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The sustainability of mussel cultivation

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The sustainability of mussel cultivation

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SUMMARY

This study investigated growth and mortality of mussels, *Mytilus edulis*, cultivated on the seabed in order to suggest new and improved management techniques that would optimise the limited natural resource of seed mussels and hence provide a more sustainable approach to mussel cultivation. In addition the environmental effects of intertidal mussel cultivation on invertebrate communities were considered.

The problems associated with an unpredictable and limited supply of seed mussels was addressed through a novel management technique in which excess seed mussels could be 'banked' at higher tidal levels in times of abundant seed fall, and subsequently moved downshore for on-growth in times of low seed fall.

Mussel growth in terms of shell length and flesh dry weight decreased with increasing tidal height and initial stocking density. Statistical models of seasonal growth and mortality as a function of shore height and initial seeding density were developed for use in the prediction, and hence management, of mussel production at a commercial scale. Additionally, intrinsic mussel mortality through density-dependent effects was addressed to obtain a better understanding of the seasonal relationship between mussed biomass and density.

Mussel cultivation had a significant effect on the invertebrate community of the underlying sediment. This was demonstrated by a change in the composition of species of the infaunal community and, at all but the areas of lowest mussel cover, a decrease in the number of individuals and number of species compared to the control areas. Within the mussel bed itself negative trends of species numbers and abundance of individuals with increased mussel shell area were also demonstrated.

Current and potential management of mussel cultivation through the use of production models was reviewed and discussed. Finally, the implications of this study were discussed in relation to the management of mussel cultivation and the future sustainability of the mussel cultivation industry.

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For their assistance in the execution of this project I would like to thank Kim Mould of Myti Mussels Ltd and Andrew Wilson of Deep Dock Ltd. I also thank the other partners in the LINK-Aquaculture project at the Centre for Ecology and Hydrology, Dorset, in particular Dr Richard Caldow, and the Shellfish Association of Great Britain.

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CONTENTS

LIST OF TABLES AND FIGURES

Chapter 1

General Introduction

ECOLOGICAL ROLE OF MUSSELS

Mussels (Bivalvia:Mytilidae) have a global distribution and are a conspicuous feature of many intertidal and subtidal habitats on both hard and soft substrata (Seed 1976). Mussel beds create a secondary habitat, composed of layers of mussels with accumulated sediment, faeces, pseudofaeces and shell debris, which supports its own highly diverse community (e.g. Tsuchiya and Nishihira 1985; 1986; Svane and Setyobudiandi 1993; Ragnarsson and Raffaelli 1999). The mussel communities have the capacity to both enhance and degrade the infaunal assemblage. Enhancement can occur through the provision of a more complex habitat substratum (on the surface of the mussel shell matrix) and through the production of an organically enriched sediment microhabitat (Tsuchiya 1980; Kautsky and Evans 1987). Degradation of the infaunal community can occur by a reduction in the number and diversity of faunal species due to competition, smothering, anoxia and removal of larvae in the water column through filter feeding (Cowden *et al.*1984; Asmus 1987; Morgan 1992; Wahl 2001).

Wherever they occur mussels are often the dominant organisms in terms of their biomass, and are key factors in the functioning of estuarine and shallow water systems (Herman 1993). The filter-feeding activities of mussels can process large volumes of water (Jørgensen 1990) and consequently the occurrence of mussel beds is an important factor that influences the abundance and structure of phytoplankton communities. The uptake of phytoplankton by large bivalve beds tends to exceed the primary production per m^2 of the seabed (Smaal and Prins 1993). Non-selective feeding by mussels can also skew the plankton community structure towards smaller faster growing species (Prins *et al.* 1995; Noren *et al.* 1999). Small microalgae have an advantage as they grow faster and therefore can out grow, in terms of population numbers, the slower growing larger microalgae (Furnas 1990). This can cause a shift in the population to higher proportions of diatoms (high growth rate species) and declines in relatively slow growing dinoflagellates (Prins *et al.* 1995).

Mussel feeding activities result in a continuous flux of particulate matter from the water column to the bivalve beds, and in many coastal ecosystems clearance time is shorter that the residence time of the water body (Smaal and Prins 1993). As a result of biofiltration and natural sedimentation mussels therefore have a large impact not only on phytoplankton populations, but also on the seston flux in the water column (Dame et al 1991). Hence, through their filter-feeding activities mussels play a central role in the exchange of material between benthic and pelagic systems (Asmus and

Asmus 1993). However, the most important ecological role of bivalve communities in estuaries and shallow coastal waters may be to act as processors and accelerators of the remineralisation of estuarine materials (Dame and Dankers 1988; Dame *et al.* 1991). Nutrients are processed in two main ways, through mussel metabolism and bacterial decomposition of organic material within the mussel bed, which tends to result in higher nutrient fluxes on mussels beds than on sediment without bivalve beds (Smaal and Prins 1993).

Apart from their active function within the ecosystem as a result of their high biomass mussel beds also provide an abundant food source for many predators. Seed mussel beds (composed of mussels < 20 mm in length) may provide a temporary food resource for fish (e.g. flounders *Pleuronectes flesus* and plaice *Pleuronectes platessa*), crabs (e.g. *Carcinus maenas)*, starfish and bird populations (Dare 1976). The main invertebrate predators on established mussel beds in Northern Europe include gastropods, starfish and decapod crustaceans (Seed 1993), while vertebrate predators include birds such as oystercatchers (*Haematopus spp.*) (Meire and Ervynck 1986; Cayford and Goss-Custard 1990; Meire 1993) and eider ducks (*Somateria mollisima*) (Dunthorn 1971; Guillemette *et al.* 1992), fish (Dare 1976) and even seals, walruses and turtles (Seed 1993).

MUSSELS AS A CROP

Mussels are the focus of important global artisanal and commercial fisheries. The wide distribution of mussels has resulted in their cultivation throughout much of the world including Europe, Asia, and North America using a variety of methods such as longline, raft and on-bottom culture (Hickman 1992). The extensive cultivation of mussels has become an activity of growing economic importance (Smaal 1991), with world-wide mussel landings in the year 2000 of 1.3 million metric tonnes valued at over $5.5 billion (FAO 2003). Europe contributes approximately 50% to the global harvest of mussels, although in the last decade European production has decreased relative to the total world production. Further developments in the European mussel cultivation sector depend upon the development of new methods of seed collection and on-growing or an expansion of production areas (Smaal in press).

In 2001 the UK mussel cultivation industry harvested approximately 14 000 tonnes of mussels with a value of over £4.5 million (DEFRA 2003). The Menai Strait in North Wales has been the source of over 75% of the UK mussel production for the past

decade. Mussels are cultivated directly on the substratum in the Menai Strait, whereas most cultivation in Scotland and Ireland is undertaken using long-line raft culture. On-bed culture involves the transfer of seed mussels from areas where they have settled naturally in abundance to lays (culture plots), with more favourable conditions (Mason 1972) where the mussels will benefit in terms of growth (Kristensen and Hoffmann 1991). Once the mussels have grown to marketable size (50 mm in the UK (Dare 1980)), they are then harvested by dredging. This is generally 18 to 36 months after the seed is laid, depending on the tidal elevation of the lay. However, the expansion and continued success of the mussel industry in the UK is constrained by the unpredictable supply of seed mussels (Dare 1980). At present little management is used in the commercial cultivation of mussels to optimise the mussel seed stocks. Survival of these seed mussels is poor as many die from either starvation or are eaten by predators. Furthermore, wild seed settlement is unpredictable such that years of very abundant seed fall can be interspersed with lean years with little or no seed fall.

IMPROVING THE POTENTIAL OF MUSSEL CULTIVATION

Improved management techniques in seabed mussel cultivation need to focus upon optimising the limited seed resource through the achievement of superior mussel growth rates in relation to initial stocking density and position on the shore. The position on the shore in terms of height above low tide will determine the time available for the mussel to feed (Baird 1966). The longer the periods that mussels are exposed to air, the slower their growth rate, and the smaller their ultimate size (Jorgensen 1976). Longer periods of exposure to air increase physiological stress due to wide variations and extremes of salinity, temperature and desiccation (Bayne *et al.* 1976). However, food availability for an individual mussel can also be affected by the presence of other mussels, and there is evidence of food depletion immediately above mussel populations, which can result in the mussels becoming food limited (Frechette and Bourget 1985a; Frechette and Bourget 1985b). The water movement above the mussel bed can be critical, as food is removed from the water column by filter feeders lower on the shore during the incoming tide before it reaches mussels at higher tidal elevations (Peterson and Black 1987). Food depletion has also been demonstrated for aggregations of mussels at high densities in which individual growth rates were reduced (Bertness and Groshoz 1985). Negative effects on mussel growth in dense aggregations have also been suggested to occur as a result of some property of live adjacent individuals (Svane and Ompi 1993; Okamura 1986). The effect of physical

pressure on a mussel shell from neighbouring mussels can result in reduced valve gape leading to reduced growth (Fréchette *et al.* 1992).

These density dependant effects can ultimately result in mussel mortality. Hence, the density of mussels influences the intrinsic mortality rate within a mussel bed and at high population densities self-thinning can occur with an observed negative relationship between individuals per unit area and average individual mass (Hughes and Griffiths 1988). Mortality within the mussel bed will also be influenced by predation pressure, which will vary according to the position of the mussel bed on the shore, with the size of the mussels, the state of tidal inundation and with the time of year. In Northern Europe, the most important predators of mussels located in the intertidal zone are birds (e.g. oystercatchers *Haematopus ostralegus*) and crabs (e.g. *Carcinus maenas*) (Dare and Edwards 1976), since starfish are mainly confined to the area of the shore adjacent to extreme low water spring tides. Crab predation pressure is generally highest in the spring and summer upon mussels up to a size limit of approximately 40 mm (Davies 1966; Hunter and Naylor 1993; Aagaard *et al.* 1995). In comparison oystercatcher predation is greatest in the winter with oystercatchers preferentially consuming the larger mussels from 25-55 mm in shell length (Seed and Suchanek 1992; Meire 1993).

A better understanding of the interacting factors that control the growth and mortality of mussel populations would enable more informed decisions to be made in the management of mussel cultivation. Improved management that sought to optimise the limited natural seed stock would also enable the industry to continue in a more sustainable manner, minimising unnecessary losses that may occur due to overstocking.

In addition to considerations of optimising the stocking strategy for mussel seed, there is an increasing environmental awareness of the potential for negative ecological effects to occur in association with mussel cultivation. Hence the future expansion of the mussel industry may be constrained by consideration of potential environmental impacts in areas that often overlap with other stakeholders. The most direct ecological impact of on-bed mussel cultivation will be on the area onto which the mussels are laid and differences in the faunal community associated with mussel beds compared to that of the surrounding sediments have been demonstrated (e.g. Dittman 1990; Guenther 1996; Commito 1987; Ragnarsson and Raffaelli 1999). Failure to quantify the scale and significance of such changes may unduly impede

expansion of the industry as a result of objections on environmental grounds and advocates of the precautionary principle. It is therefore essential that these direct impacts should be determined, together with possible consequences for birds that feed on intertidal areas and subsequently excluded from these areas through the activities associated with mussel cultivation.

The research presented herein was intended to yield data and models that would:

- improve the yield of marketable adult mussels from re-laid seed mussels in the intertidal zone by suggesting new management techniques and optimising stocking density, which would consequently maximise growth rate and reduce predation losses from birds and invertebrates.
- ascertain the environmental effects of intertidal mussel cultivation on invertebrate and avian communities.

The problems associated with an unpredictable and limited supply of seed mussels is addressed through a novel management technique (Chapter 2). Mussel growth (Chapter 3) and mortality (Chapter 4) over a range of initial seeding densities and shore heights are investigated through a large scale experimental approach in order to develop statistical models to aid in the prediction, and hence management, of mussel production at a commercial scale. Additionally, intrinsic mussel mortality through density-dependent effects is addressed to obtain a better understanding of the seasonal relationship between mussed biomass and density (Chapter 5). A study of the environmental impacts of mussel cultivation on the invertebrate community of the mud flat was run concurrently with the growth and mortality experiments (Chapter 6). In conjunction with this project the Centre for Hydrology and Ecology carried out a study to assess the impact of mussel cultivation on the bird populations of the Menai Strait. Current and potential management of mussel cultivation through the use of production models is reviewed and discussed with recommendations made for future research to improve the management and sustainability of mussel cultivation (Chapter 7). Finally, the implications of this study are discussed in relation to the management of mussel cultivation and the future sustainability of the mussel cultivation industry (Chapter 8).

In writing this thesis my intention was that each chapter should stand on its own in a format suitable for publication, whilst attempting to avoid excessive repetition.

The following chapters have already been published:

Chapter 2: Beadman, HA, RWG Caldow, MJ Kaiser and RI Willows (2003) How to toughen up your mussels: using mussel shell morphological plasticity to reduce predation losses. Mar Biol 142: 487-497.

Chapter 7: Beadman, HA, RI Willows, and MJ Kaiser (2002) Potential applications of mussel modelling. Helgoland Mar Res 56: 76-85.

