.5. Multi-dimensional scaling plot of number of individuals in a) genera and b) classes found in mussel assemblages from three habitat types (S = subtidal, R = rope, I = intertidal) at the six study sites in Maine during May 2006. Stress = 0.14 and 0.15.

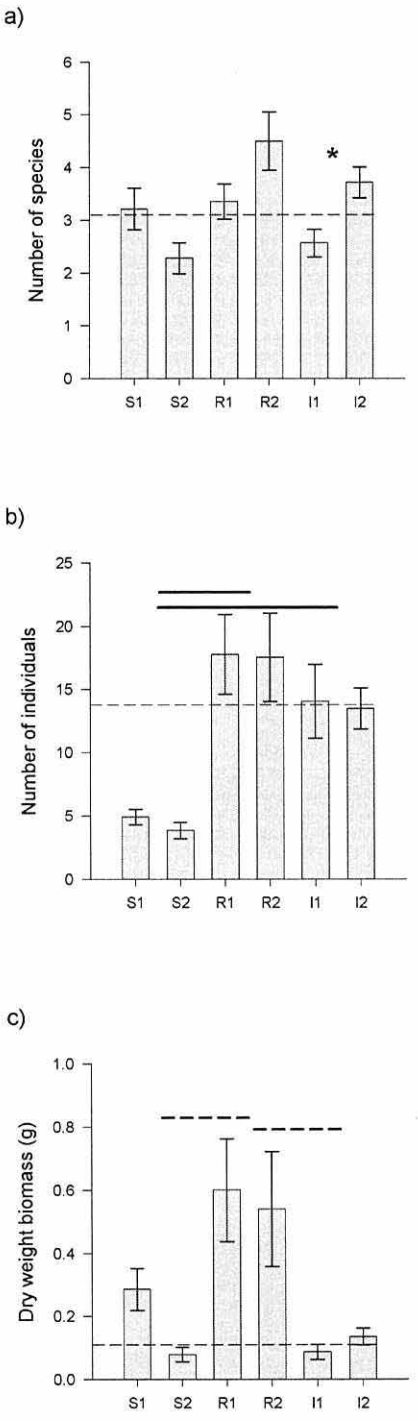
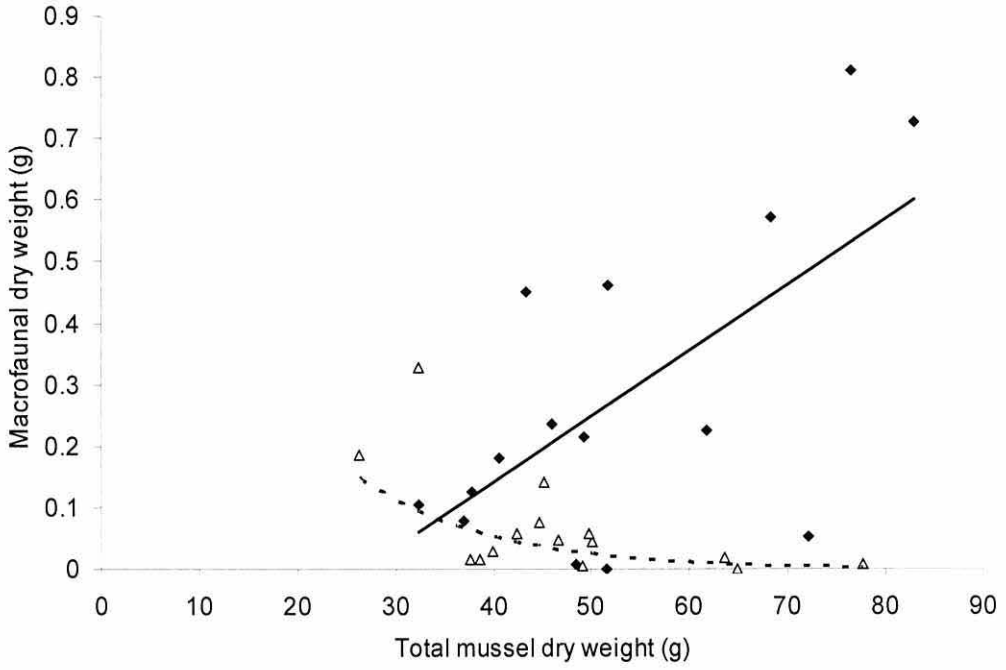


Figure 6.6. Mean species richness (a), abundance (b) and biomass (c) ±1. S.E. (n = 15) per core (79 cm^2) at the six study sites in Maine (S = subtidal, R = raft, I = intertidal). Dashed lines indicate the mean value for both intertidal sites (I1 and I2). Lines join habitats that were significantly different (Tukey's pair-wise comparisons). Asterisks indicate significant differences between sites within habitats. Symbols connecting bars: Solid = $p<0.001$, dashed or * = $p<0.05$.

a)



b)

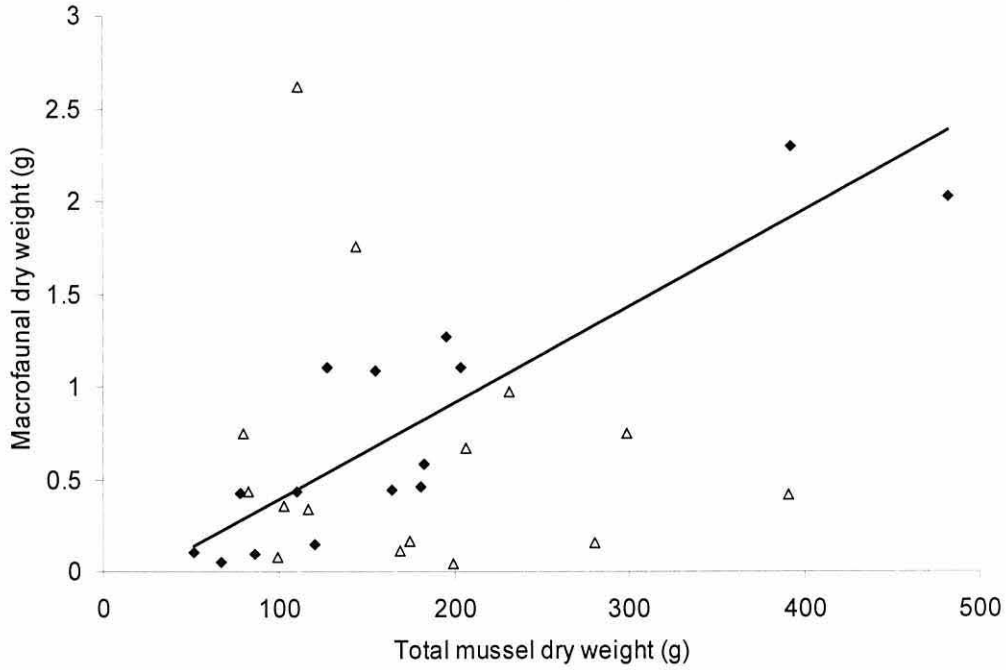


Figure 6.7. Correlation between total mussel biomass (number of mussels per core x mean dry weight) and associated faunal-biomass (n = 15) on (a) subtidal mussel beds at Old Point (S1, solid diamond, $R^2 = 0.411$) and Hadley's Point (S2, open triangle, $R^2 = 0.436$) and (b) rafts in Belfast Bay (R1, solid diamond, $R^2 = 0.788$) and at St. Helena Island (R2, open triangle, NS).

There was a significant positive linear correlation between mussel dry weight and dry weight biomass of the associated macrofauna at S1 ($F_{1,13} = 9.07$, $R^2 = 0.411$, $p = 0.010$; Figure 6.7a) and a significant negative exponential correlation at S2 ($F_{1,13} = 10.05$, $R^2 = 0.436$, $p = 0.007$). There was also a significant positive correlation between mussel dry flesh weight and associated dry weight biomass at R1 ($F_{1,13} = 48.28$, $R^2 = 0.788$, $p<0.001$; Figure 6.7b) but no correlation at R2. The intertidal sites exhibited no significant correlations between mussel biomass and the biomass of associated macrofauna.

These results show that numbers of individuals and biomass was greatest at the raft mussel cultivation sites, while on-bottom cultivation resulted in fewer individuals. Mussel cultivation did not cause major changes in the numbers of species associated with the mussel structure although there were significant changes in community composition.

6.4 DISCUSSION

The intertidal study sites supported four taxa that were not found at either the raft or on-bottom subtidal cultivation sites, namely *Gammarus oceanicus*, *Jaera marina*, *Nucella lapillus* and tubificid oligochaetes. Dredging of intertidal seed beds for cultivation in the subtidal zone is therefore likely to be detrimental to these predominantly intertidal organisms. Cultivated intertidal mussel beds, however, have been found to support increased numbers of amphipod crustaceans (Beadman *et al.*, 2004; Smith and Shackley, 2004; Chapter 5) while isopods can be abundant on subtidal mussel beds (Dolmer *et al.*, 2001) and amphipods may reach greater abundance beneath mussel rafts (Stenton-Dozey, 2001). There was a high abundance of the amphipod *G. oceanicus* at the intertidal sites in Maine (Table 6.2). Amphipods generally inhabit soft sediments providing a good food supply (Thiel, 1997) and thus benefit from the sedimentation caused by mussels (Kautsky and Evans, 1987). *G. oceanicus* in particular selects larger particles in preference to the unicellular algae consumed by some amphipods (Hudon, 1983) suggesting greater levels of detrital settlement over the intertidal mussel beds.

Changes from polychaete to oligochaete dominated worm communities in the presence of mussels in the intertidal zone have been identified in previous studies (Commito, 1987; Beadman *et al.*, 2004) together with a positive relationship between mussel and oligochaete abundance (Commito and Boncavage, 1989). By comparison, transplanting intertidal mussel assemblages to the subtidal zone appears to cause a shift to polychaete dominated worm communities. Six polychaete species which were absent at the intertidal sites were present at either the subtidal on-bottom or raft sites (Table 6.2), while the mean abundance of polychaetes per core was only 2 at the intertidal sites compared to 34 at the raft sites and 9 on the subtidal beds. Mussel rafts have also been shown to result in increased numbers of polychaetes in the underlying sediments (Stenton-Dozey *et al.*, 2001). By contrast, although an average of 18 oligochaete individuals per core was present at intertidal sites, these were absent from all other sites. The burrowing activities of oligochaetes can often prevent tubicolous polychaetes from becoming established in a particular habitat (McCann and Levin, 1989). However, cultivation of mussels in the subtidal zone appears to favour increases in the abundance of deposit feeding polychaetes such as *Amphitrite* spp. and may allow them to out-compete the much smaller oligochaetes. In terms of the biomass available to higher trophic levels, the transplantation of mussels may therefore have a positive effect.

Crimaldi *et al.* (2002) suggested that decreasing the space between adult clams reduced the chance of successful larval settlement on established beds due to changes in hydrodynamic forces. This may also account for the additional species present at S1 and S2, where mussel density was lower (Figure 6.2). However, Asmus (1987) found no correlation between the density of mussels and associated epifauna. Any such correlations are thus likely to depend on local physical conditions and larval dispersion; therefore no general assertions can be made on the relationship between mussel and associated faunal biomass. Mussel patch size is positively correlated with species richness (Tsuchiya and Nishihira, 1985), thus the practice of laying seed mussel in patches in the subtidal, as is the case in Maine, will limit the potential number of species that are found associated with the mussel patches. Conversely, leaving large areas of open sediment is likely to limit any detrimental effects to underlying infauna.

Asterias forbesi and *Nucella lapillus* were the only benthic invertebrate species recorded at the Maine sites that are known to commonly prey on *Mytilus edulis* (Hughes and Dunkin, 1984; Norberg and Tedengren, 1995), neither of which were found in high numbers. Thus benthic invertebrate predators were probably not a major factor in structuring the mussel-associated macrofaunal communities. However, although raft mussels are protected from eider ducks *Somateria mollissima* by nets both the subtidal and intertidal mussel beds, and the associated fauna, are accessible to eiders, which may have contributed to differences in the associated communities. In addition, 28 species of fishes have been recorded between Penobscot and Cobscook Bays including *Myoxocephalus aenaeus*, *Pseudopleuronectes americanus*, *Gasterosteus aculeatus* and *Microgadus tomcod* (Lazzari and Stone, 2006), all of which feed predominantly on the zoobenthos (Grabe, 1978; Langton and Bowman,1981; Laroche,1982; Bowman *et al.*, 2000). *M. tomcod* and *M. aenaeus* are most abundant in areas of *Zostera* sp. (Lazzari and Stone, 2006), which was observed around the intertidal sites in the current study, and both species feed predominantly on benthic crustaceans (Grabe, 1978; Laroche, 1982). Thus, fish may play an important role in the structuring of the macrofaunal communities, which undoubtedly support numerous predatory species on both the natural and cultivated mussels.

The increased substrate complexity resulting from the presence of mussels over a much wider range of size classes (Figure 6.2) amongst the rope-grown mussels may have contributed to the significantly greater macrofaunal densities in this habitat compared to the subtidal mussel beds. The significantly lower density of mussels at the subtidal mussel beds compared to the intertidal sites is likely to have contributed to the significantly lower number of individuals found at S1 and S2 (Figure 6.6b), supporting the positive relationship between mussel density and associated fauna previously suggested by Dolmer (2002). In addition, although the high stocking densities of mussels in the Menai Strait may result in a decline in species richness compared to lower densities of mussel coverage (Beadman *et al.*, 2004) the cultivated mussel beds in the Menai Strait harbour 27 species compared to the 19 species found in the natural intertidal mussel beds in Maine.

There was a predominantly mollusc-based community at I2 as compared to the predominantly oligochaete-based community at I1. Molluscs also predominated at R2, while at RI the community consisted predominantly of polychaetes. Lower salinity due to freshwater input from the Penobscot River at R1 may have contributed to differences in community composition compared to R2. This variability between sites will also influence higher trophic levels. Polychaetes provide an important food source for the brown shrimp, *Crangon crangon* (Dolmer *et al.*, 2001), and fish (Lopez-Jamar *et al.*, 1984), while molluscs are preyed upon by crabs, including *Carcinus maenas* and *Cancer irroratus*, *Nucella lapillus*, and starfish (*Asterias* spp.). Therefore, the predators feeding on natural or cultivated mussels are also likely to differ between cultivation sites and habitats. There will also be differences in predator communities in the intertidal and subtidal zones due to the available prey and substratum; for instance, there were more small crabs (<30 mm carapace width) on mussel beds in the intertidal zone of the Menai Strait (see Chapter 7).

The intertidal and raft sites exhibited polymodal distributions of mussel biomass, in contrast to the subtidal beds. These polymodal distributions represent a wider range of mussel sizes and differences in the mussel structure, some of which will better suit certain species than others causing greater variation in communities. The significantly higher macrofaunal biomass found on the rafts (Figure 6.6b) was in part due to the significantly higher densities (Table 6.1) but also the size of organisms found, commensurate with the larger mussels present on the rafts.

The significant positive correlations between mussel biomass and associated macrofaunal biomass at S1 and R1, compared to negative or no correlations at S2 and R2, are possibly due to the particular species inhabiting these sites. The solid substratum provided by the mussels allowed for increased abundance of barnacles at S1, where *Balanus* spp. were predominant. However, the presence or absence of barnacles is dependent on larval dispersion, and successful settlement and attachment, meaning barnacles were not as abundant at all sites. *Lepidonotus* spp., the most abundant genus at S2, is likely to have attained refuge among mussels in a similar way to *Carcinus maenas* in other locations (Thiel and Dernedde, 1994) but only up to a critical density of mussels; this link is also more ephemeral than

the barnacle-mussel symbiosis at S1. At R1 *Amphitrite* sp. was predominant probably due to the accumulated sediment, organic matter, faeces and pseudo-faeces on the mussel rafts. Tentaculate deposit feeders, such as *Amphitrite* spp., are known to feed predominantly on particles with a low weight to area ratio (Jumars *et al.*,1982), therefore sedimentation due to reduced current flow through mussel rafts (Newell and Richardson, 2000) combined with entrapment of mussel faeces could allow *Amphitrite* sp. to thrive. In contrast, *Macoma calcarea* was most abundant at R2 and, as a filter-feeding bivalve, competition with mussels for phytoplankton may have limited the beneficial effect of the substrate provided by the mussel structure at the other sites, especially where *M. calcarea* and *M. edulis* are consuming similar sized particles (Griffen *et al.*, 2004).

Biomass of the mussel-associated fauna was significantly greater at the raft sites than at either the intertidal or subtidal sites; similarly, mussel biomass was much greater on the rafts (Figure 6.3). Thus, there is at times a positive effect of mussels on biomass that is important to factor into any assessment of the environmental impacts of mussel farming. In particular, the habitat provided by mussels could offset the negative effects of mussel cultivation (Dittmann, 1990; Dolmer *et al.*, 2001; Smith and Shackley, 2004) on the underlying fauna.

In light of the current study, raft culture is arguably preferable to on-bottom culture in terms of maintaining associated faunal abundance and biomass. Furthermore, off-bottom mussel cultivation provides protection against benthic predators such as *C. maenas* and thus is a preferable form of cultivation if predation is problematic and where local conditions are suitable. Subtidal mussel beds provide a similar level of mussel-associated macrofaunal biomass to naturally occurring seed beds, and both habitats may provide an additional food source to predators feeding on the mussel beds. However, it is important to recognise that both small and large spatial scale variation in community structure exists in the naturally occurring intertidal mussel beds that will lead to differences in the communities present in subtidal mussel assemblages following transplantation. Stocking subtidal beds or ropes with mussel assemblages rich in fauna is likely to result in richer communities in the cultivated mussel assemblage, with the exception of the loss of exclusively intertidal species. Commercial

mussel assemblages derived from impoverished intertidal beds will rely predominantly on colonization, and communities will thus take longer to become established.

The finding of lower biodiversity at sites where mussels are re-laid cannot simply be interpreted as a negative effect of mussel culture on biodiversity. The removal of seed mussel from an intertidal site may allow underlying fauna to prosper in the newly exposed surface sediments, while the newly created subtidal mussel structure and associated sediment provides increased substrate for many species, particularly in the case of raft mussel culture, but possibly at the expense of subtidal infaunal organisms. To characterise fully the effects of mussel cultivation and select sites that will minimize species and biomass loss it is recommended that communities should be identified at seed beds and cultivation sites both before and after mussel transplantation. Identification of bycatch in the seed dredging process will also help to elucidate which species survive the transplantation process. The method of sampling rope-grown mussels is also recommended as a suitable means for enabling quantitative comparisons of biodiversity between suspended and on-bottom cultivation sites.

In the following chapter predictions are made about the potential impact of *C. maenas* on the commercial mussel beds in the Menai Strait. A predation model is presented and consideration is given to the effects of feeding rates on the catches made by the crab fishery. Estimates of mussel losses during the cultivation process are also presented.

CHAPTER 7

PREDICTING LOSSES OF *MYTILUS EDULIS* TO *CARCINUS MAENAS* PREDATION

ABSTRACT

A general feeding model is described which was developed based on the results presented in Chapter 3. This feeding model was applied to the *Carcinus maenas* abundance data presented in Chapter 2. The accuracy of the model was tested against a separate dataset on the feeding rates of crabs over a range of sizes. The influence of feeding rates on catches of crabs in baited traps was determined, and average catches are discussed in relation to abundance estimates. There was a significant relationship between crab feeding rates and catch per unit effort (CPUE). Crab abundance was not significantly correlated with CPUE. There was an exponential decline in the predicted losses of mussels during the cultivation process as mussels grew to larger body size. It was estimated that *C. maenas* consumed ~10% of seed mussels laid in the Menai Strait during their growth to a marketable size. Although crab abundance and size, and seawater temperature substantially influenced the number of mussels eaten over a period of 24 hours, the size of mussels was by far the dominant factor in determining losses during the cultivation process. Efforts to control crab predation, therefore, should focus on the early stages of the cultivation process and on areas where the smaller, more vulnerable, mussels are present. The coefficients and formulae presented here could be applied to other areas of *Mytilus edulis* cultivation subject to predation by *C. maenas*, and the model might also be used to assess predation in other species of commercially important bivalve molluscs.