Chapter 2

How to toughen up your mussels: Using mussel shell morphological plasticity to reduce predation losses

This work has been published in Marine Biology, Vol.142, pp487-497.

The work conducted on the bird populations was carried out by Dr RWG Caldow, Centre for Hydrology and Ecology, Dorset.

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ABSTRACT

Improvements in stocking strategy and management could increase the yield of mussels that are on-grown from harvested wild seed mussel resources and thereby enhance the sustainability of this shellfishery. A field experiment was undertaken to ascertain shell characteristics (compression strength and thickness) of seed mussels grown at different shore heights, whether these characteristics changed after a period of growth under identical conditions and if these characteristics reduced predation losses by crabs and birds. Results indicated that over the experimental period mussels grown at higher shore levels attained thicker shells of greater compressive strength that were beneficial to predation resistance and these characteristics were maintained after a period of growth at a lower shore level. A novel management plan for mussel cultivation was formulated from the results of this study by manipulating shore position according to the attainment of these predator resistant shell attributes and the spatial distribution of the main natural mussel predators (crabs and birds). This technique was expanded to address the mussel cultivation problem of low natural seed settlement.

INTRODUCTION

Mussels (Mytilidae) are susceptible to a range of subtidal and intertidal predators irrespective of whether they occur naturally or are cultivated on the seabed. The most important predators of mussels are predatory gastropods (e.g. dogwhelks (*Nucella lapillus* L.), starfish (e.g. *Asterias rubens* L.), crabs (e.g. *Cancer pagarus* L. and *Carcinus maenas* L.) and shore birds (e.g. oystercatchers *Haematopus ostralegus* L.) (Seed 1969). Understanding the mechanisms of predation and the factors that affect predation rates are of interest to cultivators of mussels who lose a substantial proportion of their crop to such predators (Dare and Edwards 1976). In this chapter the effects of a variety of alternative mussel cultivation options on the susceptibility of mussels to predation by shore crabs *Carcinus maenas* and oystercatchers *Haematopus ostralegus* are explored, and a novel mussel cultivation strategy that may be of considerable value to the commercial shellfish industry is suggested.

The relative magnitude of the predation pressure exerted on mussels by the various predatory species varies with the position of the mussel bed on the shore, with the size of the mussels, and with season. Starfish are prevalent in the subtidal and lower intertidal zones, oystercatchers only in the intertidal zone, whereas crabs feed in both areas by migrating form the subtidal into intertidal areas on the rising tide. Crabs are generally more active in the spring and summer (Hunter and Naylor 1993; Aagaard *et al.* 1995), whereas oystercatchers have a greater effect in the winter when large flocks gather in the coastal zones of northern Europe (Seed and Suchanek 1992). The impact of predation by the various predators also varies depending on the size of the mussels. Smaller mussels (less than 40mm in length) suffer disproportionately high losses from crabs, since all size ranges of crabs can crush small sized prey (Seed 1976) and with a reduced handling time compared with that required for larger mussels (Elner and Hughes 1978). Above 40 mm in length mussels attain a relative size refuge from crabs (Davies 1966). In comparison oystercatchers preferentially consume the larger mussels from 25-55 mm in length (Meire 1993). Thus, the size at which mussels are laid for cultivation and the position on the shore at which they are grown are likely to influence losses to predation.

Mussels utilise various defence mechanisms to reduce predation risk. These include the development of larger adductor muscles to increase opening time in response to high starfish predation (Reimer and Tedengren 1996), and stronger attachment to the

substratum using byssus threads in high crab predation sites (Coté 1995; Leonard *et al.* 1999). The primary means of protection from predation is, however, the shell, which mussels can modify to increase its protective capabilities. Thicker shells (Leonard *et al.* 1999; Reimer and Tedengren 1996), higher compressive strengths (Elner 1978) and thicker shell lips (Smith and Jennings 2000) are attributes of mussel shells reported from areas of high predation. A relatively thicker shell also confers an advantage to mussels in terms of protection from predation by oystercatchers that hammer mussel shells until they break (Hulscher 1996). These birds exhibit strong selection for mussels that have a thin shell (Durrell and Goss-Custard 1984; Meire and Ervynck 1986; Sutherland and Ens 1987; Cayford and Goss-Custard 1990). Clearly, the physical characteristics of mussel shells influence their susceptibility to predation by animals that use physical force to open them. Thus, any cultivation practice that can manipulate mussel growth to promote the development of thicker shells may be beneficial in reducing losses to predation.

In the UK the two principal methods used for the commercial cultivation of mussels are to grow them suspended on ropes and to lay them directly onto the seabed in low intertidal and subtidal areas. In both cases, the mussel farmer ultimately depends upon wild sources of small 'seed' mussels (these are mussels up to a size of approximately 25mm in shell length). The expansion and continued success of the mussel industry in the UK is constrained by the unpredictable supply of these seed mussels. One possible solution to this problem may be, in times of abundant, natural mussel settlement, to lay seed on high shore areas where they can ongrow. These areas are not used for cultivation under normal circumstances, as growth of mussels at high elevation is impeded (Bertness and Grosholz 1985; Seed 1969). In subsequent years, when natural settlement is low and the supply of wild seed is limited, these mussels could then be transferred down shore or subtidally to enhance growth to marketable size. Thus this would provide a more sustainable approach in mussel cultivation that depends on the natural mussel seed resource. This high shore level 'banking' may be a particularly valuable strategy if the rates of predation at higher shore levels during the banking period are low and result in lower rates of loss following transfer downshore because of an increase in mussel size and the development of thicker shells.

The aim was to determine whether: a) seed mussels grown at a range of tidal levels would develop different shell characteristics; b) whether these shell characteristics would be retained following a period of growth under identical conditions, and c) to

investigate whether these characteristics influence losses due to predation by crabs and birds. The findings of this study are then discussed in terms of management options that would reduce losses to predation in mussel cultivation practices and might enhance the use of seed mussel in times of abundant settlement and hence improve the utilisation of an ephemeral natural resource.

METHODS

The study site was located on a low intertidal mud flat adjacent to Bangor Pier on the Menai Strait, North Wales. Mussels have been commercially cultivated on the seabed at this site since the 1960s (Dare 1980).

Twelve 1m x 1m plots were arranged in a grid located in the low intertidal zone (Fig. 2.1). The grid consisted of 4 replicate plots of mussels obtained from three increasing tidal elevations: subtidal, low intertidal, mid intertidal. Possible genetic variability between mussels from the different tidal elevations was minimised by collecting these mussels from cultivated plots that had originally consisted of seed translocated from the same site. Mussels of approximately the same size were transferred from each tidal elevation to the experimental plots. Approximately 25kg of mussels were laid on each plot. The mussels were sampled at the time of their relaying in June 2001 and re-sampled in September 2001. The experimental area had a negligible slope.

Shell Thickness

Shell thickness was calculated for 30 mussels from each tidal elevation both at the beginning and end of the experiment. This was determined by a shell mass/surface area ratio. The mass of the shell was calculated by opening the mussel, cleaning and drying the shell before weighing. The surface area of the shell was approximated using the formula: $A=l(h^2+w^2)^{0.5}0.5\pi$ where A=surface area (mm^2), l=length (mm), w=width (mm), and h=height (mm) (Reimer and Tedengren 1996). This method was used rather than direct shell thickness measurements to reduce the variability in the data that may have been introduced from the exact positioning on the shell when taking the measurements.

Shell Compressive Strength

Mussels (n = 120) from each tidal elevation were compressed until they were crushed using an Instron universal testing machine with 5kN load cell. The mussels were crushed live using a flat blade crushing piece at a standard position, over the maximum width of the mussel shell, to obtain consistent measurements. When the mussels were resampled, 30 mussels from each plot were crushed in the same manner.

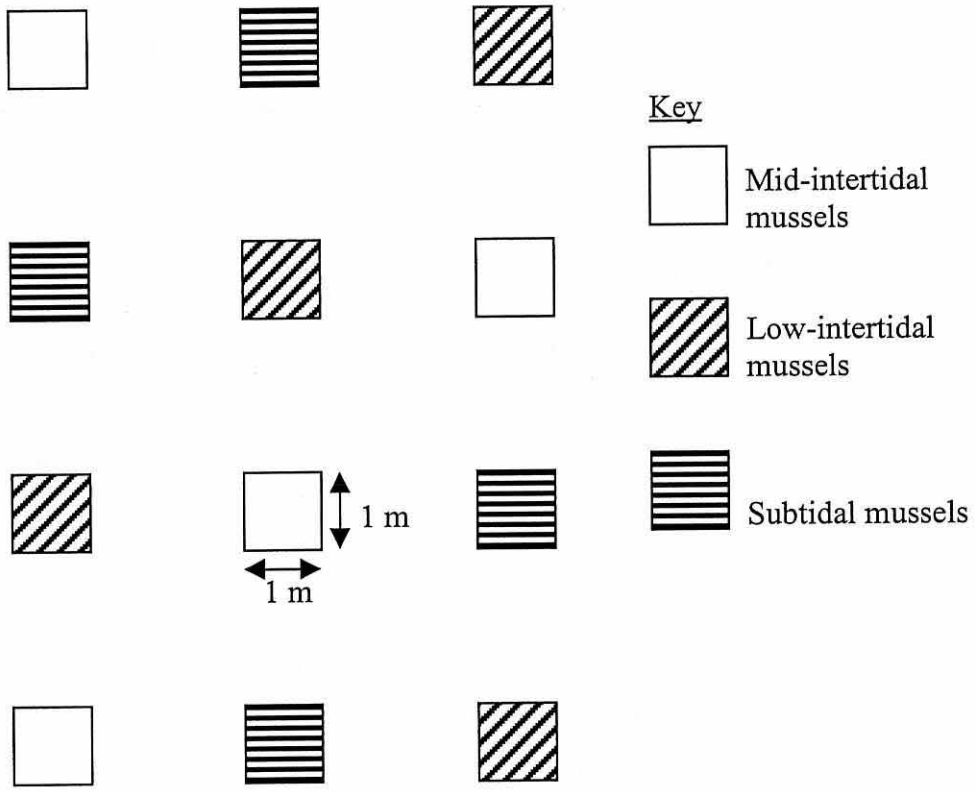

Fig. 2.1. Experimental Set Up. Bangor Pier, North Wales.

Crab Preference Experiment

A laboratory experiment was conducted using mussels from the three tidal elevations obtained on the first sampling occasion (June 2001). The experiment was not repeated at the end of the experiment (September 2001) because, according to published data (Elner 1978), the mussels were too large for the crabs to process effectively.

Male shore crabs, *Carcinus maenas*, between 60 and 80 mm carapace width were collected and acclimatised in a large tank of flowing seawater, at constant temperature. The crabs were food deprived for a period of 48 h to ensure a uniform level of feeding motivation prior to the experiment. Sixteen replicate plastic tanks were set up with a flowing sea water supply at ambient temperature. To each tank eight live mussels from each tidal height were added (total number = 24 per tank). Mussels from different tidal elevations were marked using a coloured paint spot on the shell of the mussel. The mussels ranged in size from between 32 and 41 mm but were chosen such that all sizes were represented equally for all shore elevations. At the beginning of the feeding trial a crab was added to each tank and left for a period of 10 h. After this time the crab was removed and the number of mussels from each tidal elevation, that remained uneaten, were counted.

Oystercatcher predation of 'banked' mussels

In May 2000 a mid-intertidal 'banking' area of 10 m x 10 m was seeded with small mussels (mean size 20 mm) at a density of approximately $10kgm^{-2}$. Between September 2000 and March 2001 the number of oystercatchers in this area was counted regularly throughout its daylight tidal exposure (63 counts). These data were used to calculate the average number of bird minutes spent on the plot per tidal exposure. Based on observations of the heights of the tides on which this plot was or was not exposed the total number of tides on which the plot was exposed throughout the study period was estimated. Assuming, as a worse case scenario, that bird usage was the same at night as by day the total number of bird minutes spent on the plot over the whole winter was calculated. Observations of oystercatchers foraging on a larger area of similarly sized mussels nearby (see below) yielded an estimate of the rate at which they consumed mussels when feeding in such an area. This value was combined with bird usage data to calculate the proportion of banked mussels lost to oystercatchers over the winter.

Oystercatcher-mussel interactions

The foraging behaviour of oystercatchers feeding on cultivated low-intertidal mussel beds and natural mid intertidal mussel beds were observed between September 2000 and March 2001. Observations were made on focal individuals that were classified as being either a 'stabber' or a 'hammerer' (Hulscher 1996). The size of each mussel consumed was estimated in the field as a proportion of the bird's bill length. These estimated sizes were transformed to real sizes (in mm) by a standard observer bias correction procedure (Goss-Custard *et al.* 1987). The length of time taken to handle each mussel was measured from the time of first contact to the end of swallowing the last piece of flesh. To establish whether mussels selected by oystercatchers in the two locations differ in the strength of their defences the relationship between shell length and handling time in the two areas were compared. This study has been restrict to 'hammerers' rather than the 'stabbers' in the oystercatcher population since their ability to open mussels is most likely to be influenced by the physical properties of the mussels' shells.