7.1 INTRODUCTION

Large settlements of *Mytilus edulis* occur annually (Seed, 1969a) and mussel cultivation is, therefore, generally considered to be a sustainable form of fishing. Most seed mussel beds are ephemeral as the small mussels are often subject to heavy predation and are also vulnerable to storms (Kaiser *et al.*, 1998). These natural stocks of seed mussels are, nevertheless, a finite resource. Low levels of larval settlement or losses before stocks can be fished make extensive mussel fisheries vulnerable to high annual variability in yields. Current fishing practices do not make efficient use of seed mussel stocks, often with over 90% of mussels being lost during the cultivation process (Murray *et al.*, in press). Any expansion of mussel fisheries in response to declines of stocks in other fisheries will require more efficient use to be made of seed mussel stocks. This is also the case for other bivalve fisheries. However, the effect of minimizing predation by removing predators must be weighed against the effects on the predators of the mussels and higher trophic levels. Bird populations, particularly waders, feed extensively on *C. maenas* (Sibly and MacCleery, 1982; Ellis *et al.*, 2005) and elimination of shore crabs from mussel fisheries could have negative effects on local avian populations.

C. maenas is a voracious predator of *Mytilus edulis* (Chapter 3; Elner and Hughes, 1978). It is clear that *C. maenas* will generally select smaller prey items more frequently than larger prey items (Mascaro and Seed, 2000b; Murray *et al.*, in press) but larger prey items can be consumed (Ameyaw-Akumfi and Hughes, 1987) and are selected more frequently when their proportion in the population is increased (Chapter 3; Burch and Seed, 2000). Measurements of feeding rates in any organism are undoubtedly subject to artefacts. For example, enclosure experiments conducted in the field restrict the natural movements (i.e. migration) of the predator and alter environmental conditions (Fernandes *et al.*, 1999), as well as being prone to disturbance. Exclosure experiments are perhaps the best way to establish predation level where only a single predator species is feeding on the prey species under study, and mortality induced by other factors is known to be low. However, in practice there are likely to be losses of prey items due to more than one predator, as was apparent in Chapter 5. Laboratory-based studies remove the predator from its natural environment but allow better control of the

variables not under study and the level of disturbance can be minimized allowing the maximum predation potential to be determined.

C. maenas is abundant on the mussel beds in the Menai Strait, both in the intertidal and subtidal zones. Although absent from the intertidal zone during the winter, substantial numbers of shore crabs remain on the subtidal mussels beds throughout the year (Chapter 2). Mussels are thus subject to year round predation by *C. maenas*. Methods to limit the effects of crab predation include fences, raising mussels off the seabed and removing predators (Hickman, 1992). Each of these methods must be both practicable in the area of cultivation and economically viable. To assess the economic feasibility of predator control it is necessary to determine the loss of mussels, or other cultivated species, to the predator in question. Accurate prediction of the effects of predation requires the best possible measure of absolute abundance of predators together with knowledge on feeding rates. In practice, obtaining estimates of absolute abundance is difficult. Some studies have relied upon relative measures of abundance obtained using traps (Welch, 1968; Atkinson and Parsons, 1973). Although such data may be useful in detecting seasonal changes in relative abundance, they cannot be applied to make quantitative predictions about predation.

The aim of this chapter is to incorporate the feeding model presented in Chapter 3 with the *C. maenas* abundance data presented in Chapter 2 in order to make predictions about the losses of *M. edulis* to *C. maenas*. The overall predation model is also described in more general terms to allow its potential application to other bivalve fisheries. Predictions were also tested against a validation dataset, and consideration given to the likely impact on the crab fishery and the effectiveness of the crab fishery in reducing mussel losses to crab predation. In addition, the influence of feeding rates and crab abundance on catch per unit effort (CPUE) in baited traps was determined.

7.2 MATERIALS AND METHODS

Predation model

Equations 7.1 and 7.2 below allow predictions to be made about the number of mussels that will be consumed by a crab of a given size feeding on a given size range of mussels, assuming mussel populations are normally distributed in terms of their size frequencies. The regression equation obtained from Figure 3.11 (Chapter 3) allows a temperature correction to be applied based on the mean seawater temperature at any particular time of the year (Equations 7.3 and 7.4). The number of mussels predicted to be consumed can then be adjusted accordingly to give a temperature dependent estimate of the number of mussels consumed (Figure 7.5). The results presented in Figure 3.9 (Chapter 3) also allow an adjustment to be applied based on the proportion of green or red, male or female crabs in the local population. In Chapter 3 the relationship between the mean length of mussels and the number eaten was described by a two parameter exponential function ($y = a e^{bx}$). The relationship between bivalve prey size and the number consumed by a predator can thus be described more generally as:

Equation 7.1: $$\eta_e(L) = \eta_\infty e^{-k(L - L_0)}$$

where, η_e = the number of prey items consumed, η_∞ = maximum number of prey items consumed during a given time, L = mean length of prey, and L_0 = the size of mussel at which η_∞ is found.

The parameters in Equation 7.1 are analogous to those used in the Von Bertalanffy equation, with L being equivalent to time, and η equivalent to length. The constant k can thus be estimated in a similar manner by plotting L against $\ln[\eta_L/\eta_\infty]$, where the slope is equal to k, and η_L is the number of prey items consumed at a given length. It should be noted that the number of prey items consumed may decrease below a certain prey size, in which case a simple exponential relationship is insufficient and a more

complex model is required, as is the case for the relationship between prey length and biomass consumed. Incorporating a parameter , $a_c x$, derived from the linear function ($y = ax + b$) describing the relationship between predator size and the number of prey items consumed, and a third parameter, y_0, describing the minimum size of predator able to consume mussels of length L_0, η_e can be calculated for varying crab and mussel sizes:

Equation 7.2: $$\eta_e(L, a_c) = (-y_0 + \eta_\infty e^{-k(L-L0)}) + a_c x$$

The relationship between temperature and the number of mussels consumed (C_e) was described by the quadratic function:

$$C_e(t) = -at^2 + bt - c$$

Thus, differentiating:

$$C_e'(t) = 2at + b$$

Hence, the average derivative between any two temperatures (reference and measured) can be calculated as follows:

$$C_e'(t) = 2a\left(\frac{t_m - t_r}{2} + t_r\right) + b$$

where, a and b = quadratic equation coefficients, t_r= reference temperature, and t_m = measured temperature.

Thus:

$$\delta C_e(t) = 2a \cdot \delta t\left(\frac{\delta t}{2} + t_r + b\right)$$

where, $\delta_t = t_r - t_m$. If t_r, C_e is the vertex (feeding rates are greatest) then $\delta C_e/\delta t$ is 0, thus:

Equation 7.3: $$\delta C_e(t) = a \cdot t_m + \frac{b}{2}$$

Therefore, the difference in the number of prey items consumed, τ, can be calculated:

Equation 7.4: $$\tau(C_e, t) = C_e\left(a \cdot t_m + \frac{b}{2}\right)$$

Hence, the number of prey items consumed by an individual predator at a given temperature can be predicted by:

Equation 7.5: $$\eta_t(L, x, \eta_e) = (-y_0 + \eta_\infty e^{-k(L-L0)}) + a_c x + \tau$$

where η_t is the temperature-corrected, predicted number of mussels consumed.

A simple adjustment (m) can be applied to Equation 7.6 to allow for average differences in feeding rates between male and female, and red and green crabs, or other physiological differences in other species; thus:

Equation 7.6: $$\eta_t(L, x, \eta_e, m) = m((-y_0 + \eta_\infty e^{-k(L-L0)}) + a_c x + \tau)$$

Equation 7.6 is a feeding model to predict the mussel losses resulting from an individual crab feeding during a given time period. The resulting predictions from this model can then be applied to the crab population data, which must include a measure of size (e.g. carapace width) and abundance. The size-frequency distributions of crabs recorded in the video surveys were predicted based on the mean and standard deviations of the CW of crabs measured, assuming normal distribution. From these distributions the number of mussel consumed per crab per day was predicted based on

the size of mussels at different stages of the mussel cultivation process. Normal scores, z, were calculated:

$$z = \left(\frac{x - \bar{x}}{se} \right)$$

From which the cumulative distribution was estimated:

$$x(z) = \frac{1}{\sqrt{2\pi}} e^{\frac{-z^2}{2}}$$

And thus the number of crabs in each size class:

$$f = (s_{i+1} - s_i)n$$

where s is the cumulative proportion of crabs in each size class, n is the abundance and f is the frequency of individuals in each size class.

So the number of prey items consumed by any given size class of predator can be calculated as:

$$p = f \cdot z_t$$

And therefore total prey consumption by a particular group of crabs, r, defined based on the sampling area, is calculated as the sum of the prey consumed by each size class of predator, p:

Equation 7.7: $$r = \sum_{i=m}^{n} p_i = p_m + p_{m+1} + \ldots + p_{n-1} + p_n$$

The size-frequency distributions of crabs were estimated based on the mean CW (± S.D.) in the intertidal and subtidal zones, calculated from three sites in each zone. Thus,

by summing the annual mussel consumption (Equation 7.7) by each group, r, the annual mussel losses, a, are estimated:

Equation 7.8: $$a = \sum_{i=m}^{n} r_i = r_m + r_{m+1} + \ldots + r_{n-1} + r_n$$

All of the parameters incorporated into the predation model (Equation 7.8) are shown in Table 7.1. Values of coefficients are given for *C. maenas* feeding on *M. edulis* over the range of mussel and crab sizes found on the cultivated mussel beds in the Menai Strait studied in Chapters 2 and 3.

Testing the feeding model

To assess the precision and accuracy of the feeding model an additional set of feeding trials was conducted against which the predictions of the model could be tested. The methods used were identical to those described in Chapter 3. Therefore, crabs were presented with mussels in seven length classes with 3, 5, 8, 10, 8, 5 and 3 mussels in each 5 mm length class from smallest to largest. Crabs were selected at random over a range of sizes. Crabs from 49 mm to 70 mm CW were presented with mussels. Each crab was presented with 42 mussels in the size frequency distribution described above with a modal size class selected at random and ranging from 22.5 – 25 mm to 45 – 47.5 mm length. Red and green, and male and female crabs were used and were allocated at random to a particular size frequency distribution of mussels. Temperatures and modal mussel size were also allocated at random for each crab. A total of 23 crabs were fed over 24 hour periods, and crabs were kept individually. Carapace width (widest point of the carapace) and chelal height (greatest height of the propus) were measured in each crab. Predictions of the number of mussels consumed were made using Equation 7.6.

Table 7.1. Parameters incorporated into (and output of) crab and mussel predation model. Values are given for constants based on the results presented in Chapter 3.

Parameter	Abbreviation	Unit	Value
Predicted number of prey items eaten	η_e	Mussels crab^{-1}d^{-1}	-
Minimum size of predator able to consume prey items of length L_0	y_0	mm carapace width	35
Maximum number of prey items consumed	η_∞	Number of mussels	41
Length at which η_∞ is greatest	L_0	mm mussel length	20
Mean length of prey item	L	mm mussel length	-
Number of prey items eaten	C_e	Number of mussels	-
Feeding constant	k		0.180
$\delta C_e/\delta CW$	a_c	δno. mussels δmm^{-1}	0.539
Carapace width (CW)	x	mm	-
$\delta y/\delta x$ approaching $\delta y/\delta x = 0$	a_t	No. mussels °C^{-1}	-0.492
X at $\delta y/\delta x = 0$	b_t	No. mussels °C^{-1}	12.856
y at x = 0	c_t	Number of mussels	53.120
Temperature	t	°C	-
Reference temperature	t_r	°C	13
Measured temperature	t_m	°C	-
Temperature dependent adjustment to η_e	τ	Number of mussels	-
Normal score	z	n/a	-
Number of individuals in each size class	f	Number of crabs	-
Cumulative proportion of crabs per size class	s	Number of crabs	-
Prey consumed in size class	p	Number of mussels	-
Prey consumed by all size classes	r	Number of mussels	-
Annual predation	a	Number of mussels	-

CPUE as an estimator of abundance

Data on total catches and CPUE from the commercial crab fishery (see Chapter 2) in the Menai Strait were compared to the abundance measurements and feeding rates described in Chapters 2 and 3, respectively. To establish the reliability of CPUE as an estimator of relative abundance, the influence of abundance (as measured using video

surveys) and feeding rates on the CPUE of *C. maenas* were determined. CPUE was predicted based on feeding rates at the mean monthly temperature in the Menai Strait using the function $y = -0.492t^2 + 12.856t - 53.12$ (where t is temperature, °C) and was termed the feeding index (ε). To calculate a catch index (γ), CPUE was standardized to a scale of 0 to 100, where 100 is the maximum feeding rate and 0 is no feeding. An abundance index (ρ) was calculated from abundance as measured using the video surveys (Chapter 2), and this was also standardized to a scale of 0 to 100, where 100 is the maximum abundance and 0 is no crabs. The catch index was also standardized to a temperature of 13°C, where feeding rates were highest (γ_t). Regression analysis was then used to assess the contribution of feeding rates and abundance to CPUE.

7.3 RESULTS

Mussel losses

The number of mussels predicted to be eaten by *C. maenas* using the feeding model (Equation 7.6) explained 58% of the variation in the number of mussels that were observed to be eaten ($R^2 = 0.583$, $F_{1,22} = 30.734$, $p<0.0001$; Figure 7.1). The standard error of predictions is ±6 mussels. Residual variances were equal ($p = 0.096$) and normally distributed (K-S = 0.094, $p = 0.979$). In addition, there was no significant difference between the number predicted to be eaten and the observed number actually eaten (ANOVA, $F_{1,46} = 0.05$, $p = 0.826$). The linear regression function relating the predicted and observed numbers had a slope of 1.06 and an intercept of -0.18, very close to a perfect model with a slope of 1 and intercept of 0. Thus, despite the high variability in the data, with 32% of variability unexplained, the mean predictions are accurate. Standardizing predicted numbers of mussels eaten to account for differences in chelal height did not improve the accuracy of predictions.

At any time during high water on the commercial mussel beds in the Menai Strait *C. maenas* has access to mussels ranging from around 20 mm to >50 mm (Figure 2.2; Chapter 2). At low water crabs are restricted to feeding predominantly in the subtidal

zone where mussels have a mean length >45 mm. During the first year of growth mussels increase in length by around 10 mm, by around 20 mm during the second year of growth, and by around 5 mm during their final 6 months of growth. The mean height of the intertidal mussel beds in the Menai Strait above Chart Datum (Lowest Astronomical Tide) is 2.1 m (UKHO, 2004). Consequently, they are immersed on average for 79 % of the time. Predicted losses of mussels to crabs were reduced accordingly, assuming the abundance of crabs recorded in the intertidal zone remained constant during this time.

The modal CW of *C. maenas* throughout the year was around 45 mm on both the subtidal and intertidal mussel beds (Figure 7.2). In the intertidal zone there were crabs <30 mm CW that were not present in the subtidal zone, while there were more medium-sized crabs (30 – 60 mm CW) in the subtidal zone. Crabs >60 mm CW were present in both zones in similar numbers.

Applying Equation 7.8 based on the coefficients presented in Table 7.1 and Chapter 3, and the mussel size and crab abundance data presented in Chapter 2, the predicted numbers of mussels consumed were calculated. The number and size of mussels predicted to be consumed by crabs in the intertidal and subtidal zones differed substantially (Figure 7.3). No crabs <55 mm CW will be able to consume the mussels present in the subtidal zone. Therefore, the modal CW of crabs consuming the most mussels was 62 mm in the subtidal zone compared to 50 mm in the intertidal zone. The smallest crabs observed (30 mm CW) were predicted to consume an average of 5,500 mussels $ha^{-1}d^{-1}$ in the intertidal zone during the cultivation process. The largest crabs observed (~72 mm CW) were predicted to consume an average of 10,500 mussels $ha^{-1}d^{-1}$ in the intertidal zone, while in the subtidal zone they were predicted to have consumed only 600 mussels ha^{-1} d^{-1}. Predicted mussel consumption at different stages of the cultivation process were also calculated (Figure 7.4). Predation (mussels consumed) peaked in August of the first year of cultivation when mussels were small (21 mm) and crab abundance was highest. During the first 9 months of growth, the modal CW of crabs consuming the greatest quantity of mussels increased as mussels grew from 19 mm to 29 mm in length. During the second and third years of growth, the

CW of crabs consuming the greatest quantity of mussels varied from around 60 to 70 mm. After one year of mussel growth no crabs <50 mm CW consumed any of the mussels.

Total mussel losses throughout the cultivation process due to *C. maenas* amount to 9.648×10^6 mussels ha^{-1}, or 550 kg ha^{-1} during the 33 months between seeding and harvesting, equivalent to 168.06 tonnes final weight and 10.3% of the seed mussels laid. The weight of mussels consumed ranged from 52 kg ha d^{-1} during August of the first year of cultivation when mussels were much smaller, to only 0.2 kg $ha^{-1}d^{-1}$ at the end of the cultivation period of 33 months (Table 7.2).

There was an exponential decline in the number of mussels consumed by *C. maenas* during the cultivation process (Figure 7.5), reflecting the decrease in numbers eaten by crabs with increasing mussel size (see Figure 3.5a, Chapter 3). Mussel losses decrease from 47,000 – 65,000 $ha^{-1}d^{-1}$ during the first two months of growth to only 14 $ha^{-1}d^{-1}$ in the final month of harvesting, when only crabs >60 mm CW were able to consume these large mussels. Peaks in predation occur in March and September due to increases in crab abundance and CW (see Figure 2.4 and 2.5, Chapter 2) but mussel growth is the dominant factor in reducing losses, as mussels increase from <20 mm to >50 mm in length during their 2.5-3 years of growth. The exponential decline in mussel losses reflects the exponential decline in mussels eaten with increasing mussel size (see Figure 3.5a, Chapter 3). Therefore the influence of crab size and abundance is comparatively minor in determining overall losses over the range of crab sizes and abundance recorded in the Menai Strait during this study.

The crab fishery

The mean number of *C. maenas* removed per fishing trip in 2003/2004 ranged from 6,249 ±582 crabs d^{-1} in January 2004 to 13,595 ±385 crabs d^{-1} in July 2004 (Figure 7.6a). In 2006, the mean catch of *C. maenas* per fishing trip ranged from 3,775 ±492 crabs d^{-1} in March 2006 to 25,064 ±2,304 crabs d^{-1} in September 2006 (Figure 7.6b). In

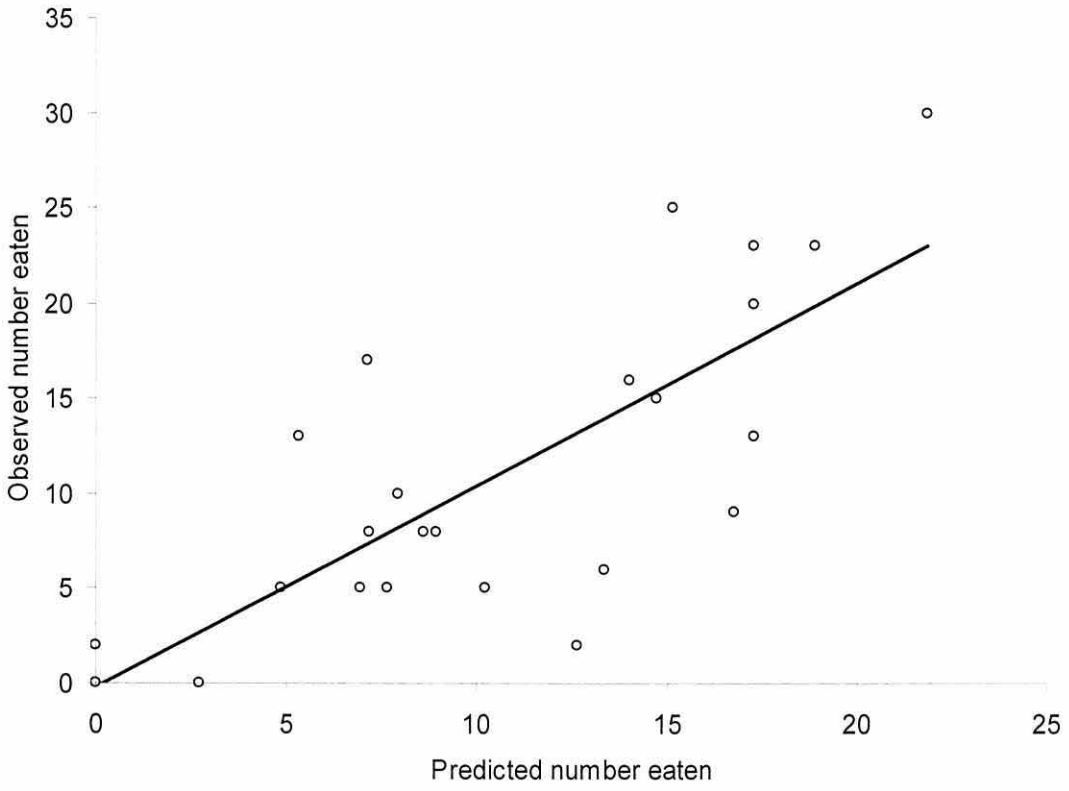


Figure 7.1. Correlation between the predicted number of mussels eaten and the observed number of mussels eaten by *Carcinus maenas* of varying size, sex and colour over several different temperatures in laboratory experiments (y = 1.06x - 0.18).

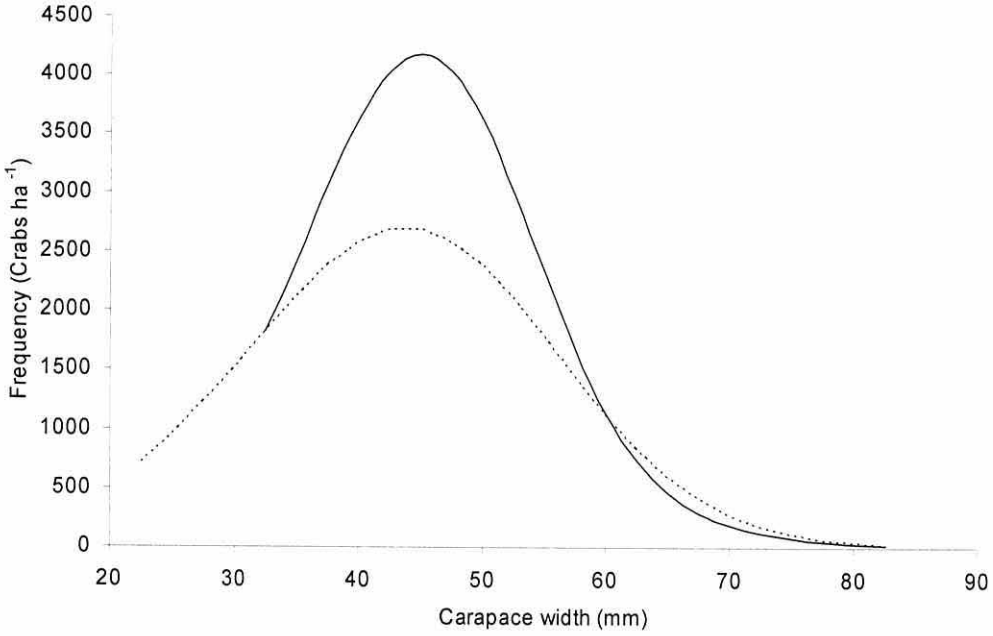


Figure 7.2. Size frequency distribution of total number of *Carcinus maenas* observed on the intertidal (dotted line) and subtidal (solid line) during 2006 based on the numbers of individuals in each 5 mm carapace width size class.

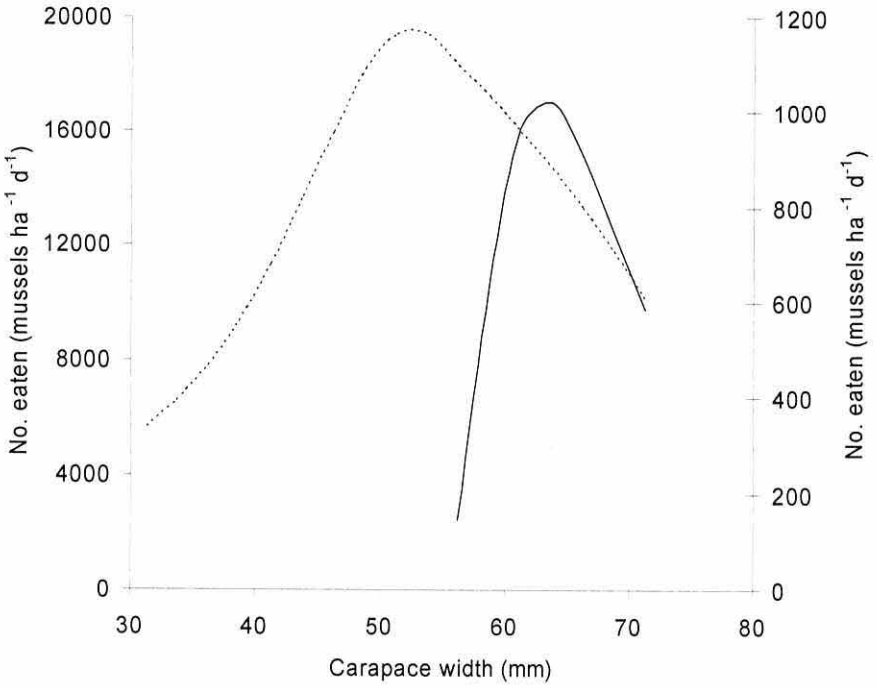


Figure 7.3. Estimated number of *Mytilus edulis* consumed by *Carcinus maenas* on intertidal (dotted line; left y-axis) and subtidal (solid line; right y-axis) mussel beds during the 3 year cultivation process.

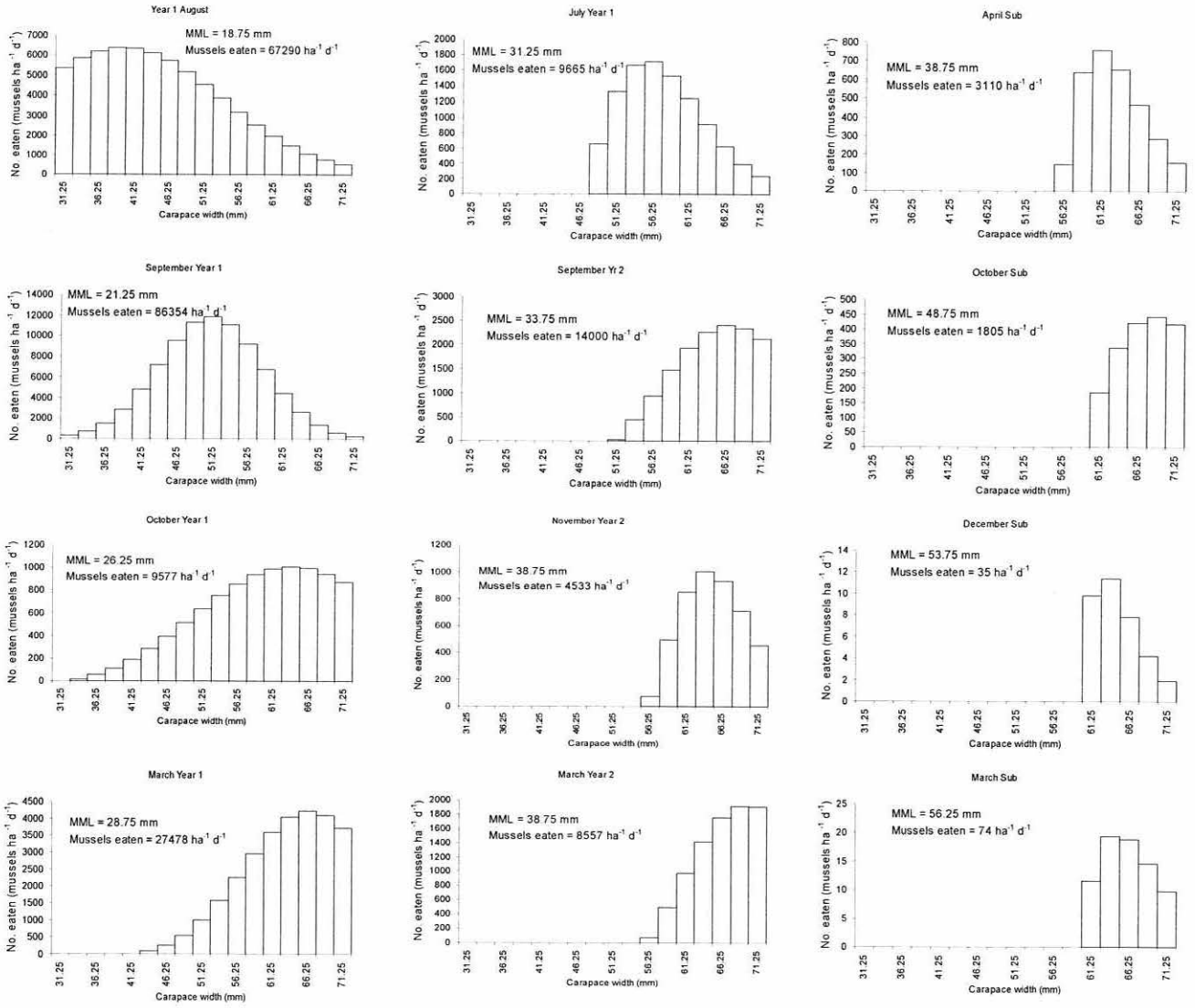


Figure 7.4. Predicted mussel consumption by *Carcinus maenas* at different stages of the cultivation process. Year 1 mussels are those in the first year of cultivation (beginning in August), year 2 mussels are those in the second year of cultivation, and subtidal mussels (Sub) are those in the final year of cultivation.

Table 7.2. Mussel losses to *Carcinus maenas* in the Menai Strait during the cultivation process.

Time (months)	Mussel length class (mm)	Losses (kg $ha^{-1}d^{-1}$)
1	17.5-20	25.20
2	20-22.5	51.77
4	25-27.5	13.72
9	27.5-30	10.54
13	30-32.5	18.29
15	32.5-35	25.92
17	37.5-40	23.40
21	37.5-40	8.45
22	37.5-40	11.30
28	47.5-50	18.42
30	52.5-55	0.33
33	55-57.5	0.24

2003/2004 the mean number of *C. maenas* removed per day within a given month ranged from 1,286 in July 2004 to 6,824 in April 2004. In 2006, the mean catch per day ranged from 1,057 in December to 4612 in April. Figure 7.7 shows the estimated crab population over the mussel beds in the Menai Strait throughout 2006 and the potential population size had no *C. maenas* been removed by the crab fishery. This is a simplification, as the removal of crabs may allow other crabs to prosper by reducing competition, and it is likely that if crabs were not removed by the fishery many would migrate offshore. Nevertheless, the minimum and maximum abundance would occur at the same times during the year even without the crab fishery, which is not responsible for the annual variation abundance.

The mean catch of *C. maenas* (±S.E.) in 2003/2004 was 4,516 ±774 crabs d^{-1} and in 2006 was 2,788 ±322 crabs d^{-1}. Thus the maximum number of mussels consumed by the crabs caught per day in 2003/4 would have been 180,640 at the smallest mussel size, falling to <4,516 at the largest mussel size. In 2006, the maximum mussel losses from the quantity of crabs caught in an average day would have been 111,520, which equates to losses per hectare of around 86,000 mussels, falling to <2,788 in total when mussels were at their largest. Crabs are also removed by the mussel fishery during the months of harvesting from October to March, but the impact is probably small as numbers of crabs remained approximately level during the winter months.

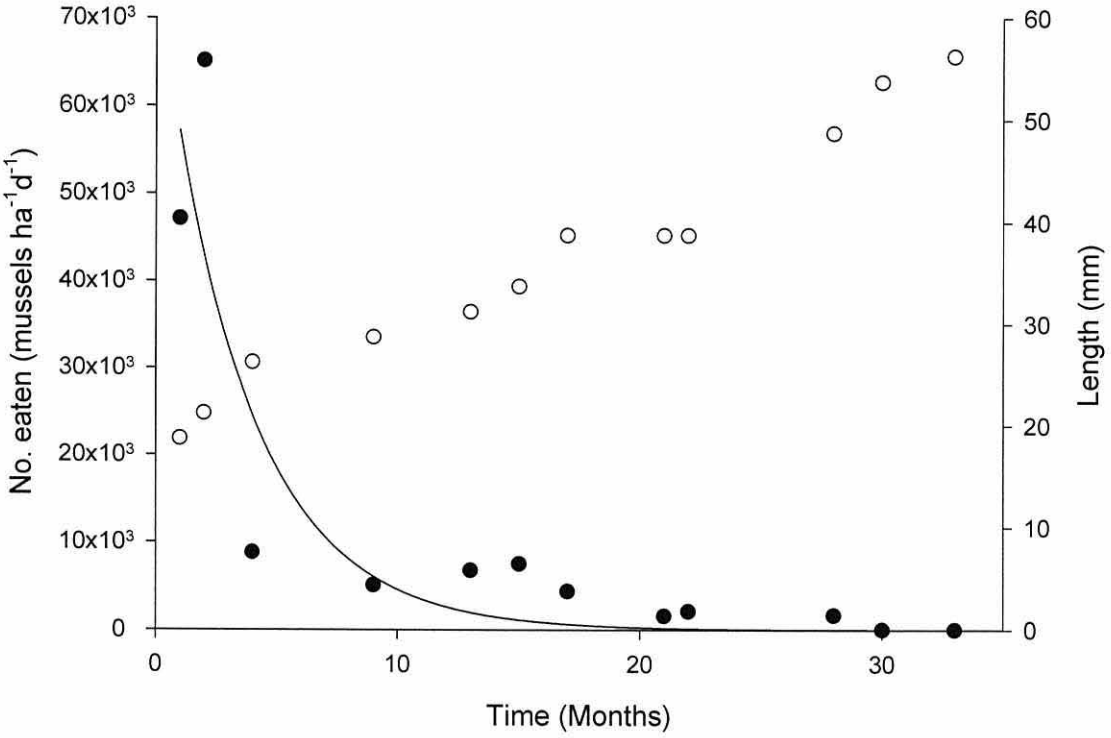


Figure 7.5. Predicted mussel losses to *C. maenas* during the mussel cultivation process (solid circles); values based on crab numbers recorded in the Menai Strait and average mussel size (open circles).

CPUE-based abundance estimates

The relationships between both temperature and feeding rates and temperature and CPUE in baited traps can be described by quadratic functions (Figure 7.8). Feeding rates peak at 13°C, declining as temperature increased to 18°C. CPUE peaks at 16°C, but levels off from 14°C, declining very slightly above 16°C. Figure 7.9 shows the relationship between the feeding index (ε) and the catch index (γ). There is a significant relationship between ε and γ ($F_{1,10} = 20.055$, $R^2 = 0.667$, $p = 0.001$); residual variance was homogeneous ($p = 0.557$) and residuals were normally distributed (K-S = 0.208, $p = 0.621$). The slope of the linear regression was 0.843, indicating that CPUE increased at a slightly lower rate than would be predicted based temperature dependent feeding rates alone, which would have resulted in a slope of 1. Estimated abundance based on video surveys and dredged samples did not match CPUE estimates of relative abundance, with peaks and troughs occurring two months before the CPUE and temperature maxima and minima (see Chapter 2). There was no significant relationship between the abundance index (ρ) and γ (Figure 7.10a), even when CPUE was adjusted to account for variations in feeding rates with temperature (γ_t, Figure 7.10b). Thus CPUE appears to be determined largely by feeding rates, which accounts for the difference in abundance as measured by the video surveys compared to relative numbers as measured by CPUE.

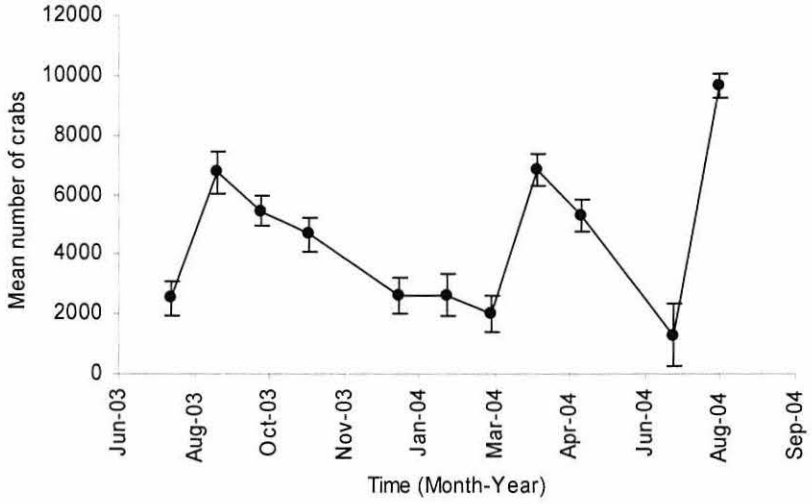
Fisheries interactions

The two fisheries, mussels and crabs, operating in the north east Menai Strait as shown in Figure 2.1 (Chapter 2), exhibit numerous interactions as summarised in Figure 7.11. In predicting the losses of mussels it is desirable to consider all possible effects acting on predation. However, time and financial constraints make this unrealistic. In Figure 7.11, 'Fishery A' can represent the mussel fishery, and 'Fishery B' the crab fishery, but interactions between other predator and prey fisheries would operate in the same way. In any ecosystem the interactions between trophic levels is complex and may be exposed to many influences. The growth of each species affects the predator-prey interactions. Mussels attain refuge from some predators by growing to larger body size,

but larger prey items are consumed as the predators themselves increase in size. Environmental variables may affect predator and prey differently both in terms of mortality and growth. Natural mortality in the predator species will be beneficial to the prey species, and removal of the predator species may also help to reduce mortality in the prey species. In the Menai Strait, the *C. maenas* fishery exists largely to reduce crab predation on the mussel beds. Many crabs are also removed during the mussel harvest. Having been cleared of mussels and some of the predators, the subtidal mussel beds are then ready for re-stocking with mussels from the intertidal zone. The intertidal zone is then ready for re-seeding with mussels, providing a new food source for resident crabs together with those accidentally imported with the mussels.

In summary, mussel losses due to *C. maenas* predation are much greater during the first few months after being laid than later in the cultivation process when mussels have grown to larger body size. The model presented reduces the need for large scale data collection in order to make predictions about the impact of crab predation. With further experimental work the predation model could potentially be applied to other bivalve fisheries subject to predation. Feeding rates are responsible for two-thirds of the variation in baited trap CPUE and baited traps are therefore not considered to be a good method for estimating crab abundance.

a)



b)

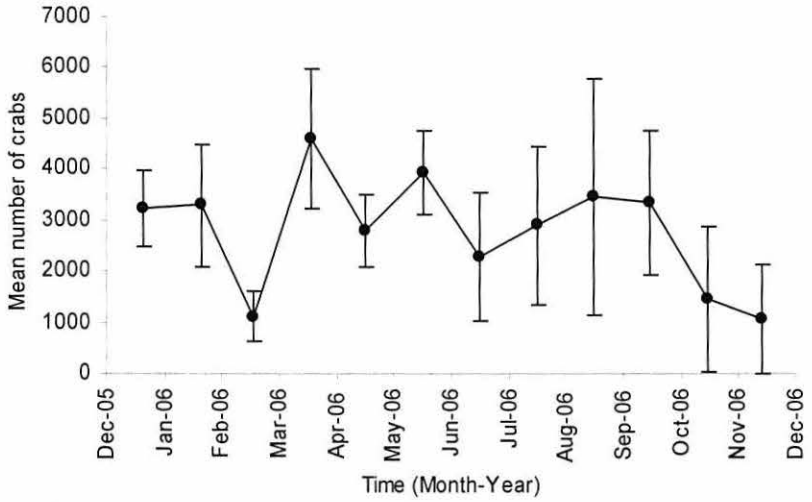


Figure 7.6. Mean catch of *Carcinus maenas* day^{-1} over mussel beds in the Menai Strait during a) 2003/2004 and b) 2006. Error bars indicate ±1 S.E.