Statistical Analysis

The shell thicknesses of mussels translocated from each tidal elevation were compared at the beginning and end of the experiment using analysis of covariance (ANCOVA). Where a significant effect was found in the interaction term (slopes of lines were significantly different) separate ANCOVAs were carried out between each treatment. Changes in shell thickness over time for mussels from each tidal height were compared using ANCOVAs. ANCOVAs were also used to analyse shell compression strength data in the same way, again employing separate ANCOVAs between each treatment where a significant effect was found in the interaction term. In the crab feeding experiment differences in the numbers of mussels taken was assessed by a one-way ANOVA. When significant differences were identified Tukey-Kramer (T-K) multiple comparison tests were conducted. Oystercatcher handling times were assessed and compared using an ANCOVA. All statistical analysis was undertaken using MINITAB 12.

RESULTS

Shell Thickness

The shell thickness of the mussels sampled in June was lowest for mussels from the subtidal zone and highest for those from the mid-intertidal zone (Fig. 2.2). There was a significant difference between shell thickness at each tidal level (ANCOVA subtidal v low-intertidal $F_{1,55}=27.33$ $P<0.0001$, subtidal v mid-intertidal $F_{1,53}=7.63$ $P<0.05$, low-intertidal v mid-intertidal $F_{1,54}=13.58$ $P<0.05$). Three months after the initial translocation of the mussels the data for the replicates within each treatment were pooled, as there was no significant difference between them. The previously observed trend was maintained with an increasing shell thickness from the subtidal (initial position) to the low-intertidal (initial position) mussels (Fig. 2.3) (Table 2.1). Shell thickness was significantly different between each (initial) shore height (ANCOVA subtidal v low-intertidal $F_{1,231}=7.17$ $P<0.05$, subtidal v mid-intertidal $F_{1,233}=7.50$ $P<0.05$, low-intertidal v mid-intertidal $F_{1,231}=8.75$ $P<0.05$). However, the regression lines converge suggesting that the largest mussels (>50mm) had similar shell thickness regardless of initial shore height. There was no significant difference between the start and end of the experiment for the intertidal mussels using the shell mass/surface area ratio method to determine shell thickness (ANCOVA June:September, Low-intertidal $F_{1,142}=1.47$ $P=0.281$, Mid-intertidal $F_{1,141}=0.17$ $P=0.684$). The mussels translocated from the subtidal zone significantly increased in shell thickness over the duration of the experimental period (ANCOVA June:September, Subtidal $F_{1,145}=3.96$ $P<0.05$).

Shell Compressive Strength

On the first sampling occasion (June 2001) the shell compressive strength for the smallest mussels was very similar for each tidal height. However, with increasing mussel size there was an increase in compressive strength from the subtidal to the low-intertidal to the mid-intertidal zone (Fig. 2.4). The compressive strength of all but the smallest mussels from the subtidal zone was significantly less than both the low and mid-intertidal zone mussels (ANCOVA subtidal v low-intertidal $F_{1,246}=40.54$ $P<0.0001$, subtidal v mid-intertidal $F_{1,251}=68.12$ $P<0.0001$). However, there was no significant difference between the compressive strengths of the low and mid-intertidal mussels (ANCOVA low-intertidal v mid-intertidal $F_{1,252}=2.47$ $P=0.117$).

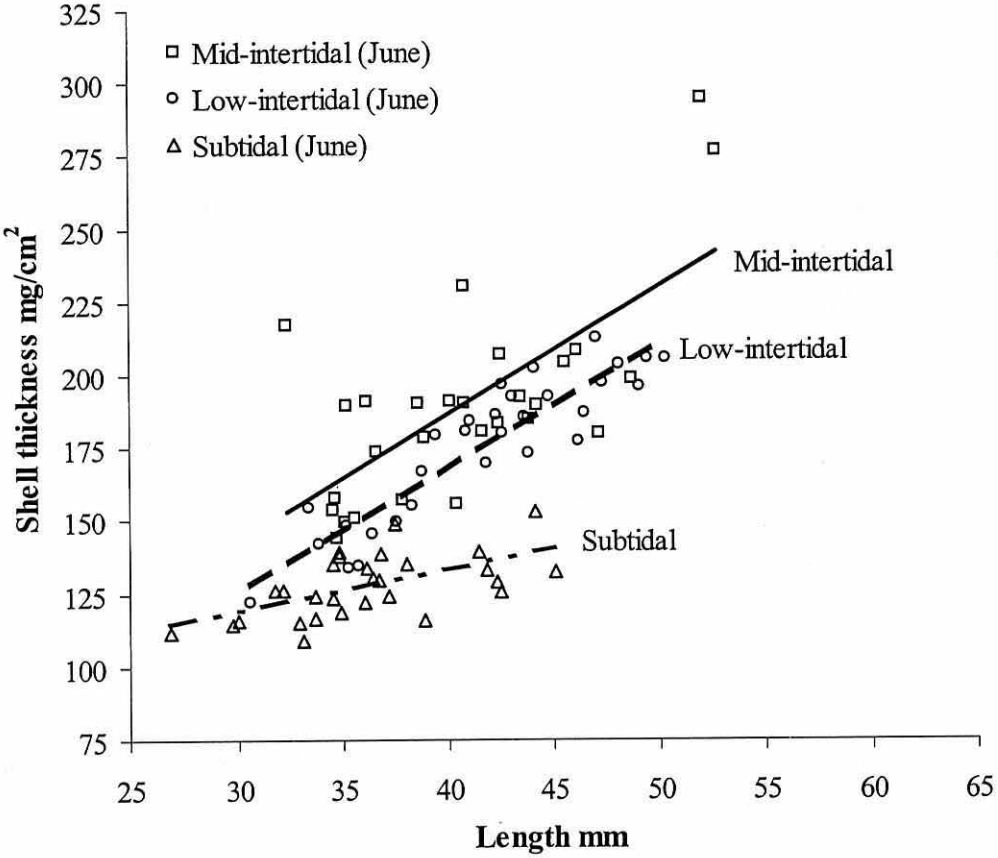

Fig. 2.2. Shell thickness of mussels from subtidal, low-intertidal and mid-intertidal areas measured at the time of the experimental translocation in June 2001.

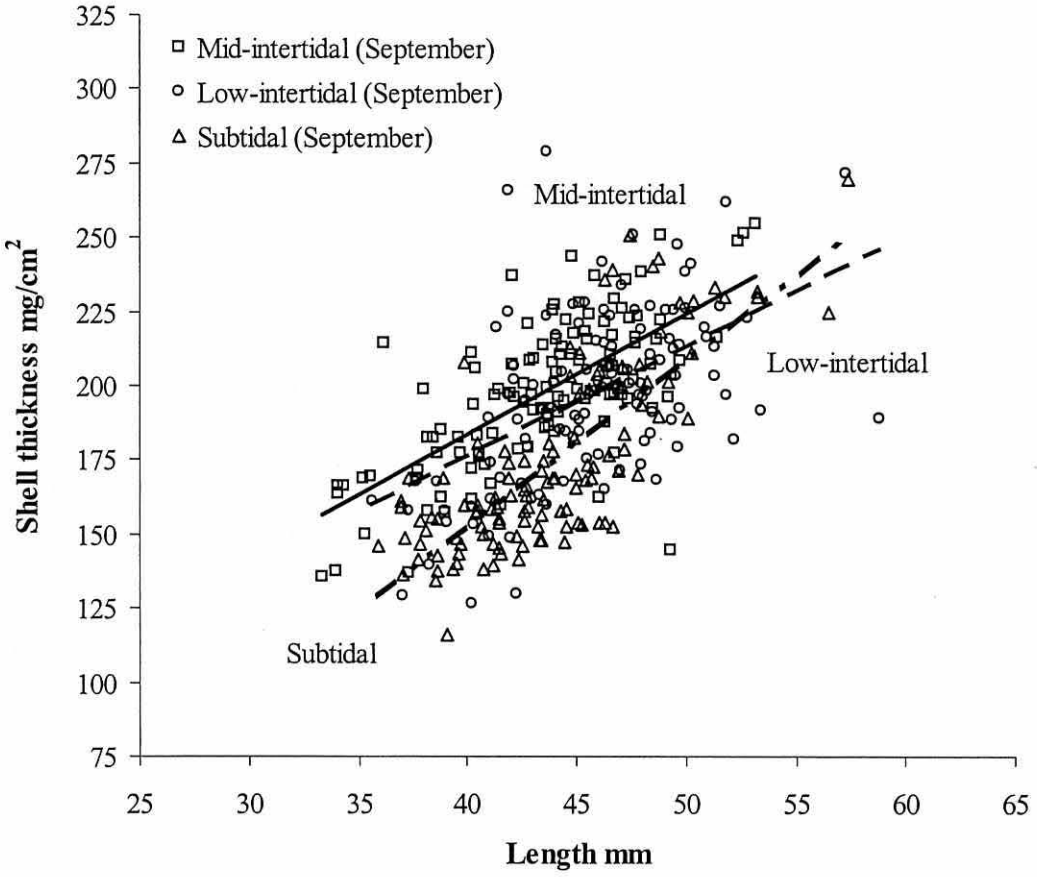

Fig. 2.3. Mussel shell thickness in September 2001, translocated from subtidal, low-intertidal and mid-intertidal areas after three months of growth under identical low-intertidal conditions.

Table 2.1. Regression Analysis of mussel shell length against shell thickness, compression strength and morphological characteristics for June and September sampling of mussels initially from the Subtidal (S) Low-intertidal (L-I) and Mid-intertidal (M-I).

Length v Shell			Regression equation		Regression ANOVA			r^2
			Slope (+/- SE)	Intercept (+/- SE)	DF Reg., error	F	p	
Thickness mg/cm^2	June	S	1.706 ± 1.006	62.84 ± 36.60	1,28	2.88	0.101	0.061
		L-I	4.281 ± 0.364	-3.12 ± 15.30	1,28	138.1	<0.001	0.825
		M-I	6.268 ± 1.304	-57.76 ± 54.54	1,28	23.1	<0.001	0.433
	Sept	S	5.662 ± 0.423	-73.95 ± 18.61	1,117	179.1	<0.001	0.601
		L-I	3.734 ± 0.589	26.55 ± 27.10	1,114	40.21	<0.001	0.254
		M-I	4.067 ± 0.400	20.63 ± 17.48	1,116	103.5	<0.001	0.467
Compres -sion $KNx10^{-1}$	June	S	0.034 ± 0.006	0.2044 ± 0.233	1,123	31.5	<0.001	0.197
		L-I	0.124 ± 0.009	-2.431 ± 0.313	1,123	212.3	<0.001	0.630
		M-I	0.127 ± 0.009	-2.433 ± 0.326	1,128	194.9	<0.001	0.601
	Sept	S	0.057 ± 0.009	0.081 ± 0.367	1,146	41.11	<0.001	0.216
		L-I	0.143 ± 0.011	-2.503 ± 0.499	1,148	184.5	<0.001	0.552
		M-I	0.144 ± 0.009	-2.457 ± 0.366	1,157	272.3	<0.001	0.632
Width mm	June	S	-0.005 ± 1.264	23.64 ± 45.98	1,28	0.0	0.997	0
		L-I	0.437 ± 1.680	2.935 ± 1.680	1,28	119.2	<0.001	0.803
		M-I	0.485 ± 0.051	1.214 ± 2.13	1,28	90.6	<0.001	0.756
	Sept	S	0.008 ± 0.005	21.19 ± 0.302	1,117	2.75	0.100	0
		L-I	0.332 ± 0.267	7.44 ± 1.23	1,117	155.4	<0.001	0.567
		M-I	0.427 ± 0.021	3.046 ± 0.913	1,117	417.0	<0.001	0.779
Height mm	June	S	0.334 ± 0.027	0.739 ± 0.972	1,28	156.7	<0.001	0.843
		L-I	0.388 ± 0.028	-0.262 ± 1.158	1,28	197.4	<0.001	0.871
		M-I	0.418 ± 0.041	-0.922 ± 1.712	1,28	104.0	<0.001	0.780
	Sept	S	0.016 ± 0.004	15.213 ± 0.253	1,117	15.2	<0.001	0.107
		L-I	0.344 ± 0.249	1.608 ± 1.145	1,117	190.7	<0.001	0.617
		M-I	0.402 ± 0.024	-0.514 ± 1.060	1,117	275.3	<0.001	0.629
Mass mg	June	S	0.101 ± 0.007	-2.015 ± 0.251	1,28	216.1	<0.001	0.881
		L-I	0.206 ± 0.007	-5.429 ± 0.308	1,28	792.8	<0.001	0.965
		M-I	0.340 ± 0.041	-10.23 ± 1.731	1,28	67.3	<0.001	0.696
	Sept	S	0.008 ± 0.003	2.972 ± 0.171	1,117	7.86	<0.05	0.055
		L-I	0.211 ± 0.018	-5.520 ± 0.818	1,116	139.8	<0.001	0.543
		M-I	0.232 ± 0.010	-6.257 ± 0.443	1,117	521.2	<0.001	0.815