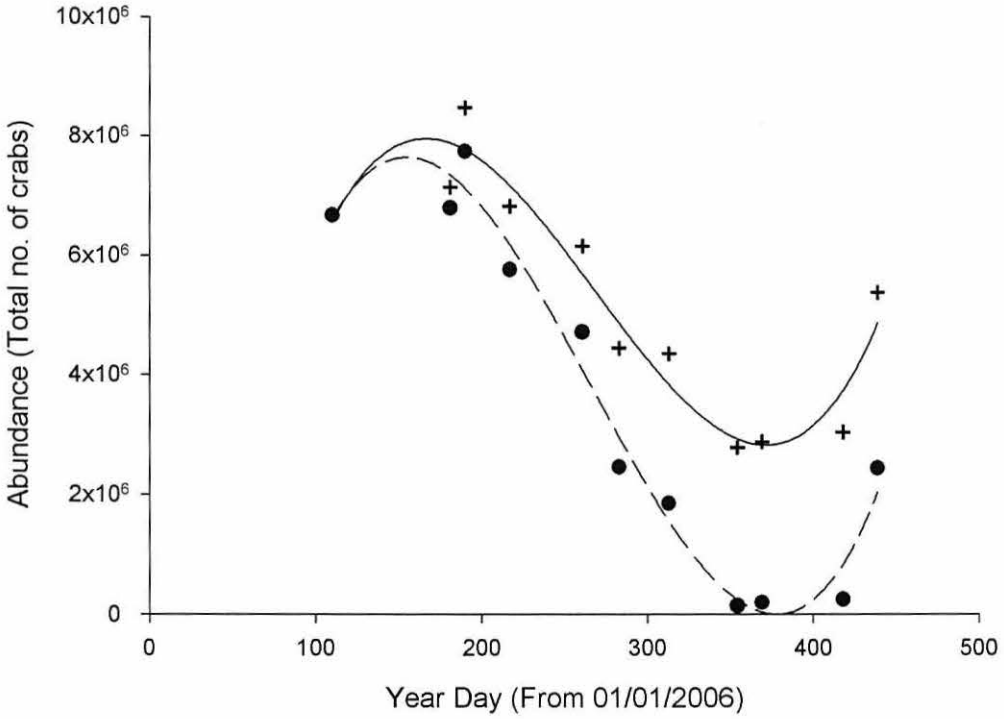


Figure 7.7. Estimated total population of *C. maenas* over the mussel beds in the Menai Strait (•, dashed line) and possible population if no *C. maenas* were removed by the crab fishery (+, solid line).

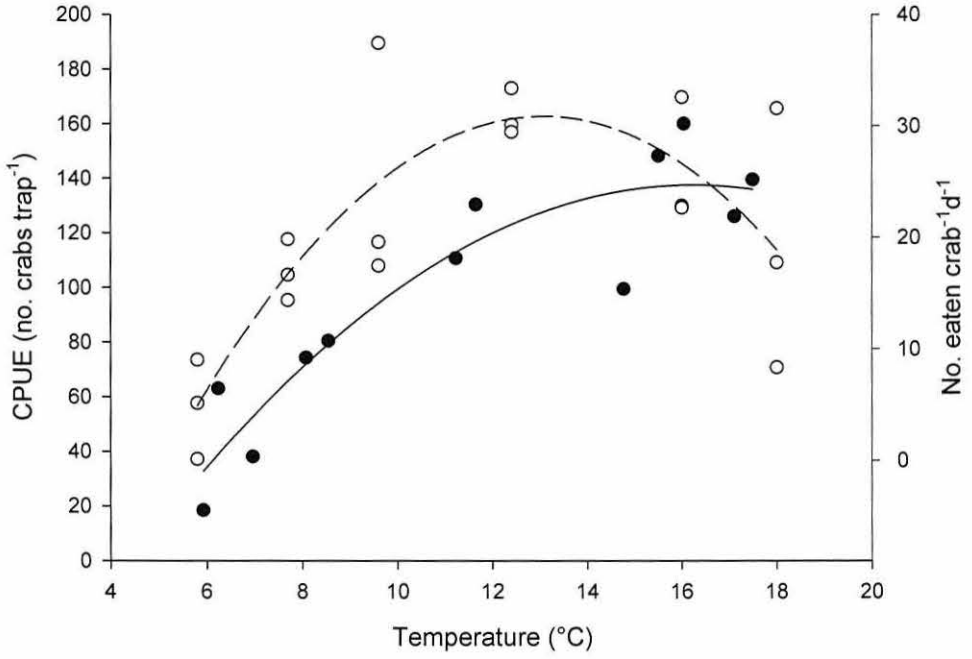


Figure 7.8. Variation in mean monthly CPUE in baited traps (solid) and feeding rates (open) with temperature.

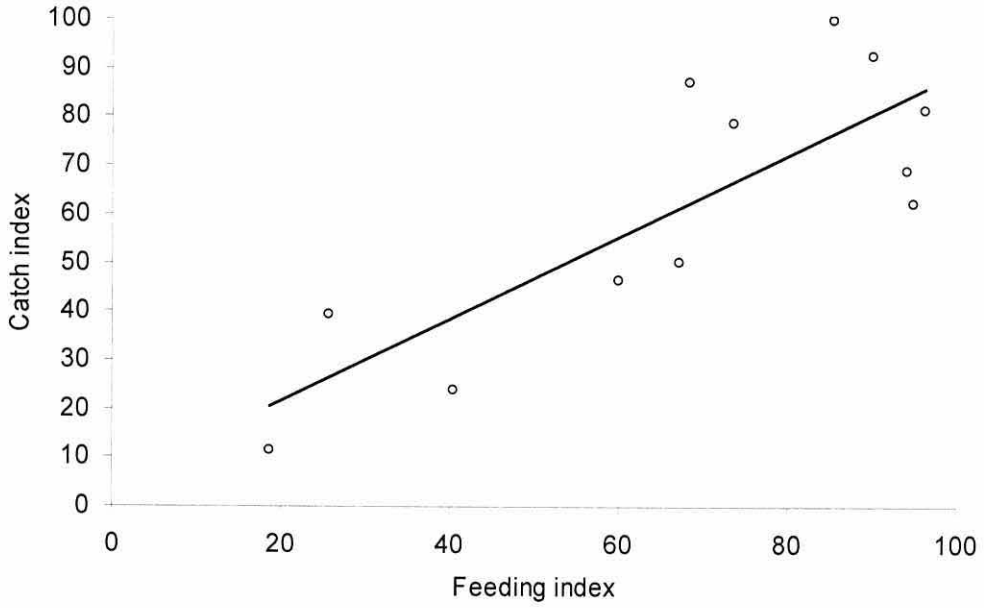
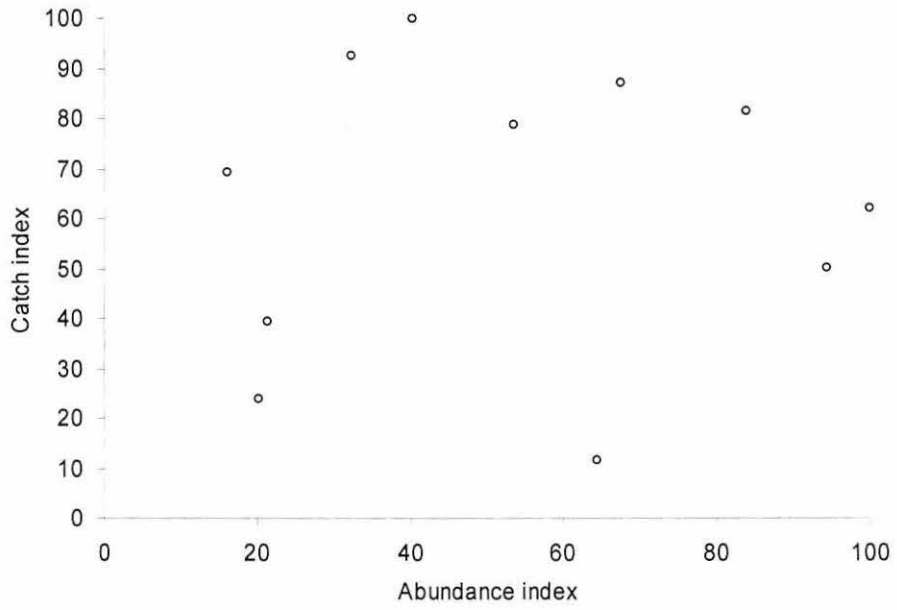


Figure 7.9. Correlation between feeding rates at mean monthly temperatures in the Menai Strait and CPUE in baited traps (y = 0.843x +4.641). Values are standardized to a scale from 0 (No catch/not feeding) to 100 (maximum catch/feeding rates).

a)



b)

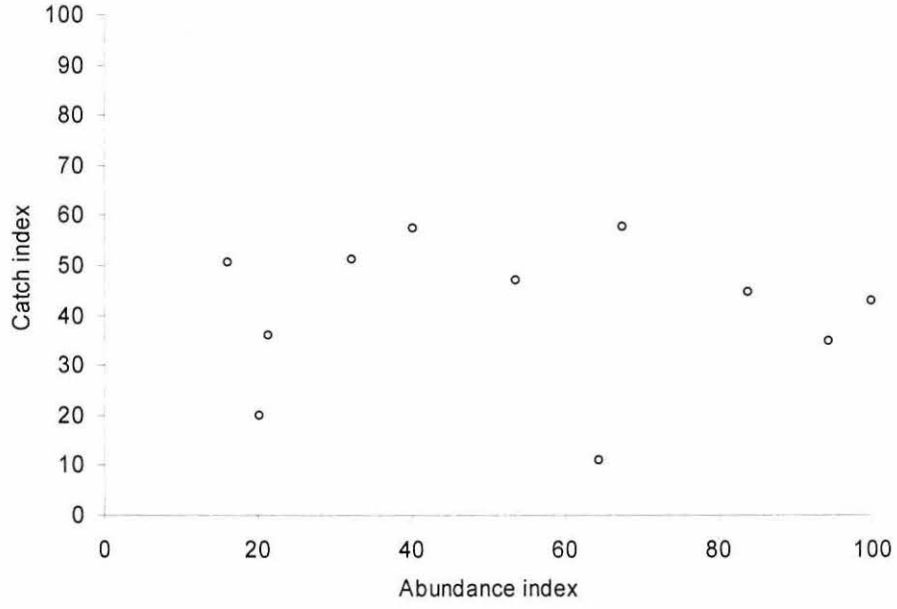
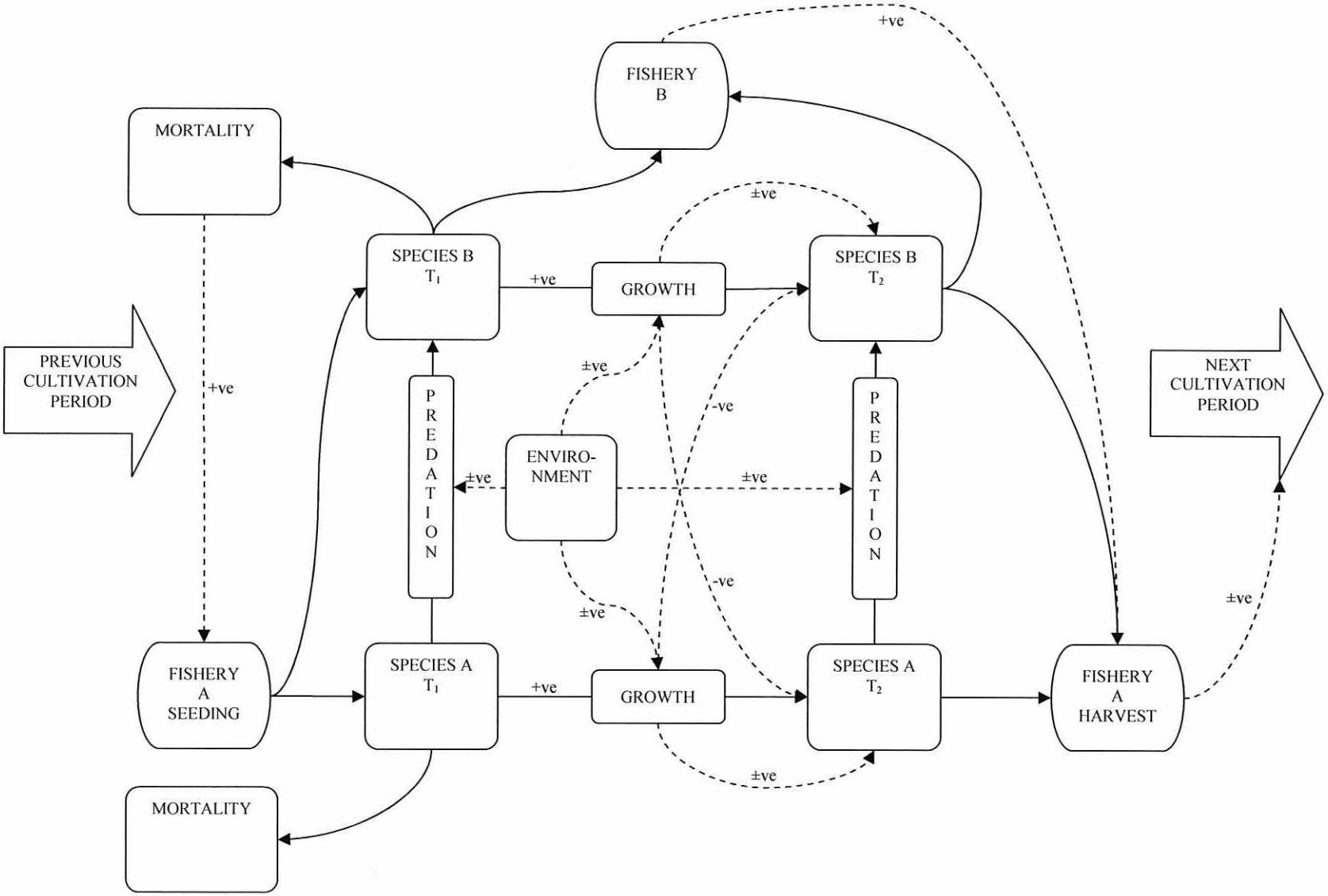


Figure 7.10. Estimated abundance versus CPUE (a) and estimated abundance standardized to maximum feeding rates based on mean monthly temperature versus CPUE (b) in the Menai Strait. Values are standardized to a scale from 0 (No catch/none recorded) to 100 (maximum catch/abundance).

Figure 7.11. Schematic representation of fisheries operating on two trophic levels over time from T_1 to T_2. Solid arrows indicate the transfer of biomass. Dashed arrows indicate other effects (positive or negative). The effects of 'Fishery A' will feedback into 'Environment' and 'Species B' in the next cultivation period. 'Fishery B' operates continuously removing predators causing mortality in 'Fishery A'. 'Mortality' may result from higher predators feeding on both species A and B (highest losses at T_1) together with disease, pollution and physical factors. In terms of the Menai Strait fisheries, 'Fishery A' is the *Mytilus edulis* fishery, and 'Fishery B' is the *Carcinus maenas* fishery but similar interactions are likely to occur between predator and prey fisheries in general.


+ve
FISHERY B
MORTALITY
±ve
SPECIES B T1
+ve
GROWTH
SPECIES B T2
PREVIOUS CULTIVATION PERIOD
+ve
±ve
-ve
NEXT CULTIVATION PERIOD
PREDATION
ENVIRO-NMENT
±ve
±ve
PREDATION
-ve
±ve
±ve
FISHERY A SEEDING
SPECIES A T1
+ve
GROWTH
SPECIES A T2
FISHERY A HARVEST
±ve
±ve
MORTALITY

7.4 DISCUSSION

The crab and mussel fisheries operating in the Menai Strait are closely linked. As mussels grow they attain refuge from some predators; similarly, as predators grow they are able to consume larger prey items. The effect of growth in mussels is clear in Figure 7.5, with a seven-fold decrease in the numbers consumed during the first few months of cultivation, despite increasing crab abundance during this time. Increase in body size was not apparent in the local *C. maenas* population based on the mean carapace width of crabs found during the course of the study. The removal and import of crabs by the fisheries, natural mortality and inward and outward migration to and from the study area may have masked the growth of individuals. Had *C. maenas* growth in body size matched mussel growth then mussel losses would not have declined so rapidly. However, even the largest crabs (~70 mm CW) only consumed small numbers of the largest occurring mussels (>45 mm) due to the greater time required to open these mussels, and thus energy gains will be lower from these large mussels (see Figure 3.4b, Chapter 3). Therefore, any influence on growth in either predator or prey will also influence predation rates. For instance, increasing the stocking density of mussels would result in slower growth rates (Campbell and Newell, 1998) that would in turn prolong the period over which the mussels are especially vulnerable to crab predation. The gain to crabs may then result in their more rapid growth increasing the size range of prey which could be eaten. Increased mussel losses and concomitant lower densities would then encourage faster growth. These sorts of interactions and their cascade effects will occur continuously and may be very subtle, but they will contribute to the overall variability in mussel losses to crab predation. However, assuming that the sum of effects will be neutral, some influences will be positive and some negative for predator or prey, then mean predation levels will remain predictable. Similar interactions will occur in any ecosystem, and are not restricted specifically to crab and mussel fisheries.

Predictions made using models of biological systems are inevitably subject to errors due to natural variability. Throughout the experiments conducted in this

study, some crabs consumed little or nothing, despite being presented with food, while others consumed far more than was typically observed. The results presented in Figure 7.2 show that the accuracy of predictions on feeding rates was high. Therefore, as long as predictions are made based on a reasonably large sample then predictions will be useful in assessing the effects of crab predation on mussel beds.

The mean length of seed mussels collected from Morecambe Bay was 19 mm. Mussels on seed beds that were to be used to stock subtidal beds in Maine were larger (see Chapter 5), with mean lengths of 23 mm and 26 mm at the two different intertidal study sites. The seed beds studied in Maine were not ephemeral, with some mussels over 50 mm in length, unlike the seed mussels collected from Morecambe Bay, which tend not to survive from one year to another. This may partly explain why the Maine fishery does not suffer from excessive crab predation. The cultivation sites in the Menai Strait do not possess established natural mussel populations. The large numbers of crabs found in the seed mussel samples, together with those already present in the Menai Strait are at least partly responsible for the absence of any established naturally occurring local mussel populations; the exceptionally strong currents in the Menai Strait are also probably detrimental to the settlement of mussel larvae.

Mussel losses could be expressed as number of mussels eaten, biomass or energy consumed. Rovero *et al.* (2000) stated that the time taken to handle and consume prey items was the best measure of the cost of feeding, rather then energy, due to the weakening of the relationship between prey size and profitability when energy is the measure of cost. By extension, the number of mussels consumed during a given time would also provide a good measure of size selectivity and feeding rates. In any practical application of the model presented in this study biomass is likely to be estimated from the relationship between mussel length and biomass. Although such relationships are strong (Appendices A5 and B1), there is an error associated with these predictions. As there are good relationships between crab size (and mussel size) and number of mussels eaten, using 'number of mussels' as

a measure of losses is preferable to using biomass or energy as this is what was measured in the experiments presented in Chapter 3.

Losses of mussels to *C. maenas* decrease exponentially with mussel growth (Figure 7.6). Thus to minimize the number of mussels lost to crabs, it is during the first year of growth that most effort should be expended on protecting the mussels, either by increasing predator removal or by using physical barriers to exclude predators (Davies *et al.*, 1980). Reducing seed mussel losses will also require less exploitation of natural seed mussel stocks. However, it is only once mussels reach a marketable size, around 45 mm length, that they have any commercial value. Whilst it is clear that in the Menai Strait only the largest crabs are able to feed on mussels of this size, losses of these mussels total ~6 mussels $crab^{-1}d^{-1}$, amounting to 540 mussels $crab^{-1}$ during the final six month of growth in the subtidal zone. It is during the first year of cultivation that mussels are most vulnerable to crab predation. After the mussels have grown for one year and reached a length of ~31 mm, most crabs in the Menai Strait will be unable to consume them. By the end of the cultivation process <100 mussels d^{-1} are consumed, as they are too large for all but the largest crabs to consume. Relaying seed mussels at a larger size would eliminate the highest levels of mortality caused by crab predation, as is experienced in the Menai Strait, but the longer seed mussels are left at their source the higher the risk of their being lost to storms or predators *in situ*.