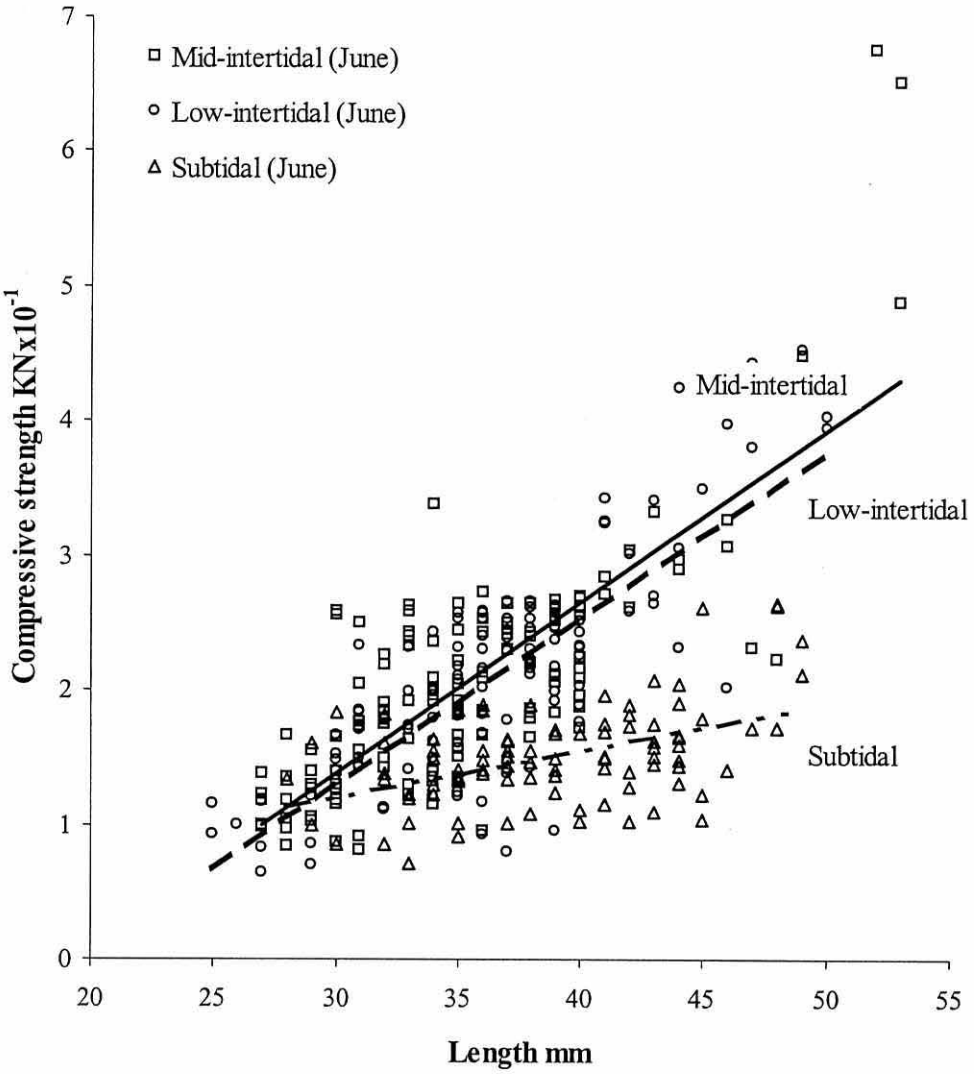

Fig. 2.4. Mussel shell compressive strength from the subtidal, low-intertidal and mid-intertidal areas, measured at the time of the experimental translocation in June 2001.

The replicates within each treatment were pooled from the second sampling occasion (September 2001), as there were no significant differences between them. The pattern in shell compression strength was maintained with an increase in shell strength with increasing tidal elevation up the shore for all except the smallest mussels (Fig. 2.5). Again, all but the smallest mussels that were initially from the subtidal zone still had significantly lower compressive strengths than equivalently sized mussels from the other tidal elevations (ANCOVA subtidal v low-intertidal $F_{1,294}=35.96$ $P<0.0001$, subtidal v mid-intertidal $F_{1,303}=45.59$ $P<0.0001$). The low and mid-intertidal zone mussels were not significantly different in terms of their compressive strength (ANCOVA low-intertidal v mid-intertidal $F_{1,306}=1.23$ $P=0.269$).

Comparisons of shell compression strength between the start and the end of the experiment for mussels from each (initial) tidal height were all significantly different (ANCOVA June:September, Subtidal $F_{1,270}=210.83$ $P<0.0001$, Low-intertidal $F_{1,272}=42.02$ $P<0.0001$, Mid-intertidal $F_{1,286}=57.98$ $P<0.0001$). Shell compressive strength increased for the mussels from each (initial) tidal height (Fig. 2.5). However, the slopes of the regression lines for each tidal height remained similar over time and thus the difference in compressive strengths between initial tidal heights was maintained for the duration of the experiment.

Crab feeding preference

The number of mussels from each initial tidal height that were eaten by crabs varied significantly (ANOVA $F_{2,45}=19.74$ $P<0.001$) (Fig. 2.6). The number of mussels eaten from the subtidal zone was significantly higher than the number of mussels eaten that originated from either the mid or low intertidal zone (T-K $P<0.001$). There was no significant difference between the number of mussels eaten that originated from either the low or mid intertidal zones (T-K $P=1.00$).

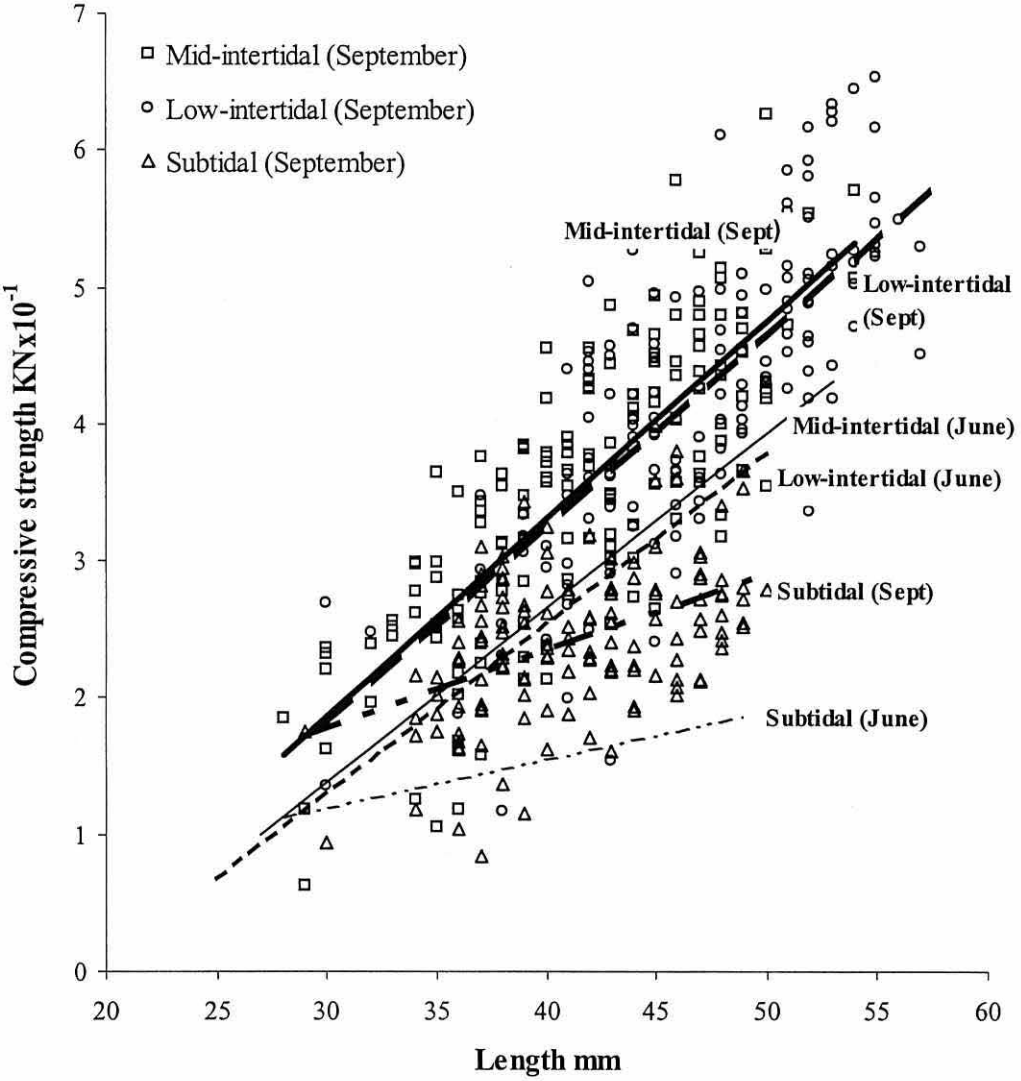

Fig. 2.5. Mussel shell compressive strength in September 2001 of mussels initially from the subtidal, low-intertidal and mid-intertidal areas, after three months growth under identical low-intertidal conditions. Also shown for comparison are the regressions through the equivalent June measurements depicted in Fig. 2.4.

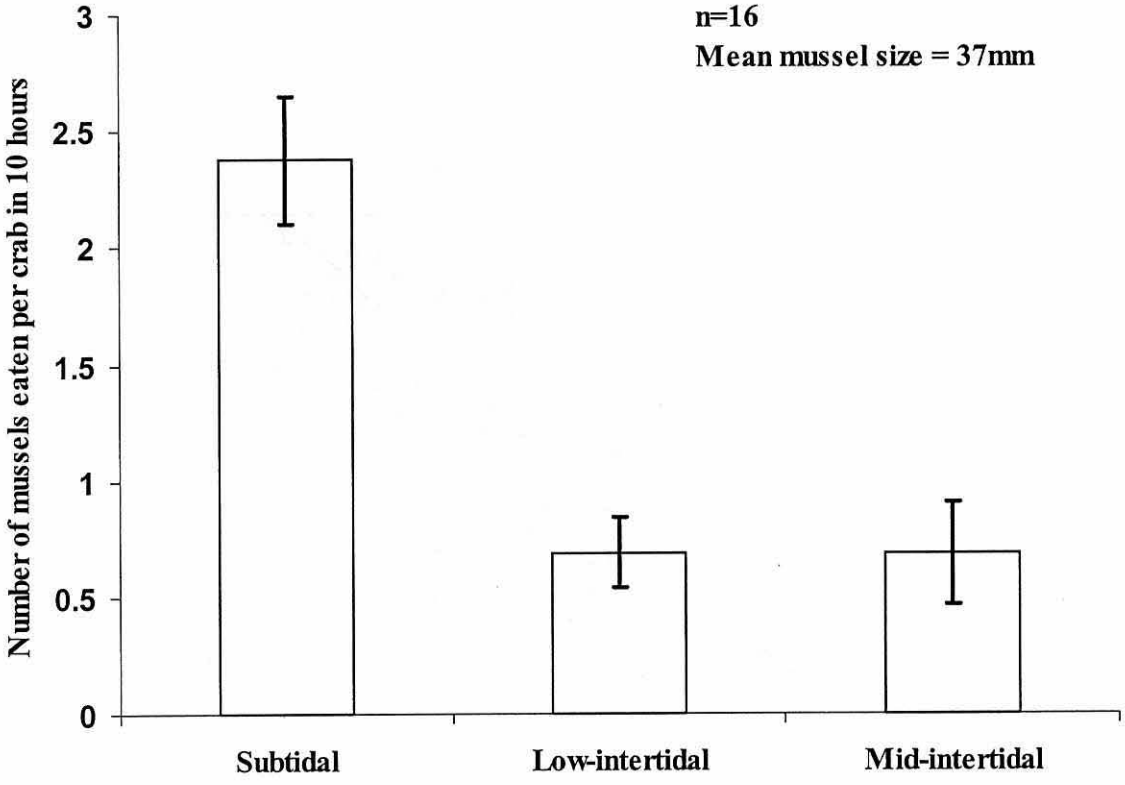

Fig. 2.6. Numbers of mussels from subtidal, low and mid-intertidal areas eaten by crabs (± SE mean).

Oystercatcher Predation of 'banked' seed mussels

Oystercatcher usage of the 'banked' area of mussels varied considerably throughout the exposure period (Fig. 2.7). Usage was greatest just after exposure on the receding tide, diminished towards low tide and then recovered just prior to re-immersion. Overall, an average of 70 bird minutes was spent in the area on each tide. Based on the total number of tides for which the patch was exposed over the whole winter (n=191) and an intake rate of 0.52 mussels per minute achieved by birds feeding on the nearby area, oystercatchers removed 7,000 banked mussels over the course of the winter. Given an initial population of 177,775 mussels (2,735 mussels m^{-2} * 100 sq m * 65% cover) this equates to a loss of only 4% of the initial stock.