There was no clear change in the mean size of *C. maenas* in the local population during the study period, presumably due to the removal and recruitment of crabs from and to the population, in addition to inward and outward migration. The percentage of ovigerous females in the Menai Strait peaked in January, with eggs hatching until May (see Chapter 2). It takes around one year for *C. maenas* zoeae to reach puberty (Crothers, 1967); therefore, young crabs contribute to the increase in numbers observed over the mussel beds from January until summer. Large numbers of crabs, over a range of sizes, are also imported to the Menai Strait with seed mussels. Seed mussels are laid at a density of 50 t ha^{-1} at a mean length of ~19 mm. If no mussels were lost throughout the cultivation process and

mussels reached a mean length of 56 mm their weight would have increased 36-fold, reaching 1775 t ha^{-1}. However, only two to three times the weight laid remain once they have attained a marketable size (pers. obs.); thus, losses amount to ~92-4%. Based on the population size of *C. maenas* from April 2006 to March 2007 and the monthly averages of the number of mussels consumed (Figure 7.6), it is estimated that predation by *C. maenas* accounts for ~10.3% of the losses (~9.5% of the seed mussels laid) over the entire cultivation process. Annual variations in the *C. maenas* population size will alter total losses suffered but mussel size is likely to remain the most important factor in determining crab-induced mortality. Disease, competition, smothering, storm damage, and predation by birds, starfish and other crab species will account for the remaining losses.

It is clear that CPUE is related to feeding rates of *C. maenas*. Both feeding rates and CPUE increase sharply with temperature up to 13-14°C; thereafter, feeding rates decline while CPUE begins to level off (Figure 7.9). There was no relationship between crab abundance and CPUE even when standardized to account for temperature-dependent variations in feeding rates. *C. maenas* and other crab species such as *Macropipus holsatus* undertake annual migrations offshore (Venema and Creutzberg, 1973). Welch (1968) suggested that increases and decreases in *C. maenas* abundance are associated with rising and falling temperature. However, the estimates used by Welch (1968) were based on baited trap catches and the observations of fishermen. There is no doubt that extremely low winter temperatures may result in mass mortality of *C. maenas* and other species (Crisp *et al.*, 1964). Thus, there is a clear advantage in *C. maenas* migrating to deeper water during the winter. Welch (1968) and Naylor (1963) suggested that annual migrations by *C. maenas* occur in response to changing temperature. Atkinson and Parsons (1973) observed that annual migrations by *C. maenas* occurred around 8°C; below this temperature more crabs were observed in the subtidal zone. However, Atkinson and Parsons (1973), like Welch (1968) estimated abundance using baited traps. Thus, although there appears to have been a general consensus that the annual migrations of *C. maenas* occur in response to

temperature, the only studies that support this hypothesis based abundance estimates on catches in baited traps. Had abundance estimates in the present study been based on the CPUE data, the conclusion may also have been reached that *C. maenas* migrated annually in response to seasonal temperature changes. However, in the light of the difference in video-based and CPUE-based estimates of abundance (Chapter 2), the observed relationship between temperature and feeding rates (Chapter 3) and the relationship observed between day length and crab abundance (Chapter 2), it seems likely that *C. maenas* uses day length rather than temperature as a cue for its seasonal migrations and also that CPUE does not provide a good estimate of abundance.

It is apparent, however, that temperature does exert a large influence on the behaviour of *C. maenas*. Tidal and diurnal locomotor rhythms in *C. maenas* can be altered by varying temperature (Naylor, 1958; 1963). Temperature also exerts the greatest effect on cardiac activity in *C. maenas* (Aagaard, 1996), and avoidance of extreme temperatures is probably an important reason for the annual migrations of *C. maenas*, even if this is not the actual cue which initiates migration (see Chapter 2). Avoidance of high temperatures may be as important as avoidance of low temperatures, as offshore migration also begins before the peak in summer temperature (see Chapter 2). The population dynamics of *C. maenas* in the Menai Strait are influenced by the removal of crabs in both the mussel and crab fisheries, as well as the accidental import of crabs with the seed mussels. The annual movement of mussels from the intertidal zone to the subtidal zone may also cause mortality in the *C. maenas* population. In spite of this complexity, it is clear the CPUE of the crab fishery does not accurately reflect the local abundance of *C. maenas*.

Abundance estimates based on CPUE should be viewed with caution. Although CPUE may follow a similar trend to abundance, showing an annual rise and fall, this may be due predominantly to temperature-dependent feeding rates. It has long been recognised that catches using baited traps are dependent not only on abundance but upon the activity of the animal (Crothers, 1968) and traps are

potentially size and sex biased (Williams and Hill, 1982). In the present study, feeding rates are by far the dominant factor in influencing CPUE, which does not reflect absolute abundance. In addition, the distribution of crabs may also affect CPUE and other measures of abundance. Mosknes (2004) identified density-dependent dispersion in juvenile *C. maenas* populations, caused by interference competition for space in nursery habitats, suggesting that this was an important limitation on population size. Cultivated mussel beds provide refuge for juvenile *C. maenas* in the Menai Strait (Chapter 3) but refuges for adult crabs are more limited; thus density-dependent migration may occur in larger crabs over the cultivated mussel beds in the Menai Strait. The crab fishery will undoubtedly prevent some mussel losses. An estimated 2,961,000 crabs were removed by the fishery in 2006 (see Chapter 2). With potential feeding rates of 40 mussels $crab^{-1}d^{-1}$, such a large number of crabs will have caused substantial mussel losses.

In summary, the feeding model presented in this Chapter explained 58 % of the variation in feeding crab rates and was accurate in predicting mean levels of predation. The predation model could be used to predict the effects of other predators on other prey species, greatly reducing the amount of experimental work required to determine the losses of a prey species to a consumer. Most of the mussel losses occurring in the Menai Strait result during the first year of cultivation, in particular during the first few months when mussels are still small and vulnerable to crab predation. Therefore, efforts to remove crabs or protect mussels should focus on the early stages of the cultivation process. CPUE does not reflect *C. maenas* abundance in the Menai Strait. Catches in baited traps are determined largely by feeding rates, which vary with temperature; the relationship between day length and crab abundance presented in Chapter 2 verify this finding. Future studies should therefore not rely on the use of baited traps to assess species abundance. Further investigations are required to determine exactly why *C. maenas* migrates. Although avoidance of low temperatures is likely to be a factor, avoidance of high temperatures may be equally important. Other factors such as predation by over-wintering birds, especially waders, preying on crabs should also be considered. The relative costs (increased energy requirements, risk of predation,

extremes of temperature) and benefits (food supply, higher growth rate) of migrating must also be given further consideration.

In the following and final chapter the results presented in this thesis and the main conclusions that can be drawn from them are briefly discussed. Some management recommendations are made concerning the reduction of mussel losses to crab predation, and important areas of future research are also identified.

CHAPTER 8

GENERAL DISCUSSION

Previous studies have examined various aspects of prey selection by the shore crab *Carcinus maenas* including size selectivity (Elner and Hughes, 1978) and prey preference (Mascaro and Seed, 2000a). Consideration has also been given to losses of mussels to predators during the cultivation process (Dare and Edwards, 1976; Saier, 2001). However, no studies have specifically quantified the impact of shore crabs on commercial mussel beds during the course of the cultivation process. An important aim of the research presented in this thesis was to determine the abundance of *C. maenas* on and around the commercial mussel beds in the Menai Strait throughout the year (Chapter 2). Only by obtaining estimates of absolute abundance could the effects of crab predation upon the mussel populations be determined.

The high densities of *C. maenas* found throughout most of the year over the mussel beds in the Menai Strait undoubtedly represent a major source of mussel losses. Seasonal variation of *C. maenas* abundance was described using a sine wave function. This model of abundance not only helped quantify the variation in crab abundance during the course of this study but it also reduces the quantity of data required to assess the crab population in the future. *C. maenas* was absent from the intertidal zone during the winter but migrated extensively over and around the mussel beds during the rest of the year. These annual migrations appear to occur in response to changing day length, preceding changes in temperature by two months. No other studies have related crab migration to day length; however, crabs do exhibit circadian rhythms (Naylor, 1958) and are more active in darkness (Naylor, 1960). Other animals, particularly birds, use day length as a cue for migration (Gwinner, 1996). Crabs can avoid extremes of temperatures by commencing their offshore migration before the onset of maximum summer temperatures and onshore migration after the lowest winter temperatures. However, large numbers of crabs remain onshore during the

summer months and thus migration of the crab population occurs gradually with densities peaking when day length is greatest and reaching a minimum when day length is shortest. Importantly, the use of day length as a cue for migration makes the movements of crabs much more predictable than if crabs were responding to temperature, which is more variable.

Catch Per Unit Effort (CPUE) in the baited traps used in the commercial Menai Strait crab fishery increased with temperature up to 16°C. Welch (1968), Atkinson and Parsons (1973) and Dare and Edwards (1976) also found significant relationships between temperature and CPUE, but this does not necessarily reflect a relationship between temperature and abundance. In this study there was a significant relationship between feeding rates and CPUE in baited traps, while abundance was not significantly correlated with CPUE; it is likely, therefore, that baited trap catches will be a poor estimator of crab abundance. Most *C. maenas* in the local population on the commercial mussel beds moulted once, with males moulting predominantly in May and females mostly in June. This broadly corresponds with the peak in tidal migration by *C. maenas* in the Menai Strait during June and July (Dare and Edwards, 1981).

Cultivated mussels are often subjected to heavy mortality by several predators, including *C. maenas* (Le Roux *et al.*, 1990; Frandsen and Dolmer, 2002; Floyd and Williams, 2004). In Chapter 3 feeding experiments were conducted, the results of which formed the basis of the predation model presented in Chapter 7. Increasing the mean length of mussels presented to crabs resulted in an exponential decline in the number of mussels consumed. The numbers consumed were greatest at ~13°C, decreasing at higher and lower temperatures. Previous studies examining temperature and feeding rates in crabs failed to establish clear relationships between these variables (Wallace, 1973; Elner, 1980). Metabolism increases linearly with temperature, but feeding rates are not directly related to metabolism (Wallace, 1973; Robertson *et al.*, 2002). For example, *Octopus vulgaris* migrates offshore in summer, possibly to reduce metabolism and thus the requirement for the intake of food (Katsanevakis *et al.*, 2005); shore crabs may migrate offshore for the same reason. The coefficients and formulae presented in this chapter were used, with crab abundance data, to estimate the potential losses

of mussels to crab predation and they could also be used to predict future losses of mussels. The predation model could also be applied to other areas of *Mytilus edulis* cultivation subject to predation by *C. maenas*, and may be used to estimate losses of bivalves to predators in general, although coefficients will differ and some further experimental work would be required to estimate these coefficients for other species.

The results presented in Chapter 4 indicate that *C. maenas* is able to identify the most profitable areas in which to forage and handle prey. Crabs responded to interference from conspecifics by increasing their searching efficiency, with important implications for how populations will be distributed in the wild. The ideal free distribution (IFD) model proposed by Fretwell (1972) is suitable for simple systems where prey is consumed immediately and the predator is not selective. However, the IFD model is inappropriate, in its simplest form, for many other predator prey interactions (Tregenza, 1994), including crabs and mussels, and the tendency to increase searching efficiency in response to competition will further influence the distribution of crabs. Moreover, it allows crabs to adapt to a decrease in resource quality due to greater competition. In doing so crabs will be able to maintain energy intake and growth rates; thus natural selection would favour such adaptive behaviour. Mixing larger mussels with smaller mussels could help to reduce losses from crab predation on cultivation sites. It would be of considerable interest to determine whether the behaviour observed in the present study occurs over larger spatial scales.

Mussel beds harbour numerous species which, in addition to mussels, may be preyed upon by *C. maenas* (Elner, 1981; Raffaelli *et al.*, 1989). Several studies have reported that mussel cultivation results in substantial changes in benthic communities (e.g. Romero *et al.*, 1982; Beadman *et al.*, 2004). *C. maenas* can consume large quantities of mussels as well as others molluscs, annelids and crustaceans (Ropes, 1968; Grosholz and Ruiz, 1995; Mascaro and Seed, 2001). A total of 27 taxa were recorded on the intertidal mussel beds in the Menai Strait (Chapter 5). More taxa (19) were found exclusively in the mussel layer than in the underlying sediments (4) and it is these animals that will be most accessible to crabs. There were no significant differences in the numbers of mussels consumed

by *C. maenas* in the presence of other macrofauna as compared to when mussels alone were presented. Therefore, it can reasonably be assumed that the quantity of mussels consumed by crabs is not affected substantially by the presence of other prey species on the commercial mussel beds in the Menai Strait.

The potential ecological impacts of mussel cultivation, as described in numerous studies (Romero *et al.*, 1982; Stenton-Dozey *et al.*, 1999; Smith and Shackley, 2004), are widespread; however, these studies have focused primarily on the differences in biodiversity between mussel and non-mussel covered areas. The biodiversity associated with cultivated mussel assemblages depends partly on the source of the mussels and on the new habitat created by the method of cultivation (Chapter 6). Changes from polychaete to oligochaete dominated worm communities in the presence of mussels in the intertidal zone have been identified in previous studies (Commito, 1987; Beadman *et al.*, 2004) together with a positive relationship between mussel and oligochaete abundance (Commito and Boncavage, 1989). There was a shift from oligochaete to polychaete dominated worm communities caused by moving mussels to the subtidal zone in Maine, USA, while in the Menai Strait the cultivated intertidal mussel beds harboured high numbers of tubificid oligochaetes. Few amphipod crustaceans were found on subtidal commercial mussel beds or among rope-grown mussels in Maine but they were common on the intertidal commercial beds in the Menai Strait and on the naturally occurring intertidal mussel beds in Maine. Thus, both cultivated and naturally occurring mussel beds can harbour similar fauna. The cultivation method and tidal height (subtidal or intertidal) of a mussel assemblage is likely to be a much greater influence on the associated macrofaunal community composition than whether mussel assemblages are cultivated or naturally occurring and both will potentially be subject to crab predation.

The abundance of crabs in the Menai Strait is potentially subject to high variability. In addition to the predictions made about the impact of *C. maenas* on commercial mussel beds in this thesis the results presented can also be used to reduce the requirement for data collection to make estimates of mussel losses in the future. *C. maenas* abundance can be modelled using cubic or sine wave functions. Thus predictions about the abundance of crabs at any given time can be

made based on estimates of minimum and maximum abundance. Clearly the greater the temporal resolution of abundance estimates the better the predictions about the effects of predation will be. Dare and Edwards (1981) monitored the tidal migration of *C. maenas* using underwater television images and recommended this as a method for assessing the abundance and behaviour of crabs; this technology has also proved invaluable in the present study and is recommended for future studies of crab population dynamics.

Dare and Edwards (1976) recorded mussel mortality rates of 75 – 80% during the first year of growth, falling to 22 – 57% during the second year of growth. From the results of the present study it is estimated that *C. maenas* is responsible for ~10% of the number of mussels lost during the cultivation process. Losses show a significant exponential decline with time, reflecting the parallel decline in crab feeding rates as mussels grow to a larger body size. Although crab abundance and size, as well as seawater temperature substantially influenced the number of mussels eaten, the size of mussels was by far the dominant factor in determining mussel losses. Therefore, efforts to control crab predation should focus on the early stages of the cultivation process and on areas where the smaller, more vulnerable, mussels are present.

Every tonne of mussels imported to the Menai Strait as seed would reach a weight of ~36 tonnes total wet weight during three years of growth assuming that no mussel mortality occurred. Therefore, every tonne of mussels lost during the early stages of cultivation represents a much greater loss after three years of growth, when mussels are ready to harvest. At 2007 prices, mussels are valued at around £500 per tonne. The total weight of mussels harvested annually from the subtidal cultivation areas described in this study typically ranges from 2,500 – 5,000 tonnes. A 10.3% increase in the harvest weight if no losses due to crab predation occurred would therefore amount to between £128,750 and £257,500 over the cultivation process.

In summary, *C. maenas* is clearly a major predator of mussels cultivated in the Menai Strait. Small mussels are particularly vulnerable to crab predation but as they grow to a larger body size they increasingly attain refuge from crab predation.

Therefore, the shore crab fishery should be concentrated around mussels in their first year of growth. In addition, restricting crab fishing to the summer months would represent the most efficient use of this method of predator control. Large numbers of *C. maenas* are inadvertently imported with seed mussels. Removal of these crabs prior to laying the seed mussels would allow an immediate reduction of mussel losses, as well as lessening future predation that results from the imported crabs. Mixing larger mussels with newly laid seed would potentially increase the time crabs spend handling and selecting mussels and thus could help to further reduce mussel losses. Future studies on the seasonal migrations of *C. maenas*, particularly during their offshore winter migrations, would be of especial interest. Establishing the complex relationships that exist between temperature, metabolism, feeding rates and migration is also suggested as a fertile area for future research.

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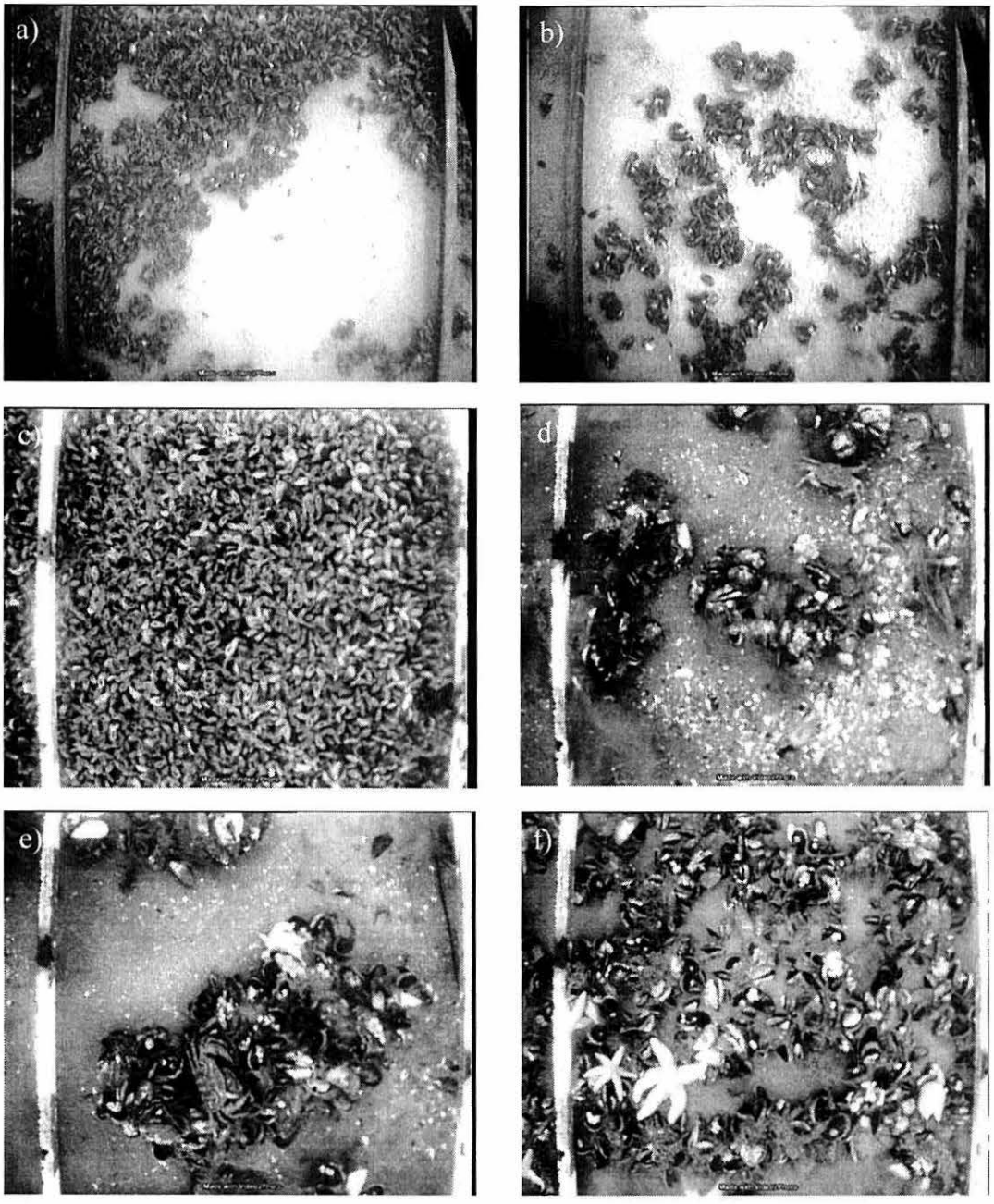
APPENDIX A1

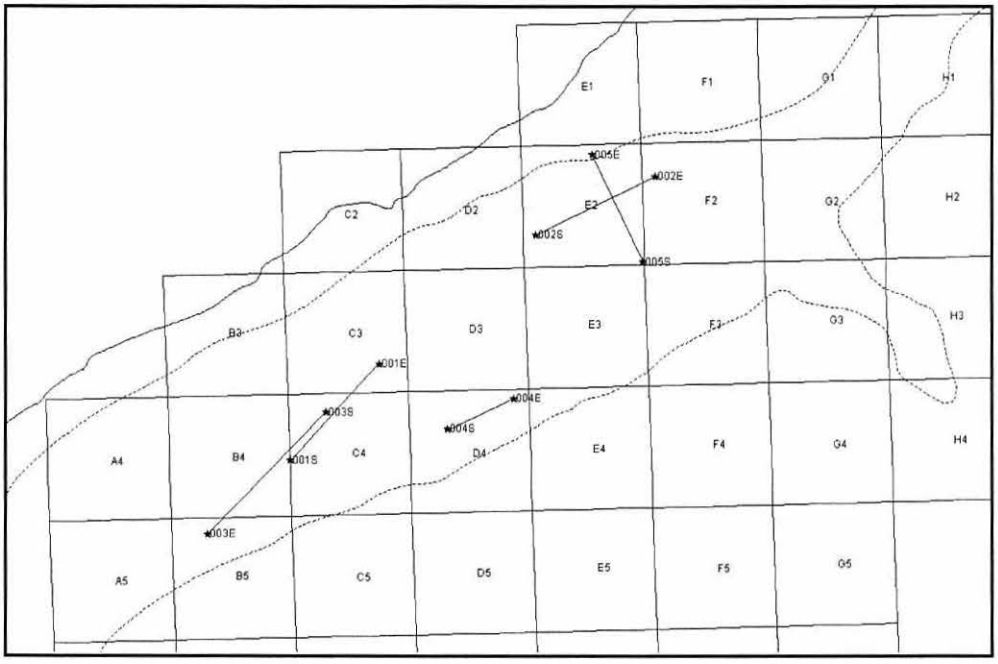
MUSSEL BED IMAGES



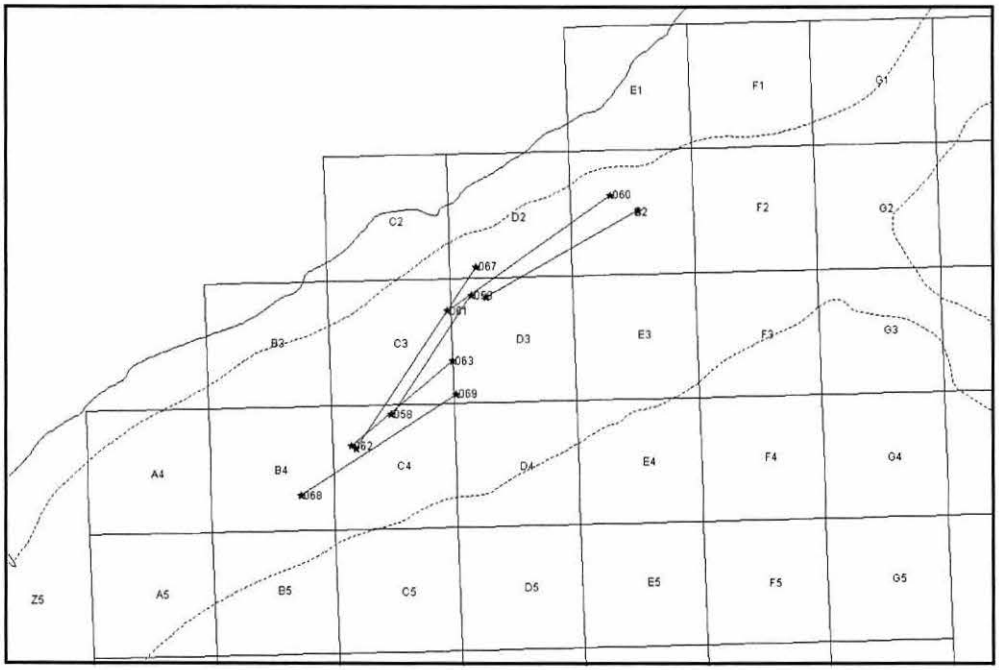
Examples of the images extracted from video footage which were used to estimate the abundance of *C. maenas*. Video was recorded both on and around intertidal (a, b, c) and subtidal (d, e, f) commercial mussel beds in the Menai Strait. The quadrat visible in the images measures 0.5m x 0.5m. *Carcinus maenas* individuals are visible in images b, d and e. *Asterias rubens* is also visible in images e and f.