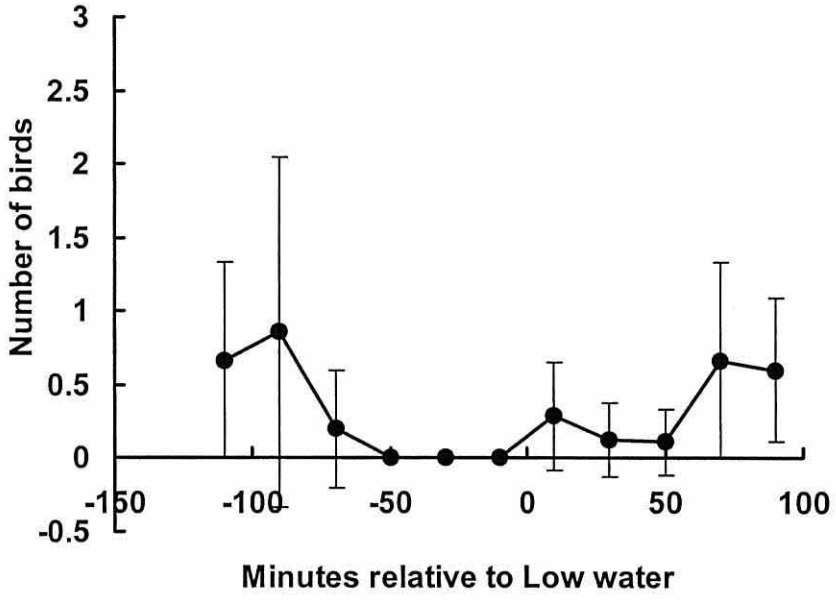

Fig. 2.7. The mean (± 2 SE) number of oystercatchers foraging on a 10 x 10 m area of seed mussels 'banked' at mid-intertidal levels as a function of time relative to low water.

Oystercatcher-mussel interactions

The relationship between handling time and mussel length differed significantly between mid-interidal areas and low-intertidal areas (ANCOVA $F_{1,117}$=31.66 P<0.001) (Fig. 2.8). Oystercatchers opened smaller mussels in approximately the same time at each location but took considerably longer to handle larger mussels in the mid intertidal area than in the low intertidal area.

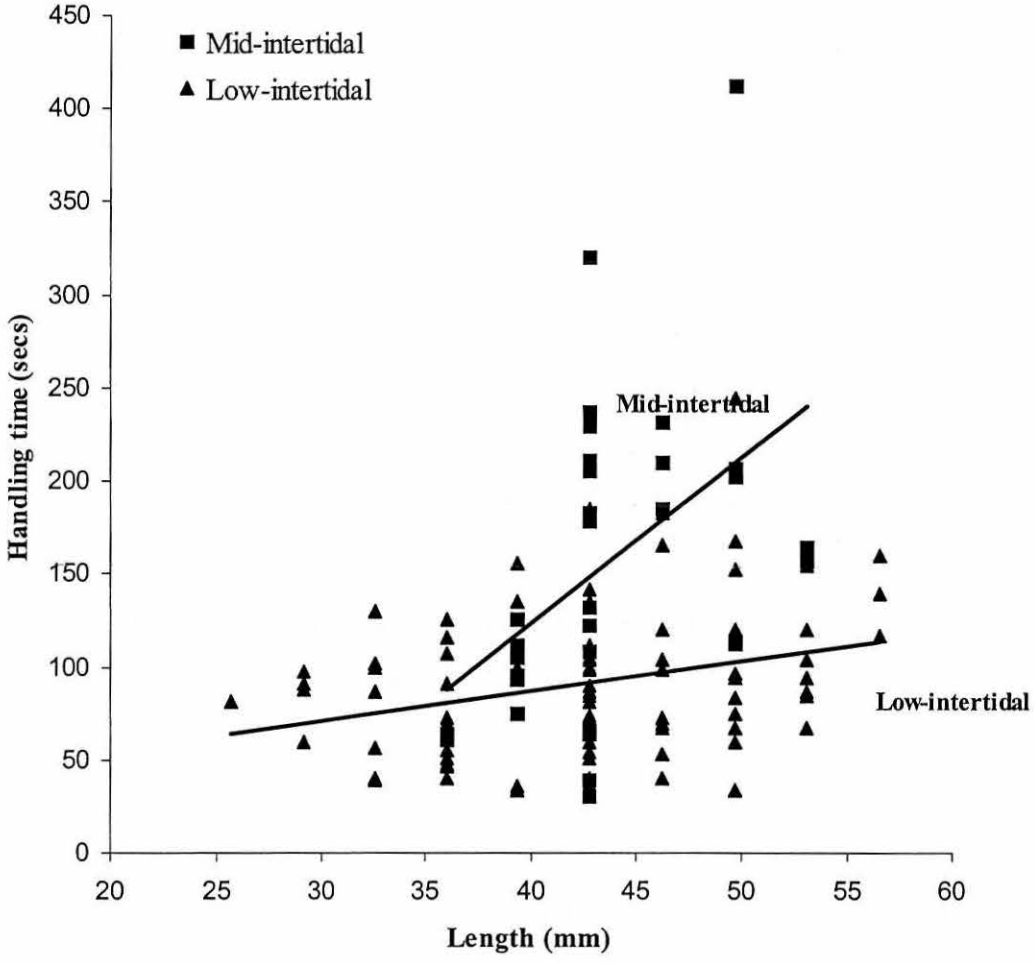

Fig. 2.8. Oystercatcher handling time of mussels from the mid and low intertidal.

DISCUSSION

The mussels sampled at the beginning of the experiment indicated that for mussels of all sizes, shell thickness increased with increasing tidal height. This concurs with previous observations (Seed 1976), and has been attributed to the slower growth of the animals at higher tidal elevations. However, the compressive strength of the mussels did not reflect this finding. The mussels from the subtidal zone had significantly lower compressive strengths than the mussels from the intertidal zone, but there was no significant difference between the mussels sampled from the low and mid-intertidal zones. This difference in the pattern of variation in compressive strength and shell thickness across tidal zones may influence the predatory efficiency of crabs and oystercatchers.

When offered mussels at the start of the experimental translocation trial, crabs preferred subtidal mussels but showed no distinction between mussels from low and mid-intertidal areas. This suggests that the compressive strength rather than the overall thickness of the shell dictates crab dietary preference. Smith and Jennings (2000) demonstrated that exposure to waterborne cues from crabs that predated upon mussels induced an increase in shell thickness in a particular area of the mussel shell (the shell lip). Greater compressive strength confers two advantages to an individual mussel. First it limits the number of predators that have sufficient strength to crush it (Boulding 1984; Elner 1978). Second, even for those predators that can crush it, increased compressive strength increases its handling time. This decreases the profitability of the mussel to the predator (defined as the energy gain per unit time handling) and hence reduces the likelihood that it will be taken by an optimally foraging predator (Robles *et al.* 1990; Boulding 1984). Moreover, because handling time determines the asymptotic level of feeding rate in many predator-prey systems (e.g. Holling 1959; but see Caldow and Furness 2001) greater compressive strengths will reduce the number of mussels that can be consumed by each predator per unit time (Boulding 1984). This is likely to be a particularly important consideration in tidally migrating predators that have very restricted feeding opportunities (e.g. shore crabs) (Seed 1993).

The handling time-length relationship calculated for oystercatchers differed markedly between low and mid-intertidal areas. Oystercatchers handled small mussels equally quickly in both areas but took increasingly longer to do so in the higher shore area when dealing with larger mussels. This finding, coupled with the similarity of the compressive strength and difference in shell thickness between these areas, suggests

that shell thickness rather than compressive strength is the most important shell characteristic for oystercatchers. Shell thickness is known to be an important component in mussel selection by oystercatchers (Durrell and Goss-Custard 1984; Sutherland and Ens 1987 and Cayford and Goss-Custard 1990). As in the case of crabs, increased shell thickness and associated handling time increases the chance that a particular mussel will be abandoned without being opened and will decrease the number of mussels a bird is able to consume over a given time (Meire and Ervynck 1986).

After growth at the same tidal height for three months (June-September) the shell compressive strength of mussels from each (initial) tidal height had increased. Crab numbers at the site are highest over the warmer summer months (Aagaard *et al.* 1995; Hunter and Naylor 1993), so the observed increased compressive strength may indicate a morphological response to waterborne cues resulting from crab predation on mussels (Leonard *et al.* 1999; Smith and Jennings 2000). Although the shell compressive strength increased for all of the mussels, it appeared to increase equally for the mussels from each initial tidal height (Fig. 2.5). The morphological advantage in mussel shell compressive strength acquired by the 'banked' mussels during their previous growth at higher shore elevations was therefore maintained, and the mussels that were transplanted from the subtidal zone would therefore be selected preferentially by predators.

Mussel shell thickness did not significantly increase over the experimental period for the intertidal mussels using the shell mass/surface area ratio method. Since compressive strength altered this may suggest that a more sensitive method of determining shell thickness, particularly at the shell margin where new shell growth would have occurred, may provide a more instructive measurement. A significant increase in shell thickness was detected for the mussels from the subtidal zone. The mussels translocated from the subtidal zone were significantly thinner than those from the intertidal zones at the start of the experiment, hence the relative increase in shell thickness over the experimental period may have been greater allowing for this detectable difference. It is possible that the apparent increase in shell thickness for the mussels transplanted from the subtidal zone could be the result of predator selection over the duration of the experiment due to crabs and oystercatchers only taking the thinnest shelled mussels. However, it is unlikely that this explains the full extend of the change in shell thickness as the largest sized mussels (>40mm) displayed the most noticeable increase in shell thickness. These mussels would be too large for the crabs

to eat and oystercatchers are unlikely to have had a significant impact when the transplantation experiment was conducted, as numbers are relatively low in the summer months.

Management Options

Our findings indicate that mussel growth at higher shore elevations is associated with high levels of shell thickness and compressive strength. Both of these properties can provide protection from predators. Moreover, these protective adaptations are maintained after periods of on-growing when transplanted to areas lower on the shore. Although mussel growth is retarded at higher intertidal levels due to shorter immersion times (Bertness and Grosholz 1985; Seed 1969), it would seem that mussel cultivators could manipulate their management practices to reduce losses to predation by initially stimulating the growth of shell thickness in areas higher up the shore. Although there will be a trade off between these predator resistant shell adaptations and the slower mussel growth at higher tidal elevations, the mussel grower has access to a finite area of leased seabed that is composed of both intertidal and subtidal areas. The following management suggestions have been made in light of this to maximise the benefits of growth at a particular shore height. Initially, seed mussels could be laid at the higher shore elevations where they will develop thicker shells. In the presence of abundant, alternative areas of mussels on which to feed at lower intertidal levels oystercatchers clearly show little interest in these small, thick-shelled and hence relatively unprofitable mussels. Furthermore, the elevated height on the shore will be associated with reduced crab numbers (Aagaard *et al.* 1995; Hunter and Naylor 1993). When the mussels have reached a greater size they could be transferred further down the shore where they would on-grow to marketable size at a faster rate. Their increased size and the maintenance of their relatively high compressive strength will result in reduced losses from crab predation. The relatively thicker shells of the mussels will also be a deterrent to oystercatchers that will also have a more limited time in which to feed upon the mussels at these lower-level ongrowing areas.

These results indicate that 'banking' at times of abundant spatfall could be a valuable option. When natural spatfall is high and an abundant supply of wild seed means that the normal areas of cultivation have been fully utilised, the excess seed could be laid at much higher tidal elevations – banked rather than laid at even higher densities downshore. By 'banking' excess mussels separately, the other mussels in the on-growing area will suffer less density-dependent mortality (Heral 1993) and the

banked mussels, although they will grow more slowly, will obtain thicker shells of greater compressive strength that will then improve their resistance to predation. In subsequent years, when natural spatfall is low and wild seed is in short supply, these 'banked' mussels can then be transferred further downshore where they will grow to marketable size at a faster rate, with the added advantage of being less susceptible to predation. Adoption of this practice is likely to (i) even out the unpredictable supply of seed mussels for on-growing, (ii) reduce density effects in the principal on-growing areas and (iii) reduce the losses to predators. All of these have obvious benefits in terms of commercial profitability.

Chapter 3

Factors affecting the growth of mussels in large scale beds

ABSTRACT

At present there is little management used in the commercial cultivation of mussels on the seabed to achieve superior mussel growth rates in relation to initial stocking density and position on the shore. The aim of the present study was to investigate these effects on the seasonal growth rate of mussels in the intertidal zone in order to aid shellfish management. A large-scale field experiment was conducted in which mussels were grown over a range of initial seeding densities and shore heights in order to provide data relevant to mussel cultivators. Data were obtained of mussel growth in terms of shell length and flesh weight and used to develop statistical models of seasonal mussel growth as a function of initial stocking density and shore height. Mussel shell growth rate was higher over the summer than the winter months and decreased with increasing initial seeding density and shore height. Mussel flesh weight displayed a seasonal pattern increasing from April to September, and then declined over the autumn and winter. Mussel flesh dry weight decreased with increasing shore height and initial seeding densities. The results of the study and the use of the statistical models to predict mussel growth are discussed with a view to improving the management of cultivated mussels and hence enabling a more sustainable approach to the cultivation of mussels on the seabed.

INTRODUCTION

Mytilid mussels are found throughout the world and form a key component of many marine communities (Herman 1993; Seed 1976). Within the distributional limits of *Mytilus edulis*, both at wider geographic and local scales, growth varies among individuals and between populations. The most significant parameter in determining growth rate food supply (Seed 1976; Page and Hubbard 1987). Food quality and quantity is highly variable both spatially and temporally in temperate estuaries and turbid coastal waters (e.g. the Menai Strait). Spatial variability is brought about by hydrodynamic factors (tidal and wind driven processes), together with patchiness in plankton abundance in the water column, and the activities of populations of bivalves themselves (Bayne 1993). Within this variability food availability in temperate climates is generally lowest over the winter and highest over the summer months (Widdows *et al.* 1979), resulting in rapid growth over the spring and summer, and slight or no growth during the colder winter months (Seed 1969; Bayne and Widdows 1978). Winter growth has been reported in the River Exe estuary, Devon (McGrorty 1997), but this was greatest in smaller mussels and then declined with increasing shell length. The position on the shore in terms of height above low tide is also of importance (Sukhotin and Maximovich 1994), since this corresponds with the time available for the mussel to feed when covered at particular states of the tide (Baird 1966). The longer periods that mussels are exposed to air, the slower their growth rate, and the smaller their ultimate size (Jorgensen 1976). Longer periods of exposure to air also provide an increasingly stressful environment due to wide variations and extremes of salinity, temperature and desiccation (Bayne *et al.* 1976).

Food availability for an individual mussel can also be affected by the presence of other mussels, and there is evidence of the occurrence of food depletion immediately above mussel populations, which can result in the mussels becoming food limited (Frechette and Bourget 1985a; Frechette and Bourget 1985b). The water movement above the mussel bed can be critical, as food is removed from the water column by filter feeders lower on the shore during the incoming tide before it reaches mussels at higher elevations (Peterson and Black 1987). Food depletion has also been demonstrated for aggregations of mussels at high densities in which individual growth rates were reduced (Bertness and Grosholz 1985). This effect was most evident for smaller individuals. Apart from having an effect on growth, mussels that aggregate in groups as small as 21-28 individuals have been shown to have a reduced reproductive output (Okamura 1986). An 'edge effect' is also evident whereby those mussels located in the centre of an aggregation demonstrate the most severe

reductions in growth and reproduction compared with mussels on the edge of the aggregation (Svane and Ompi 1993; Newell 1992; Okamura 1986). Okamura (1986) suggested that these adverse effects are caused by some property of living neighbours, rather than simply the physical relief of the mussel clump.

While such considerations of the effects of group living on growth rate and reproductive output are of ecological interest, they also have relevance to commercial mussel growers whose aim is to maximise yield from limited resources and avoid unnecessary waste of a semi-wild crop.

Mussel cultivation has been practised on a large-scale on the seabed of the Menai Strait, North Wales, since 1960 (Dare 1980). This method is based on the principal of transferring seed mussels (10-25 mm shell length) from areas of natural settlement to lays (culture plots), that provide more favourable conditions (Mason 1972) where they will benefit in terms of growth and survival (Kristensen and Hoffmann 1991). Once the mussels have grown to marketable size, which is 50 mm in the UK (Dare 1980), they are then harvested by dredging. This is generally 18 to 36 months after the seed is laid, depending on the position of the lay on the shore. The condition of the mussel fluctuates through the year, with individual dry flesh weight highest in summer and autumn, when protein and carbohydrate content are highest, and decreasing through the winter to a post-spawning minimum in spring (Dare and Edwards 1975). It is important, therefore, for mussel growers that harvest occurs when the mussels are in good condition to maximise returns from the lays.

At present little management is used in the commercial cultivation of mussels on the seabed to achieve superior mussel growth rate in relation to initial stocking level and position on the shore. The aim of the present study was to investigate the effects of initial mussel stocking density and shore height position on the seasonal growth rate of mussels in the intertidal zone in order to aid shellfish management. While similar small scales manipulation have been undertaken, the present study examined these effects at a commercial scale. Hence the data generated are relevant to commercial applications and enable the development of statistical models of seasonal mussel growth as a function of initial stocking density and shore height. Growth models are developed in terms of mussel length and flesh dry weight. In order to obtain the greatest range of shore heights possible a caged mussel experiment was also set up in close proximity to the main site on an area with a steeper shore gradient. The statistical models of length and dry weight can be used to make calculations of the

time that it would take for a cohort of mussels, at a given initial density and shore height, to reach marketable size and the optimal time of year to harvest to ensure maximal flesh weight. The advantage of using such statistical models is that it allows mussel production, using several different management scenarios, to be predicted enabling informed judgements to be made in the commercial cultivation of mussels on the seabed. A better understanding of the relationship between stocking density and shore height should result in a more sustainable approach to mussel cultivation.

METHODS

Main experimental site

The study site was located on an intertidal mudflat adjacent to Bangor Pier on the Menai Strait, North Wales, at approximately low water spring tide level (Fig. 3.1). In April 2000 two squares each consisting of 16 cells 20 m x 20 m were seeded with mussels approximately 20 mm in length at one of four different stocking treatments (7.5, 5, 3, 2 kg m^{-2}) using a Latin square design (Fig. 3.1). At the time of seeding the mussels were of similar sizes hence the stocking treatments in biomass can be referred to as density treatments. However, it should be noted that the increments between treatments are linear in terms of biomass not density. These stocking levels were chosen to represent a range greater than that normally used in commercial mussel cultivation (mussels at this site have been laid at approximately 5 kg m^{-2} until recently). Each Latin square was marked with buoys and the mussels scattered over each plot from a boat. Due to the effects of tidal currents and inaccuracies of boat positioning, it was not possible to lay the mussels in precise squares, however an *a posteriori* examination of the experimental site revealed that distribution of mussels at the designated densities had occurred sufficient for the purposes of the experiment.

The experimental site was sampled at the time of seeding and a further 10 times over the following year until April 2001. Sampling was carried out most frequently over times of greatest mussel growth (May-July). On each sampling occasion four quadrats of 0.25 m x 0.25 m were taken per cell in a random manner, but in the main areas of mussel cover to avoid boundary effects. The contents of each quadrat were placed in a plastic bag, labelled and taken back to the laboratory. In the laboratory the number of mussels in each quadrat were counted, and 120 randomly selected mussels from each sample measured for their length (umbone to the edge of the posterior margin of the shell) to the nearest mm using Vernier calipers. A further 30 mussels were randomly selected from each quadrat for determination of flesh dry weight by drying in an oven at 90°C for 12 h.

Caged mussel experimental site

In addition to the main site an extra site was established at which the growth of mussel in cages designed to exclude predators was examined. This site had a steeper gradient than the mudflat at the main site. The caged site was set up in close proximity to the main site on the island of Ynys Faelog in the Menai Strait, North Wales. Cages of dimension 0.5 m (wide) x 0.75 m (long) x 0.25 m (high) were constructed from wooden frames with plastic mesh (5 mm square) sides.

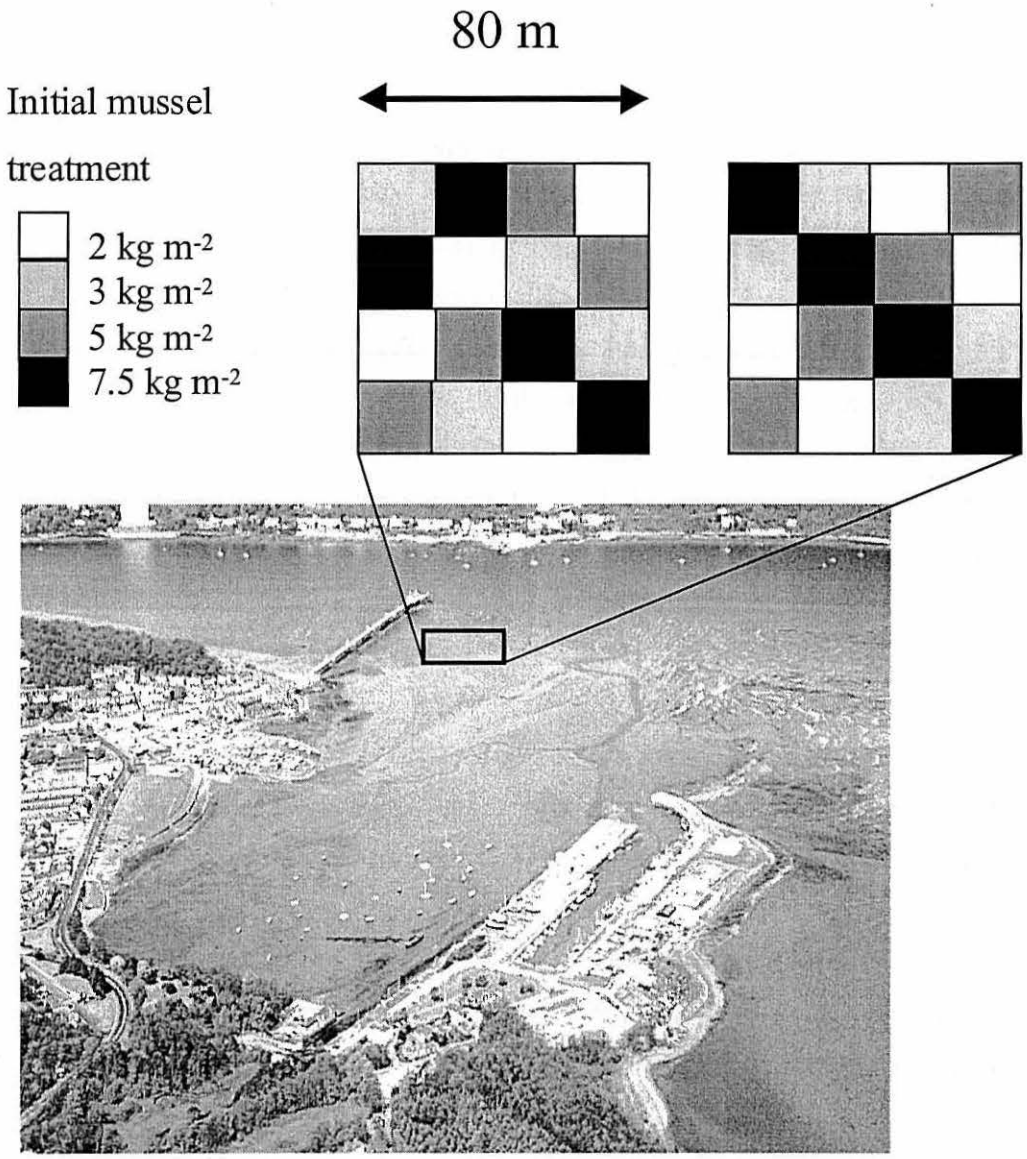

Fig. 3.1. Main site experimental set-up. Adjacent to Bangor Pier in the Menai Strait, North Wales.

The cages were supported on metal frames approximately 0.5 m above the seabed to prevent sedimentation and smothering of the mussels.

Four initial mussel stocking treatments of 2, 5, 7.5 and 15 kg m^{-2} were deployed in the cages at six shore heights spaced down the shore at regular intervals spanning approximately 70 - 210 minutes mean exposure at low water springs. A total of 24 cages were deployed on the shore. The cages were seeded with mussels in May 2000, and sampled at the time of seeding and a further 10 times over the following year until April 2001. On each sampling occasion 120 mussel from each cage were randomly selected and measured for their length to the nearest mm from the umbone to the edge of the posterior margin of the shell using Vernier calipers, before being replaced in the cage to maintain the density. A further 30 mussels were randomly selected from each cage for determination of flesh dry weight (DW) by drying in an oven at 90°C for 12 h. As the DW sampling was destructive 30 mussels from extra cages of mussels held at the same approximate density were used as replacement mussels in the experimental cages in order to maintain the correct density. The replacement mussels were marked on the shell so that they would not be sampled later in the experiment.

Statistical analysis of length data

Prior to analysis the four samples taken from each cell from the Main site were pooled. Mean length for each cell or cage on each date was calculated and plotted against time (Fig. 3.2) to determine summer (fast growth) and winter (slower growth) growth periods. The geometric mean mussel shell length for each cell or cage on each sampling date was calculated and used in the determination of the specific growth rate (SGR) for each time period between sampling dates according to Kaufmann (1981):

$$SGR = \frac{LnS_2 - LnS_1}{t_2 - t_1}$$

Where S_1 = size (mm) at the beginning of the time interval, t_1 (days); S_2 = size (mm) at the end of the time interval, t_2 (days).

For each identified growth period of the experiment (i.e. summer and winter) SGR was plotted against the log-transformed geometric mean of S_1 and S_2 to fit a Gompertz growth model of mussel growth. Regression analysis was then conducted for each of the initial seeding densities (for main site and caged site) and shore height treatments (for the caged site).

An ANCOVA was carried out on the data, comparing each treatment where the covariate was mean mussel length and the response was SGR. Least-square means pairwise tests (LSM) were also conducted between each treatment. Where there was no relationship with the length covariate a one-way ANOVA was carried out to compare initial density and shore height treatments.

When possible, linear regression models of SGR were formulated. The full model development is explained in the results and model development section. Full experimental time period models were tested for goodness of fit to the observed data using the least squares method in the software package ModelMaker3 (Cherwell Scientific 1997). All other statistical analyses were carried out using SAS version 8.2 (SAS Institute Incorporated 1999-2001).