APPENDIX A2

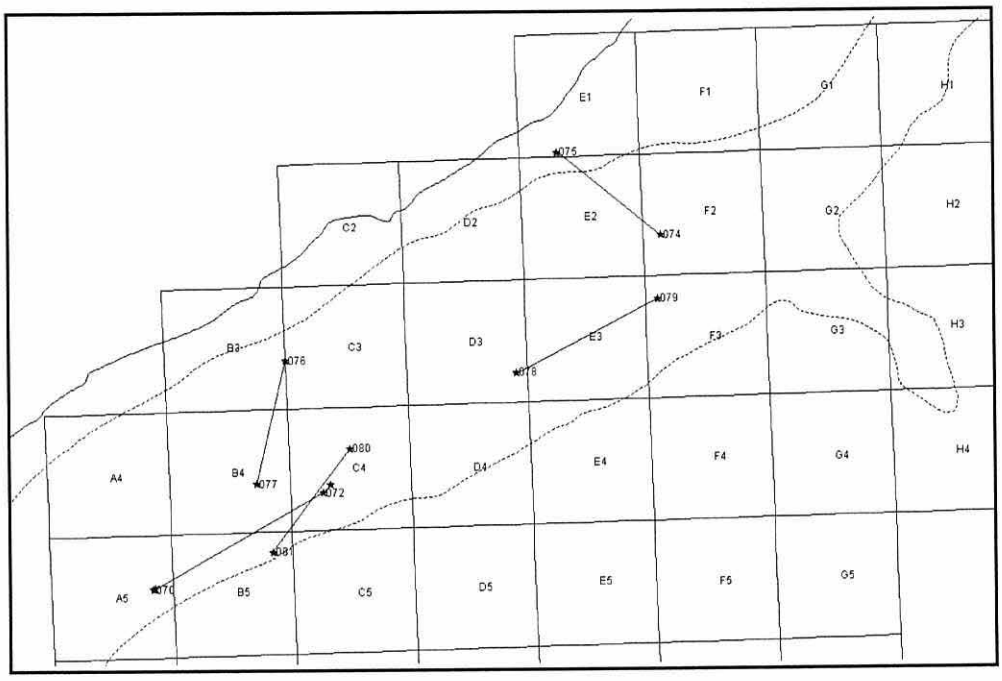
DREDGING LOCATIONS IN THE MENAI STRAIT



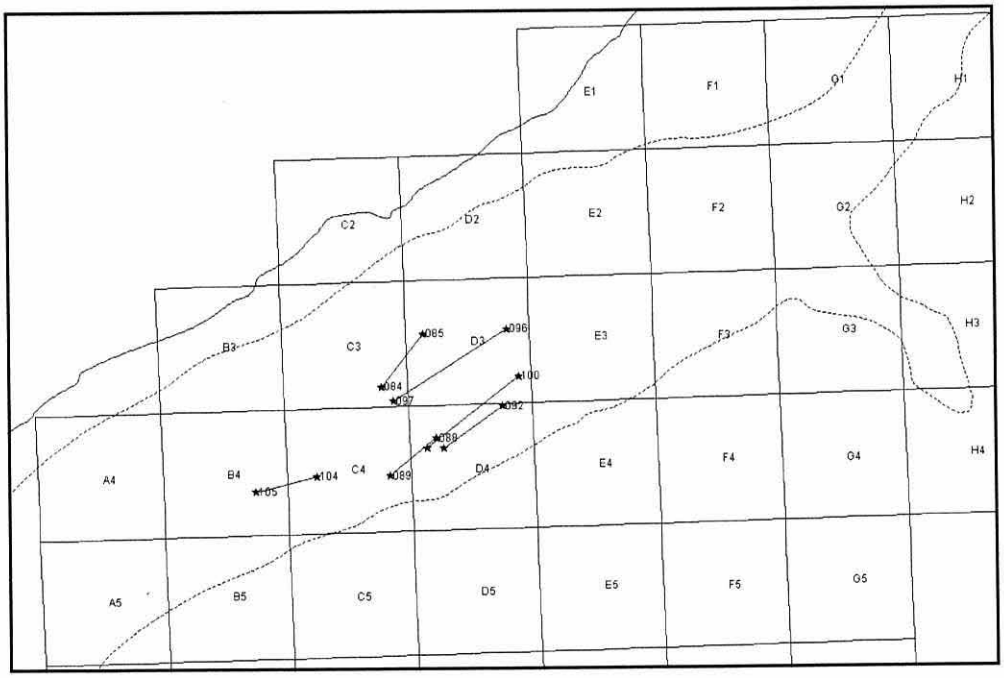
25th January 2006



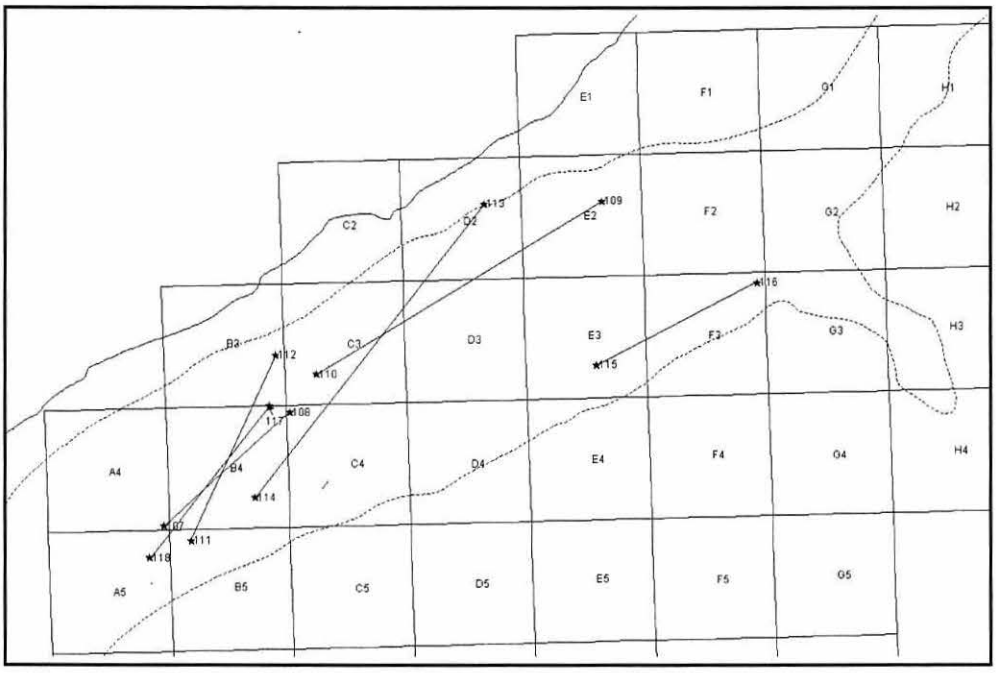
2nd February 2006



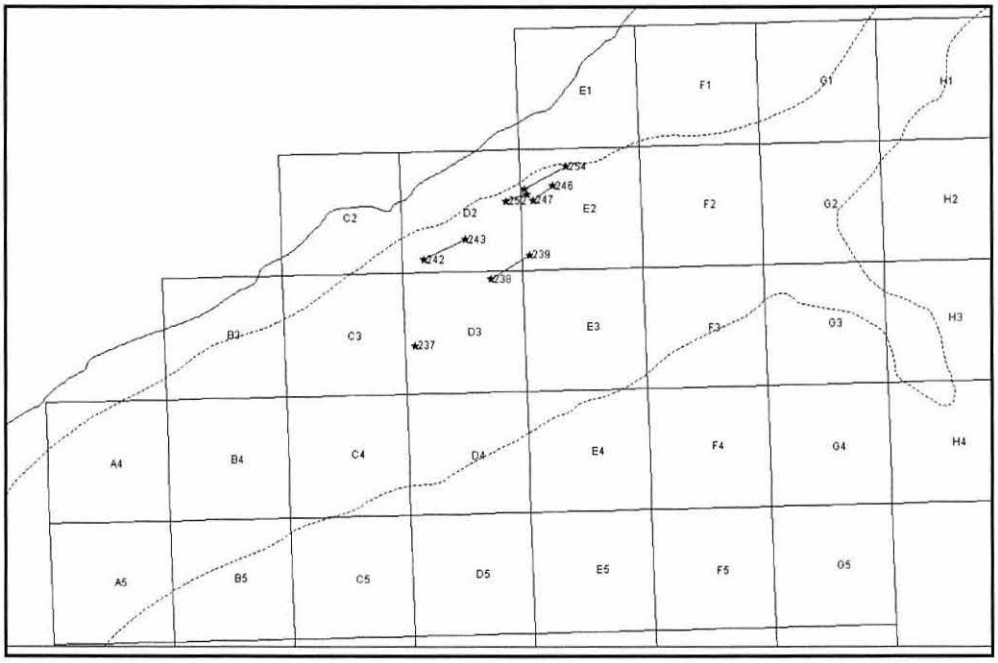
8th February 2006



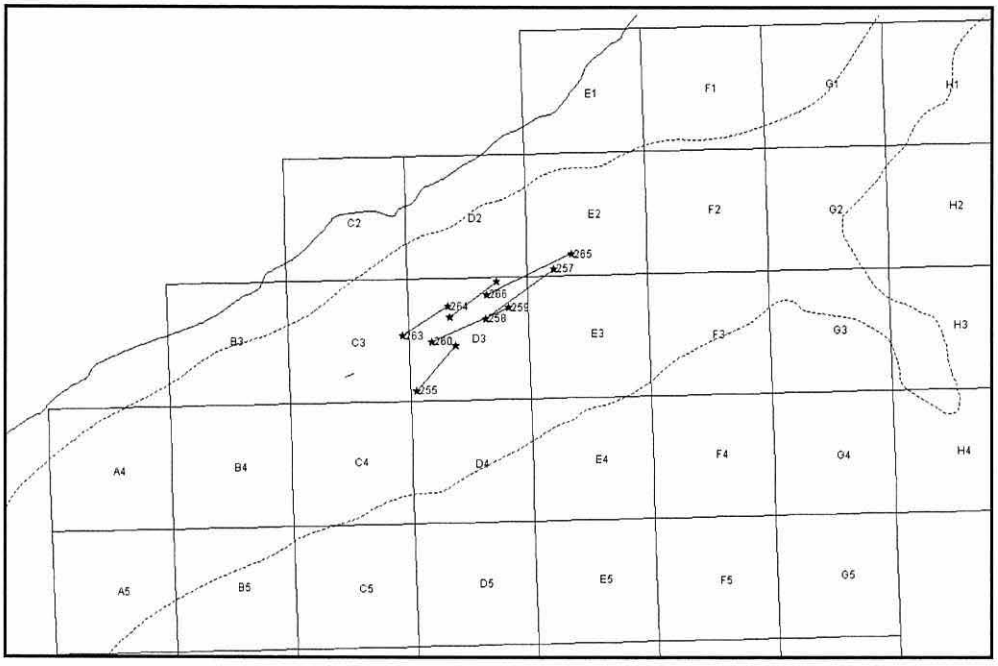
15th February 2006



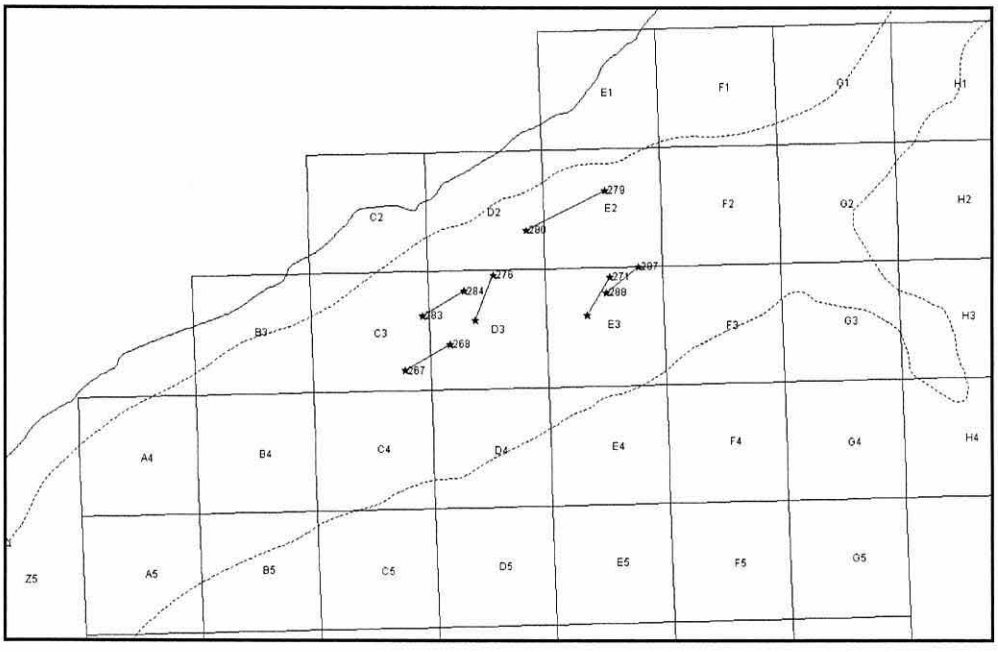
14th March 2006



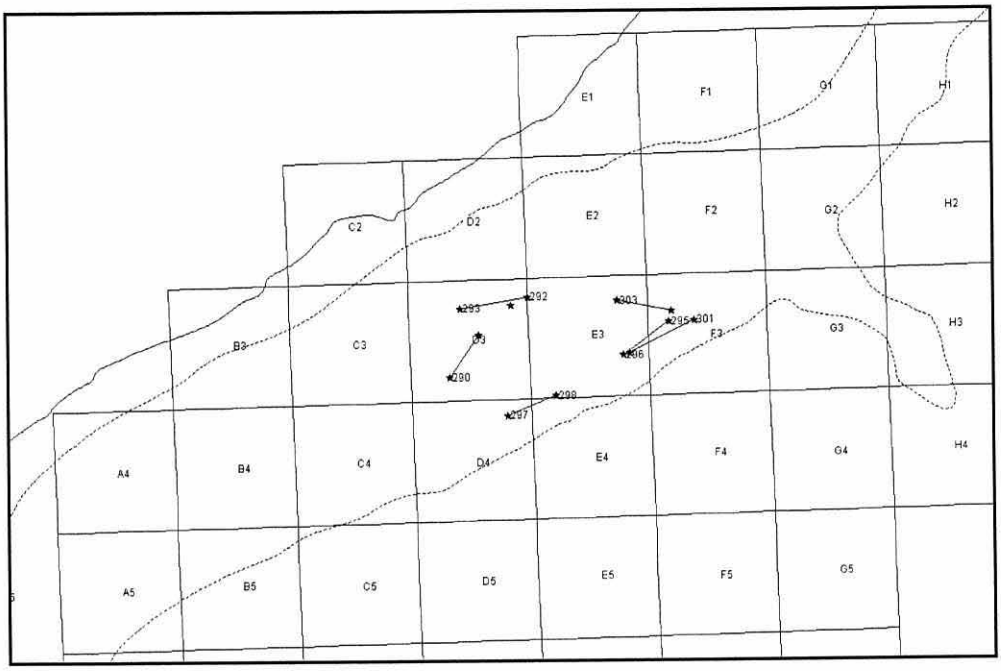
4th October 2006



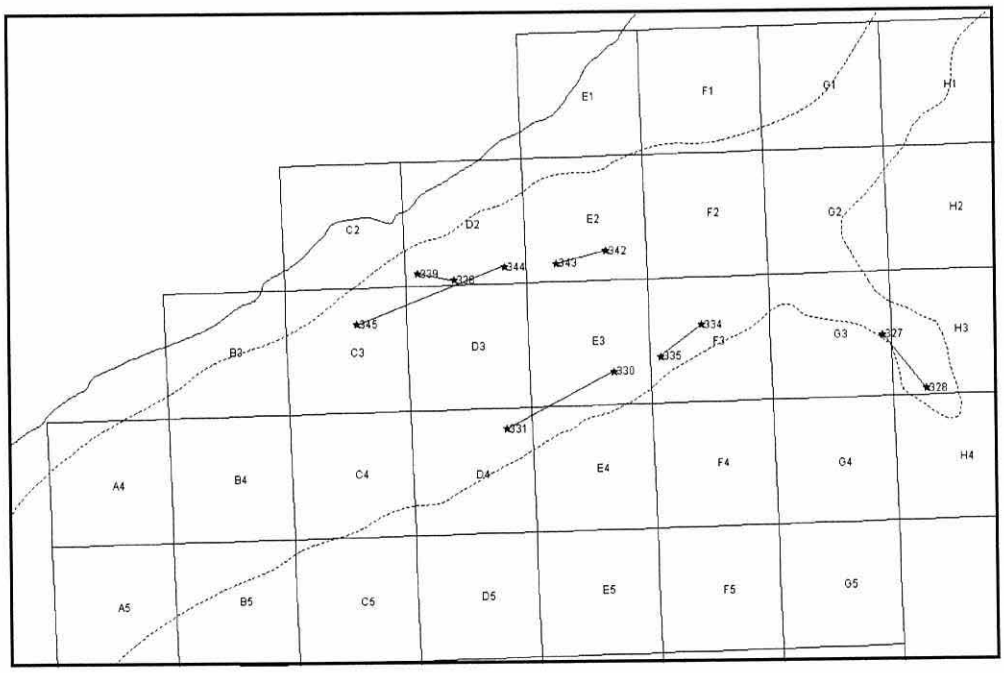
2nd November 2006



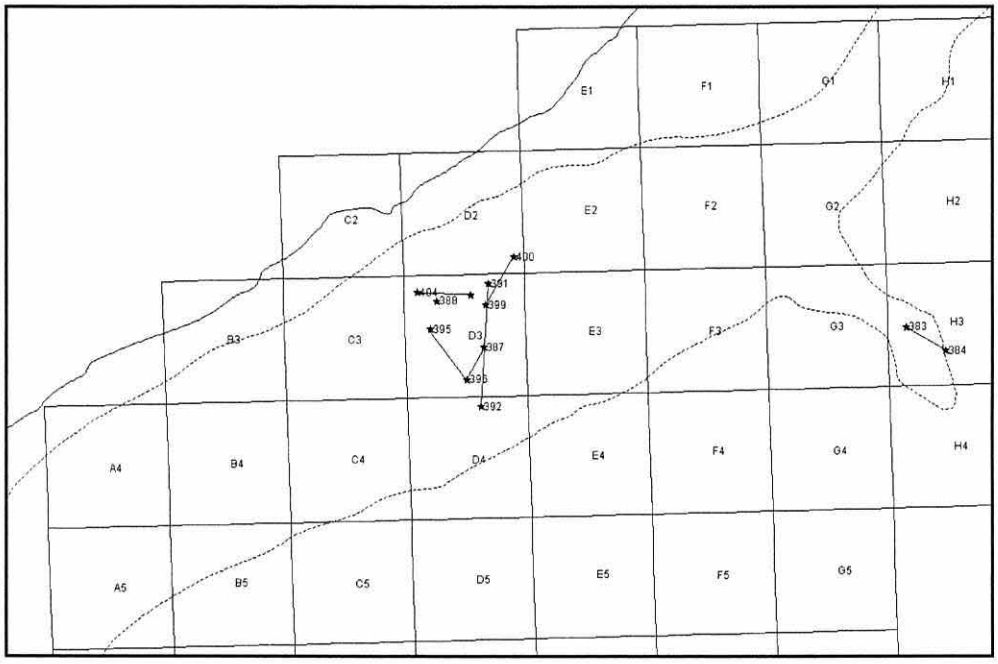
22nd November 2006



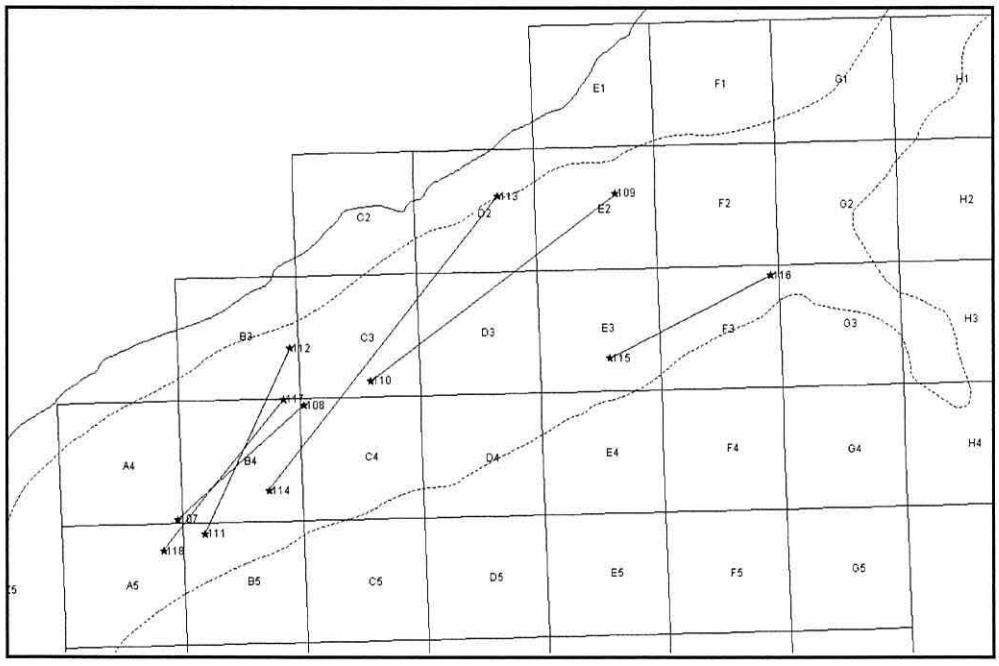
4th January 2007



24th January 2007



22nd February 2007

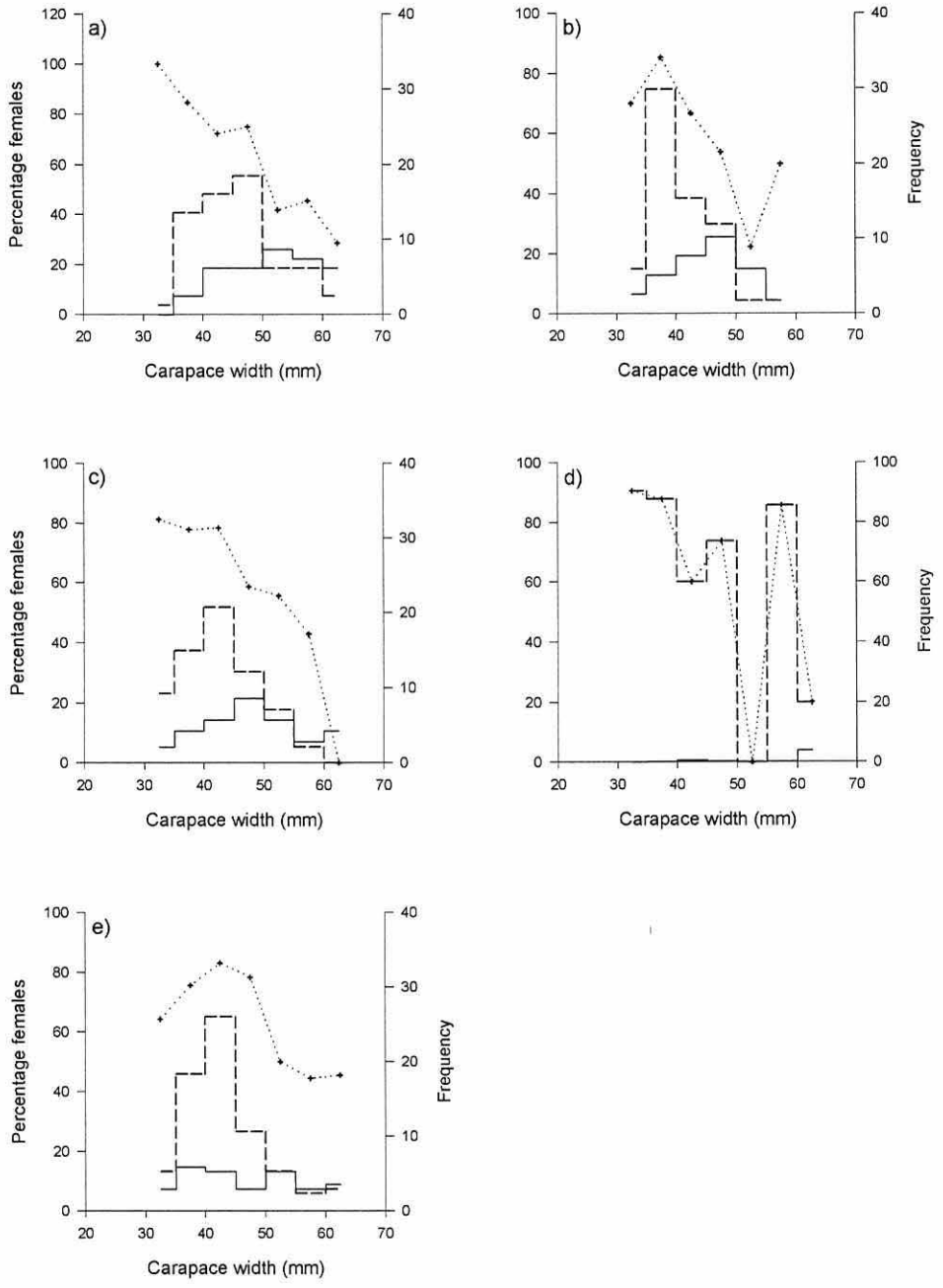


15th March 2007

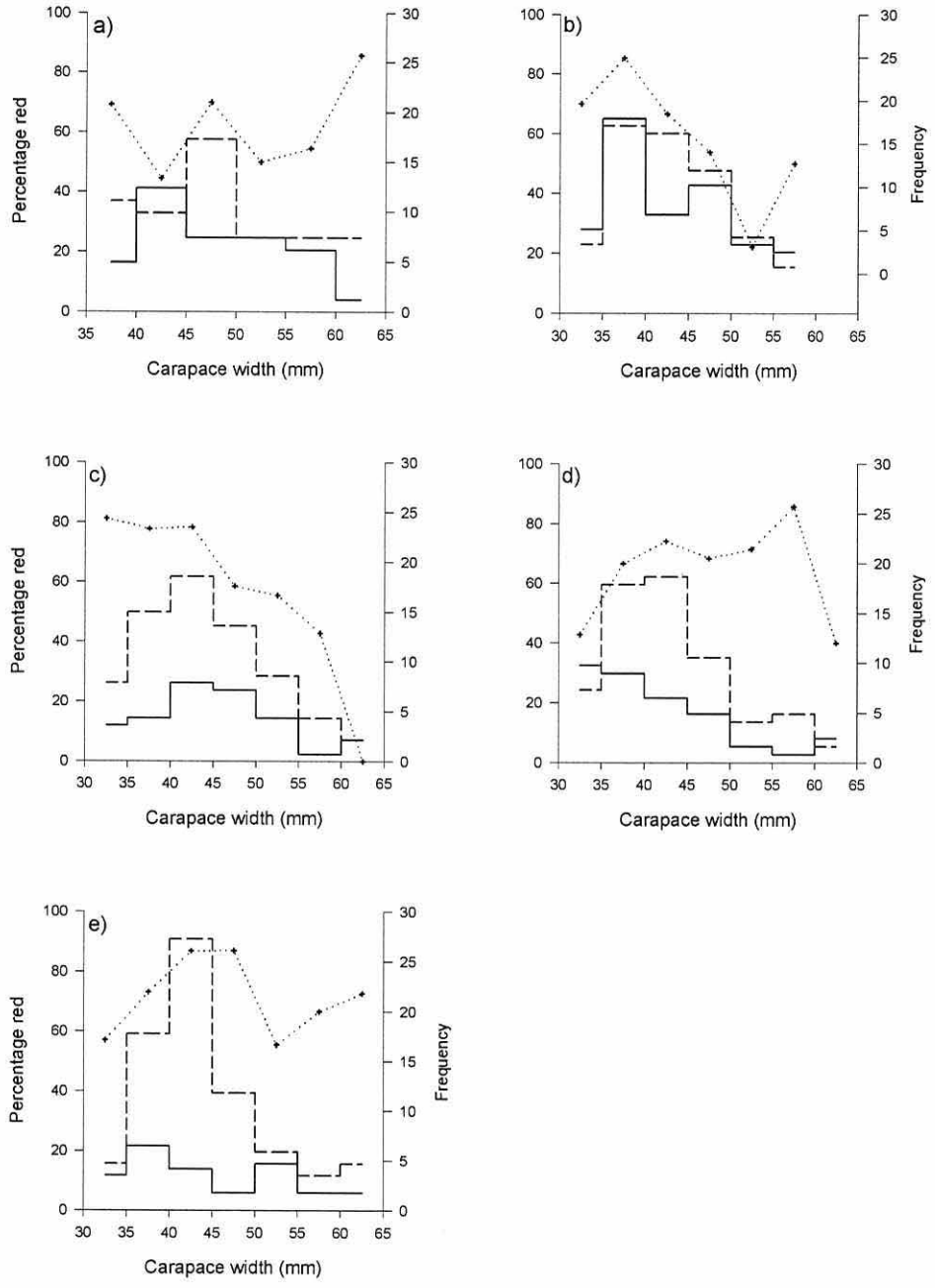
Positions of transects dredged by commercial mussel harvesting vessels on subtidal beds from which crab and mussels samples were collected. Grid squares measure 250 m x 250 m and grid is aligned to the British National Grid. Sampling dates are indicated beneath each image.

APPENDIX A3

CRAB POPULATION STRUCTURE JANUARY TO MARCH 2006



Number of male (solid line) and female (dashed line) *Carcinus maenas* collected on subtidal mussel beds in the Menai Strait, and percentage of females in each sample (crosses/dotted line) on a) 25/01/06, b) 02/02/06, c) 08/02/06, d) 15/02/06 and e) 14/03/06.

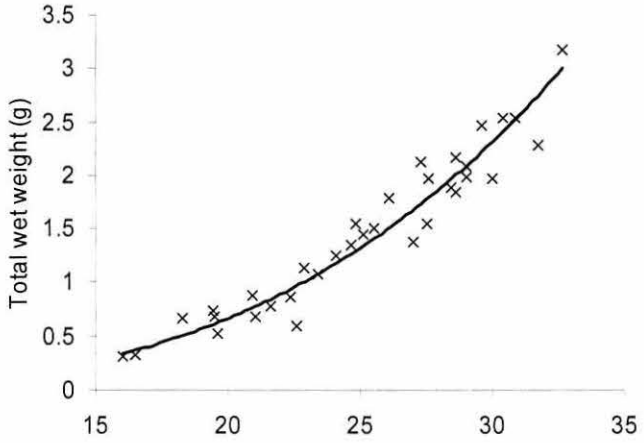


Number of red (solid line) and green (dashed line) *Carcinus maenas* collected on subtidal mussel beds in the Menai Strait, and percentage of red crabs in each sample (crosses/dotted line) on a) 25/01/06, b) 02/02/06, c) 08/02/06, d) 15/02/06 and e) 14/03/06.

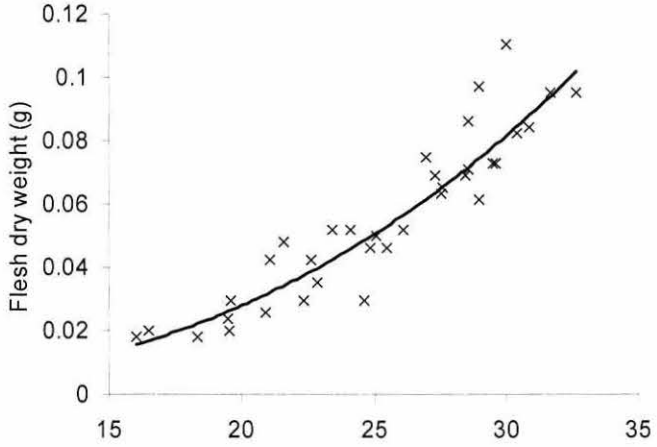
APPENDIX A4

LENGTH-WEIGHT RELATIONSHIPS OF *MYTILUS EDULIS*

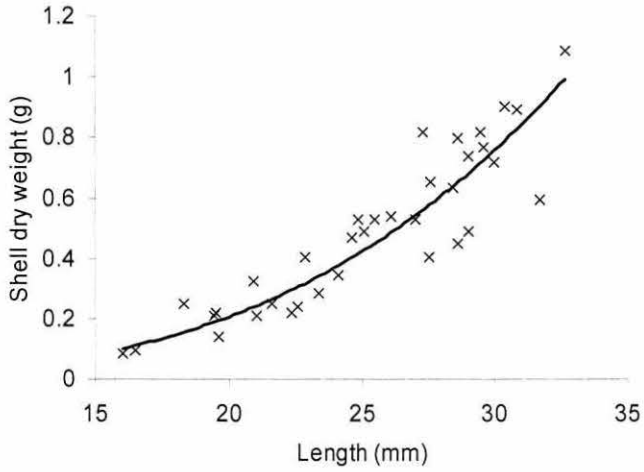
a)



b)



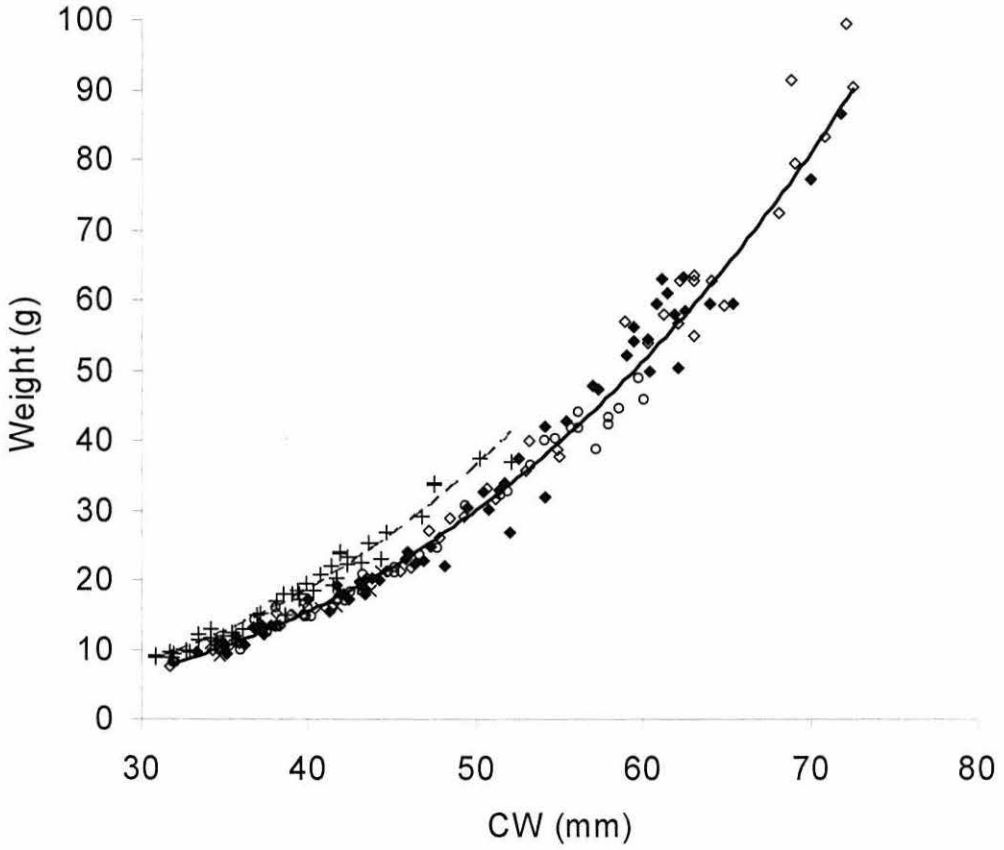
c)



Relationship between mussel length and a) total wet weight ($y = 6.65x10^{-5} x^{3.074}$, $R^2 = 0.934$), b) flesh dry weight ($y = 1.04x10^{-5}x^{2.6266}$, $R^2 = 0.879$)and c) shell dry weight ($1.39x10^{-5}x^{3.2066}$, $R^2 = 0.877$). Mussels were dredged from Morecambe Bay, July 2006.