Statistical analysis of dry weight data

Prior to analysis the samples from each initial stocking density on the main site were pooled (n=32 samples per density on each sampling occasion). The relationships between Ln(Length) and Ln(DW) were established by linear regression for each sampling date for each density (main site and caged site) and shore height (for the caged site). For the main site DW data was only available for eight of the ten sampling dates (no data 02.06.00 and 07.03.01). For the caged site data was only available for seven of the ten sampling occasions (no data for 17.05.00, 02.06.00 and 07.03.01). When possible linear regression models were formulated to represent the change in the DW/length relationship over the yearly cycle for the experimental treatments (initial density and/or shore height), transforming the date into days of the year (where January 1st was day 1). To support model development ANCOVAs were performed on each sampling data, comparing each treatment where the covariate was length and dry weight was the response variable. The statistical analysis was carried out using SAS version 8.2 (SAS Institute Incorporated 1999-2001).

The models were tested for goodness of fit to the observed data using the least squares method to provide an r^2 value, using ModelMaker2. The observed data consisted of a linear regression relationship between Ln(DW) and Ln(Length). Therefore, to obtain an actual observed DW value this relationship was used to determine the DW for the mean mussel length for that sampling date for that treatment (see 'length data' section). The same mean mussel length measurements were then used in the model to predict mussel DW.

RESULTS AND MODEL DEVELOPMENT

Length data

1. Main site

Mussel length increased over the experimental period with a fast growth period over the summer months (April-September), slowing down over the winter (September-March) and then increasing in the spring (March) (Fig. 3.2). The first 6 sampling dates from April until the end of August 2000 and the last 2 sampling dates March 2001 – April 2001 were designated as the 'summer' growth period, with dates from the end of August 2000 to the beginning of March 2001 designated as the slower 'winter' growth period.

a. 'Summer' growth period

SGR displayed a significant negative relationship with increasing Ln(Length) (Table 3.1). To demonstrate the effect of initial stocking treatment on mussel SGR a two variable regression model of Ln(Length) and initial seeding density was formulated (Table 3.1 and 3.2).

Main site summer length model

$SGR = a + b(\text{Initial Density}) + c\text{Ln}(\text{Length})$ Equation 1

Where a, b and c are fitted parameters.

This model of density and length provided a significantly better fit to the data set than the one variable model of length ($F_{1,188}=4.89$ $p=0.028$).

To support the model development an ANCOVA, with length as the covariate, was conducted on the whole data set to test the effect of initial seeding density on SGR. This test did not show a significant effect of initial seeding density (ANCOVA covariate length $F_{1,186}=214.68$ $p<0.0001$, density effect $F_{3,186}=2.01$ $p=0.114$). However, when each density treatment was compared individually to each other density treatment in LSM tests the low initial seeding density had a significantly higher SGR than the high initial seeding density (LSM low density compared to high density $p<0.05$, no significant differences between all other treatments) (Fig. 3.3).

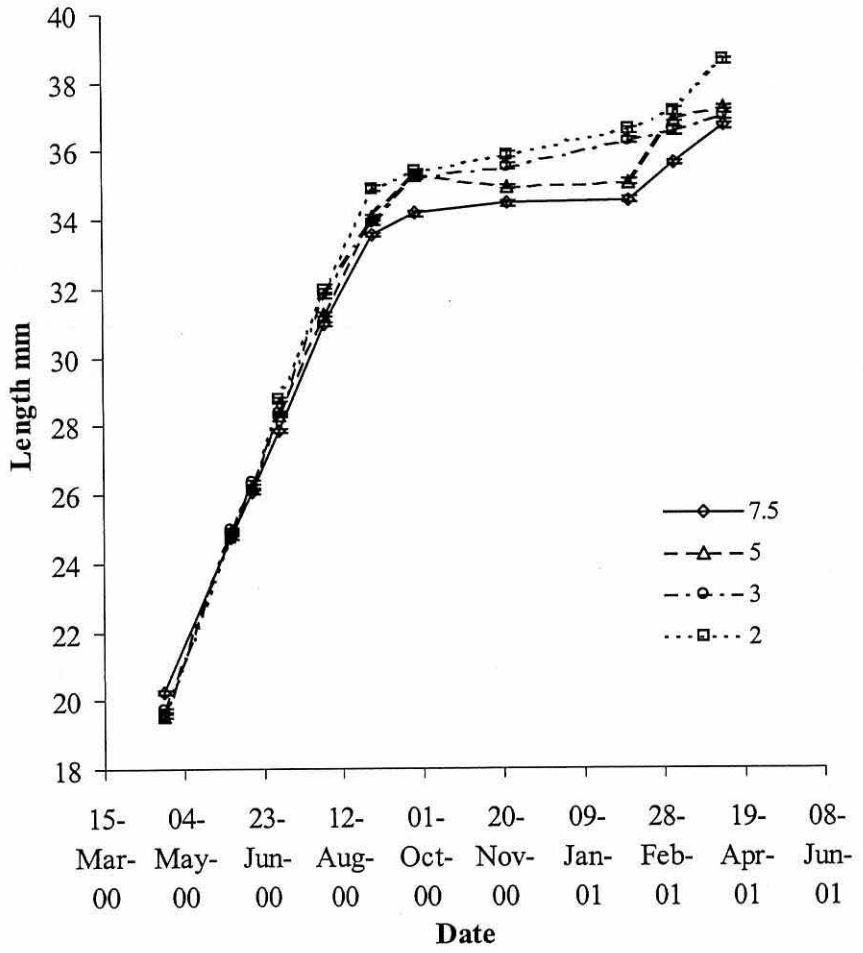

Fig. 3.2. Main Site. Mussel length from four initial density treatments (7.5, 5, 3 and 2 kg m^{-2}) (±SE mean) over experimental period from April 2000 to April 2001.

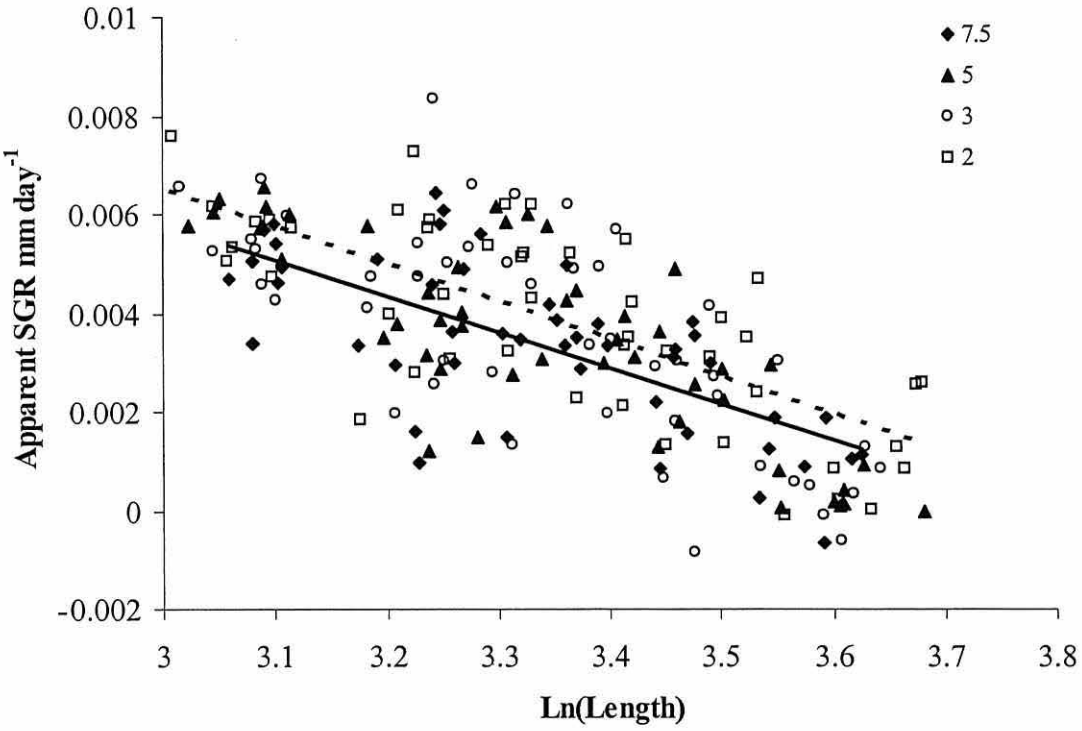

Fig. 3.3. Main Site. Apparent mussel length SGR over the 'summer' growth period for mussels from four initial seeding densities (7.5, 5, 3 and 2 kg m^{-2}). Solid line indicates linear fit to initial density treatment 7.5 kg m^{-2} data, dotted line indicates linear fit to initial density treatment 2 kg m^{-2} data.

Table 3.1. Main Site 'Summer'. Analysis of goodness of fit of regression models of i) SGR on Ln(length) and ii) SGR on Ln(length) and initial seeding density (Main site summer length model, Equation 1). Initial seeding densities High (7.5 kg m^{-2}), Medium (5 kg m^{-2}), Medium-Low (3 kg m^{-2}) and Low (2 kg m^{-2}).

Source	df	Sum of squares	Mean Square	F value	P	r^2
Length Model						
Within (explained by length)	1	0.000392	0.00039159	209	<0.0001	0.525
Unexplained	189	0.000355	0.00000188			
Total (All data)	190	0.000746				
Main site summer length model (Equation 1)						
Within (explained by length and density)	2	0.000401	0.00020037	109	<0.0001	0.537
Unexplained	188	0.000345	0.00000184			
Total (All data)	190	0.000746				

Table 3.2. Main Site 'Summer'. Parameter estimates for Main site summer length model (Equation 1).

SGR = a + b(Initial density) + c.Ln(Length)

Parameter	Estimate	SE
a	0.0317	0.00191
b	-0.000104	0.0000467
c	-0.00827	0.000563

b. 'Winter' growth period

There was no significant relationship between SGR and Ln(Length) for the entire data set or any of the individual density treatments considered alone (Table 3.3) (Fig. 3.4). Since it was not possible to establish a relationship over this time period this would suggest that a constant SGR was maintained. There was no significant difference between the initial density treatments (ANOVA $F_{3,123}=0.57$ $p=0.639$) therefore a constant SGR was assumed for all of the density treatments. An estimate was made for an average SGR of 0.0008 mmday^{-1} over the 'winter' growth period (Fig. 3.4).

Table 3.3. Main Site 'Winter'. Analysis of goodness of fit of regression model of SGR on Ln(Length) for each initial seeding density and all of the data. Initial seeding densities High (7.5 kg m^{-2}), Medium (5 kg m^{-2}), Medium-Low (3 kg m^{-2}) and Low (2 kg m^{-2}).

Source	df	Sum of squares	Mean Square	F value	P	r^2
Low Density						
Within (explained by length)	1	0.0000001	0.00000014	0.15	0.699	0.005
Unexplained	29	0.0000269	0.00000093			
Total (Low Density)	30	0.0000270				
Medium-Low Density						
Within (explained by length) Density	1	0.0000050	0.00000050	4.06	0.053	0.119
Unexplained	30	0.0000369	0.00000012			
Total (Medium-Low Density)	31	0.0000418				
Medium Density						
Within (explained by length)	1	0.0000001	0.00000008	0.05	0.822	0.002
Unexplained	30	0.0000499	0.00000164			
Total (Medium Density)	31	0.0000492				
High Density						
Within (explained by length)	1	0.0000001	0.00000007	0.05	0.818	0.002
Unexplained	30	0.0000397	0.00000132			
Total (High Density)	31	0.0000398				
Main site winter length model (all data)						
Within (explained by length)	1	0.000001	0.00000134	1.06	0.305	0.008
Unexplained	125	0.000159	0.00000127			
Total (All data)	126	0.000160				

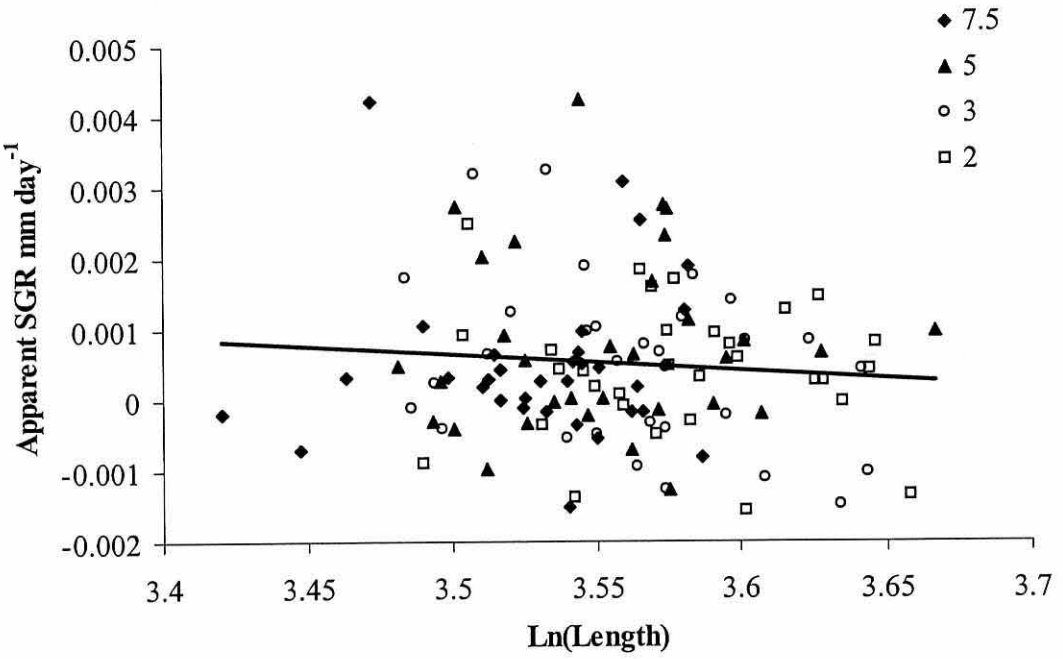

Fig. 3.4. Main Site. Apparent mussel length SGR over the 'winter' growth period for mussels grown at four initial seeding densities (7.5, 5, 3 and 2 kg m^{-2}). Solid line indicates linear fit to data from all initial density treatments.

c. Complete experimental time period

The SGR models for the 'summer' and 'winter' period have been combined to predict mussel length over the whole time period for the four initial seeding densities (Fig. 3.5). For the production of the SGR models the dates for the two growth periods were limited by the sampling dates. However, in order to make predictions of mussel shell length SGR using these growth models, the growth periods have been defined as 'summer': from the beginning of March to half way through September, and 'winter': from half way through September to the beginning of March. The combined model fits the observed data well (for initial density 2, 3, 5, 7.5 kg m^{-2} respectively r^2=0.96, 0.99, 0.98, 0.99) although an increasing discrepancy towards the end of 'winter' is apparent (Fig. 3.5).