APPENDIX A5

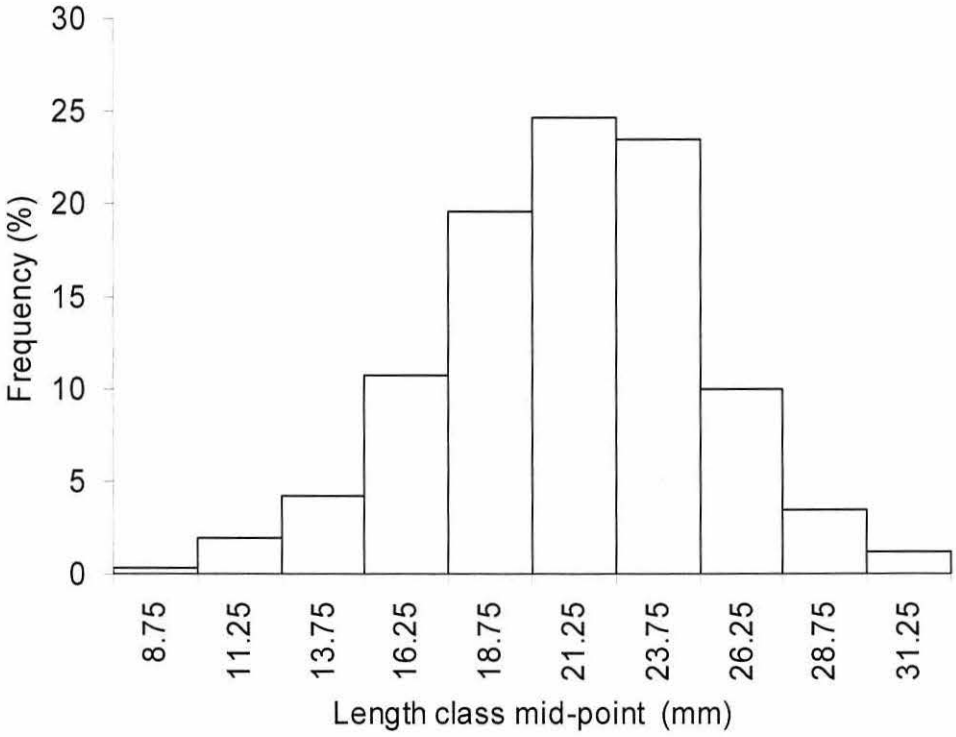
RELATIONSHIP BETWEEN CARAPACE WIDTH AND TOTAL WET WEIGHT IN COMMERCIALLY CAUGHT CRABS



Relationship between *Carcinus maenas* carapace width and total wet weight for green males (◆), green females (×), red males (◇) and red females (○) and ovigerous crabs (+). Power function regression lines were fitted to ovigerous crab data (dashed line; $y = 0.0003x^{2.964}$, 0.972) and all other crab data (solid line; $y = 0.0003x^{2.946}$, $R^2 = 0.987$). Individuals were selected over range of sizes from crabs dredged from the subtidal commercial mussel beds in the Menai Strait.

APPENDIX A6

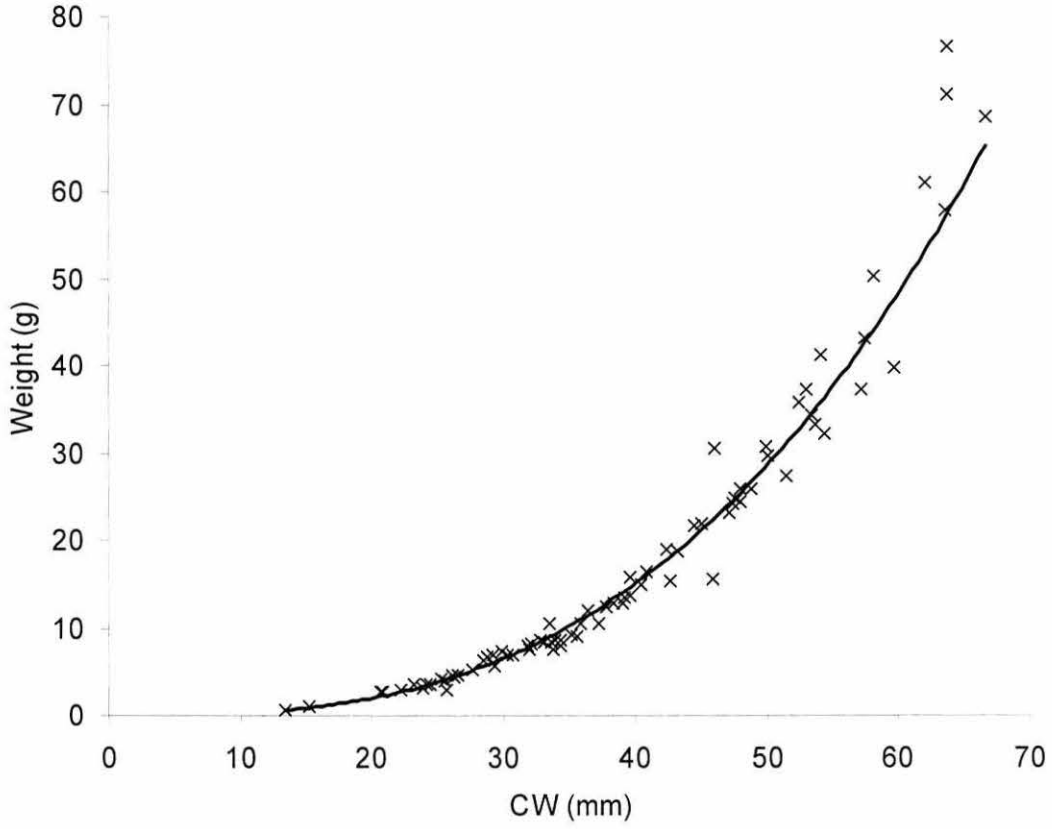
LENGTH FREQUENCY DISTRIBUTION OF SEED MUSSELS



Length frequency distribution of seed mussels collected from Morecambe Bay, July 2006.

APPENDIX A7

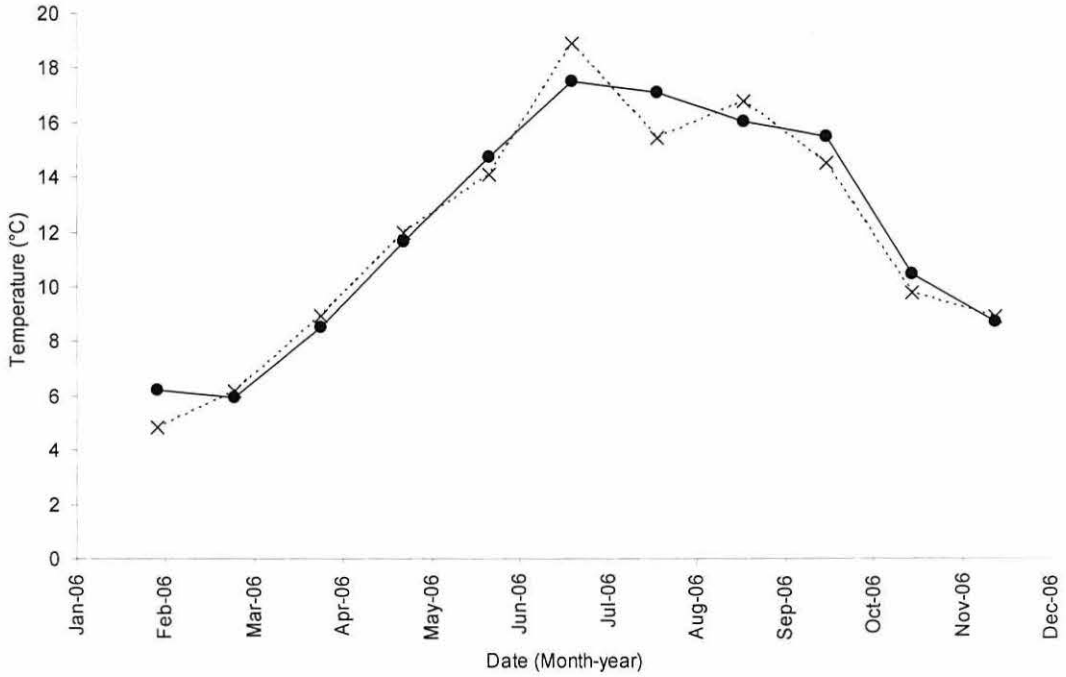
CARAPACE WIDTH-WEIGHT RELATIONSHIPS OF *CARCINUS MAENAS*



Relationship between carapace width (CW) and total wet weight of *Carcinus maenas* ($y = 0.0004x^{2.8735}$, $R^2 = 0.985$, n = 79) contained within seed mussels dredged from Morecambe Bay, July 2006.

APPENDIX A8

SEAWATER AND AIR TEMPERATURES DURING 2006

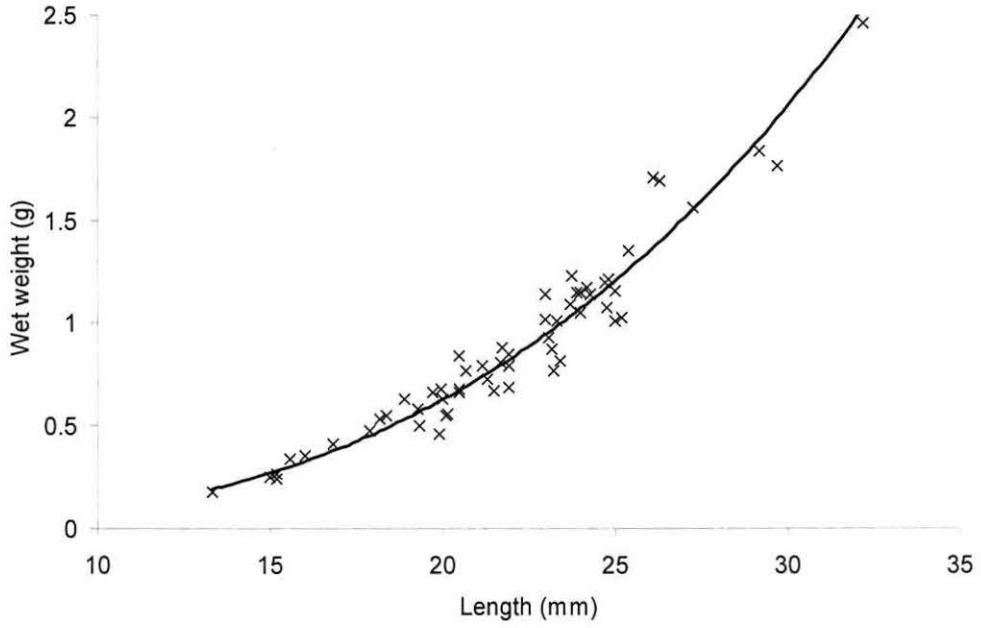


Mean monthly seawater temperature in the Menai Strait, at Ynys Faelog (•) and air temperature at Caernarfon Airport (×).

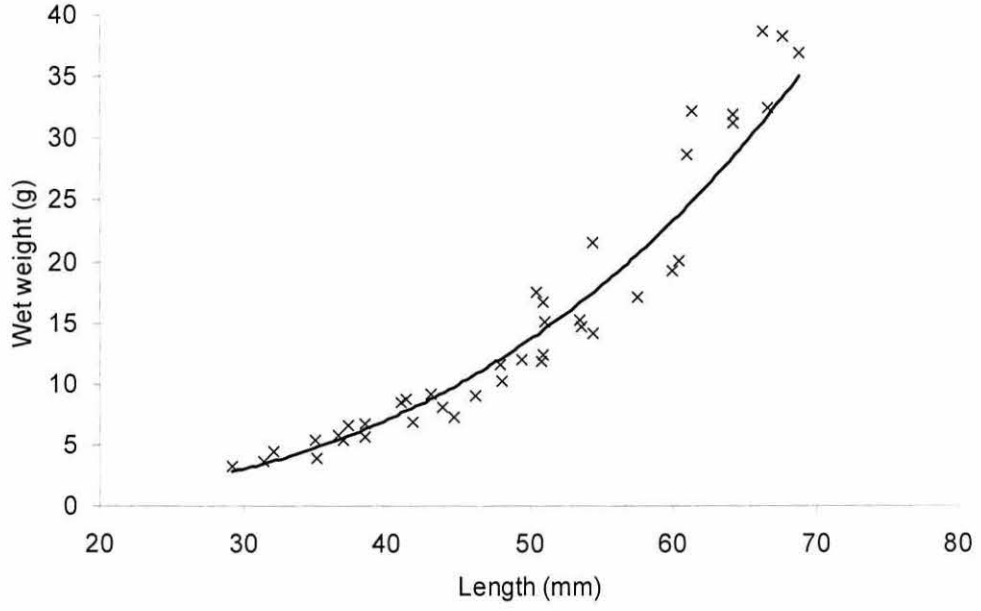
APPENDIX B1

LENGTH-WEIGHT RELATIONSHIPS OF CULTIVATED MUSSELS

a)



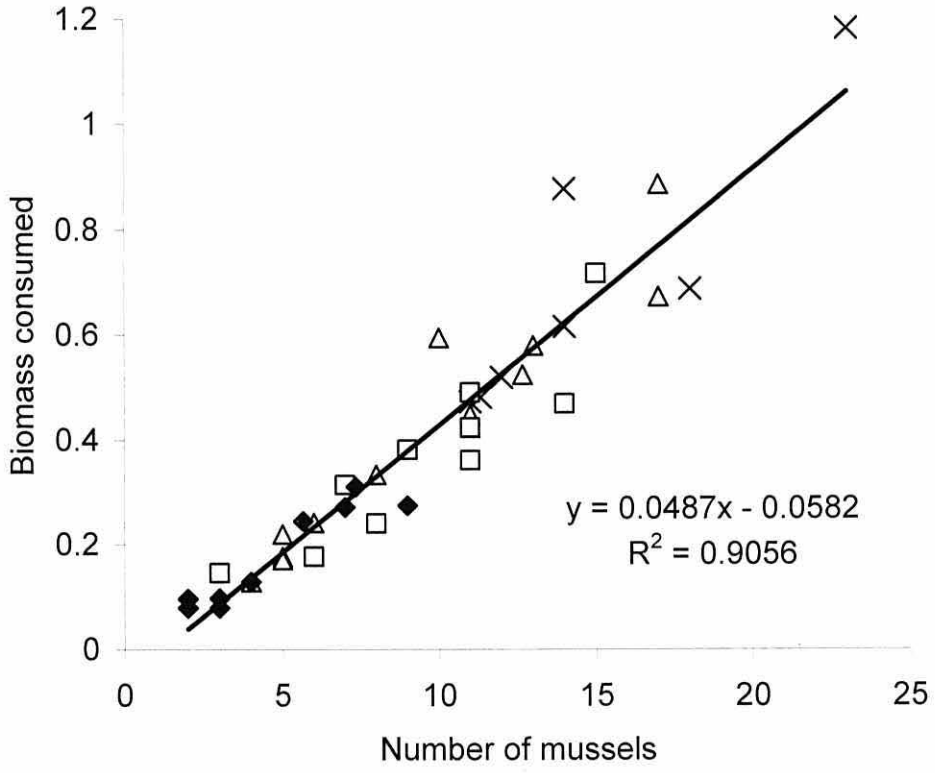
b)



a) Relationship between length and total wet weight of seed mussels collected from intertidal commercial mussel beds (site I1; Figure 2.1) in the Menai Strait ($y = 0.0001x^{2.9156}$, $R^2 = 0.951$, n = 58). b) Relationship between length and total wet weight of mussels collected from intertidal beds at Gallows Point in the Menai Strait ($y = 0.0001x^{2.9514}$, $R^2 = 0.953$, n = 40)

APPENDIX B2

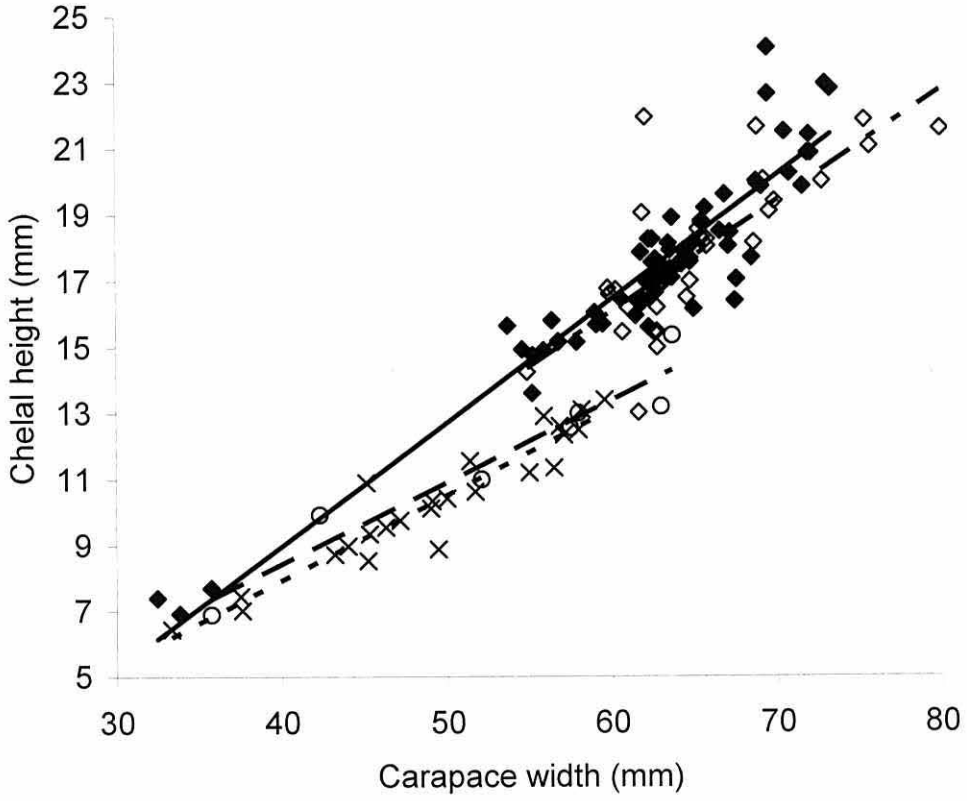
RELATIONSHIP BETWEEN MUSSELS EATEN AND BIOMASS CONSUMED BY *CARCINUS MAENAS*



Relationship between number of mussels consumed by *Carcinus maenas* of varying sizes during 8 hours and the dry flesh weight biomass consumed (y = 0.049x – 0.058, R^2 = 0.906). Symbols indicate crabs of different carapace widths: 30 – 50 mm (◆), 50 – 55 mm (□), 55 – 60 mm (Δ) and 60 – 75 mm (×).

APPENDIX B3

CARCINUS MAENAS CARAPACE WIDTH-CHELAL HEIGHT RELATIONSHIPS



Relationship between *C. maenas* carapace width and mean height of left and right chelae in green males (◆; y = 0.373x – 5.96, R^2 = 0.862), green females (×; y = 0.258x -2.398; R^2 = 0.902), red males (◇; y = 0.334x – 3.985; R^2 = 0.610) and red females (○; 0.248x – 1.476, R^2 = 0.927).