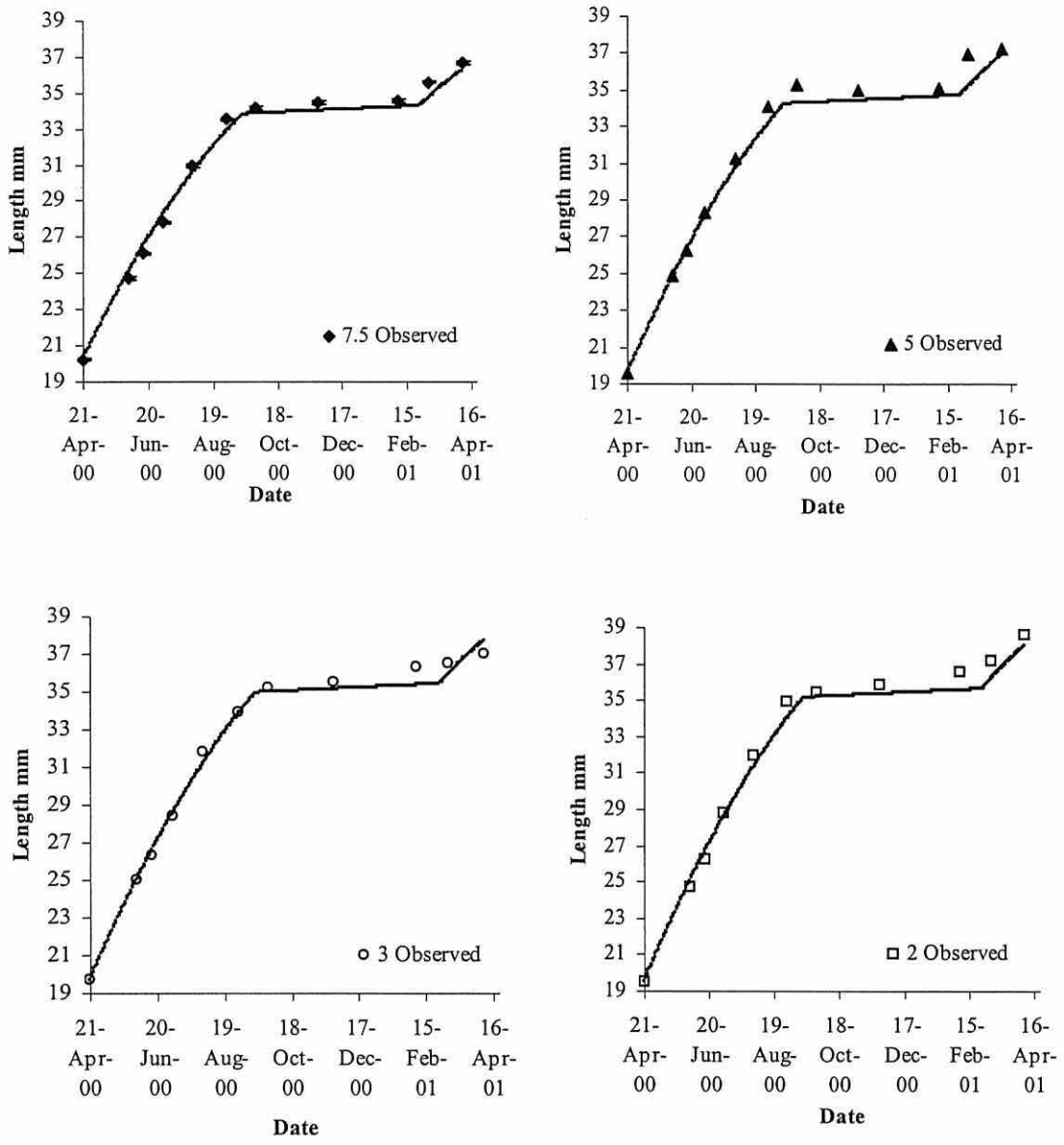

Fig. 3.5. Main Site. Predicted (solid lines) and observed mussel shell length (± SE, error bars can not be seen due to their small size) of mussels grown at four initial seeding densities (7.5, 5, 3 and 2 kg m^{-2}).

2. Caged mussel site

The same sampling time periods used on the main site for 'summer' and 'winter' growth were maintained for analysis of the caged mussel data.

a. 'Summer' growth period

Mussel shell length SGR had a significant negative relationship with increasing Ln(Length) (Table 3.4). To demonstrate the effect of shore height and initial density treatment on the relationship between SGR and length a three variable regression model of length, shore height and initial density was formulated (Table 3.4 and 3.5).

Caged site summer length model

$SGR = a + b(\text{Initial Density}) + c\text{Ln}(\text{Length}) + d(\text{Shore Height})$ Equation 2

Where a, b, c and d are fitted parameters.

The model provided a significantly better fit to the data set than the one variable model of length ($F_{2,140}=15.7$ $p<0.0001$).

Table 3.4. Caged Site 'Summer'. Analysis of goodness of fit of regression models of (i) SGR on Ln(length) and (ii) SGR on Ln(length), shore height and initial density (Caged site summer length model, Equation 2). Initial seeding densities Low 2, Medium 5, High 7.5 and Very High 15 kg m^{-2}. Shore heights 70, 100, 130, 160, 190 and 210 minutes exposed at mean low water springs.

Source	df	Sum of squares	Mean Square	F value	P	r^2
Length Model (all data)						
Within (explained by length)	1	0.000151	0.00015095	24.5	<0.0001	0.147
Unexplained	142	0.000875	0.00000616			
Total (All data)	143	0.001003				
Caged site summer length model (Equation 2)						
Within (explained by length, density and shore height)	3	0.000311	0.00010368	20.1	<0.0001	0.303
Unexplained	140	0.000715	0.00000510			
Total (All data)	143	0.001030				

Table 3.5. Caged Site 'Summer'. Parameter estimates for Caged site summer length model (Equation 2)

SGR = a + b(Initial Density) + c.Ln(Length) + d(Shore Height)

Parameter	Estimate	SE
a	0.0353	0.00433
b	-0.0000672	0.0000394
c	-0.00871	0.00124
d	-0.0000220	0.00000409

To support the development of the caged site summer length model an ANCOVA was carried out to test the effect of shore height on SGR, with length as a covariate, and was found to have a significant effect (ANCOVA covariate Length $F_{1,134}$=49.41 $p<0.0001$, initial density $F_{3,134}$=1.33 $p=0.267$, shore height $F_{5,134}$=5.90 $p<0.0001$). To establish between which shore heights there were significant differences LSM tests were conducted comparing each shore height to every other shore height, and the biggest differences were found between the highest and lowest shore levels (Table 3.6). Additionally, to establish if shore height had a significant effect on SGR at all initial seeding densities, each set of initial density treatment data was analysed separately by ANCOVAs, with length as a covariate. In this analysis shore height only had a significant effect in the medium (5 kg m^{-2}) initial density treatment (ANCOVA medium initial density length covariate $F_{1,29}$=21.7 $p<0.0001$, shore height $F_{5,29}$=3.48 $p<0.05$. All other tests not significant at $p<0.05$). It should be noted that for the high initial density treatment the length covariate did not have a very good relationship with SGR treatment (ANCOVA high initial density, length covariate $F_{1,29}$=3.82 $p=0.0604$). LSM pairwise tests were conducted comparing each shore height to every other shore height to establish between which shore heights there were significant differences. A significant effect of shore height on SGR was found for the medium (5 kg m^{-2}) and very high (15 kg m^{-2}) initial density treatments and between the highest and lowest shore levels (Table 3.7).

Table 3.6. Caged Site 'Summer'. Pairwise tests – Least square means for the effect of shore height on mussel length SGR with covariate Ln(length) for HO: LSMean (i) = LSMean (j). (Shore heights 70, 100, 130, 160, 190 and 210 minutes exposed at mean low water springs).

Bold print indicates significance $p<0.05$.

	Shore Height (minutes exposure)				
i/j	70	100	130	160	190
100	0.842				
130	0.218	0.300			
160	**0.017**	**0.028**	0.234		
190	**0.001**	**0.002**	**0.029**	0.307	
210	**<0.001**	**<0.001**	**0.002**	**0.039**	0.278

Table 3.7. Caged Site 'Summer'. Pairwise tests – Least square means for the effect of Shore Height on mussel SGR for each initial density (Low 2, Medium 5, High 7.5 and Very High 15 kg m^{-2}) with the covariate Ln(Length) for HO: LSMean (i) = LSMean (j). Shore heights 70, 100, 130, 160, 190 and 210 minutes exposed at mean low water springs.

Bold print indicates significance $p<0.05$.

Shore Heights Compared		Initial Density			
i	j	Low	Medium	High	Very High
70	100	0.708	0.549	0.651	0.503
	130	0.669	0.674	0.881	0.115
	160	0.366	0.201	0.549	**0.034**
	190	0.108	**0.041**	0.315	**0.023**
	210	**0.058**	**0.005**	0.246	**0.005**
100	130	0.425	0.314	0.763	0.344
	160	0.206	0.068	0.879	0.126
	190	**0.052**	**0.011**	0.564	0.098
	210	**0.026**	**0.001**	0.445	**0.021**
130	160	0.629	0.383	0.649	0.542
	190	0.228	0.094	0.379	0.445
	210	0.129	**0.013**	0.287	0.133
160	190	0.461	0.401	0.666	0.871
	210	0.282	0.081	0.526	0.349
190	210	0.722	0.334	0.828	0.427

Initial density did not have a significant effect on SGR in the full ANCOVA (ANCOVA covariate Length $F_{1,134}=49.41$ $p<0.0001$, initial density $F_{3,134}=1.33$ $p=0.267$, shore height $F_{5,134}=5.90$ $p<0.0001$). However in LSM pairwise tests, where each initial density treatment was compared to every other, a significant difference was apparent between the highest and lowest initial seeding densities (LSM low initial density compared to high initial density $p<0.05$. All other comparisons not significant at $p<0.05$). Analysis of the data within each shore height revealed that there was no significant effect of density on SGR (ANCOVAs with length as covariate, initial density effect $p>0.05$ for all shore heights, LSM tests comparing each initial density to every other $p>0.05$, for each comparison at each shore height).

b. 'Winter' growth period

There was no significant relationship between SGR and Ln(Length) over the winter period (Table 3.8) (Fig. 3.6). Since it was not possible to establish a relationship over this time period it would suggest that a constant SGR was maintained. There was no significant difference between the initial density treatments or shore heights (ANOVA initial density $F_{3,87}=2.04$ $p=0.113$, shore height $F_{5,87}=0.38$ $p=0.860$) and therefore a constant SGR was assumed for all of the treatments. To be consistent with the main site an estimate was made for SGR of 0.0008 mmday^{-1} over the 'winter' growth period.

Table 3.8. Caged Site. 'Winter'. Regression analysis of SGR and Ln(Length) for whole data set (shore height 70, 100, 130, 160, 190 and 210 minutes exposed at mean low water springs, initial density Low 2, Medium 5, High 7.5 and Very High 15 kg m^{-2}).

Source	df	Sum of squares	Mean Square	F value	P	r^2
Caged site winter length model (all data)						
Within (explained by length)	1	0.000002	0.00000247	2.32	0.131	0.024
Unexplained	94	0.000100	0.00000107			
Total (All data)	95	0.000103				

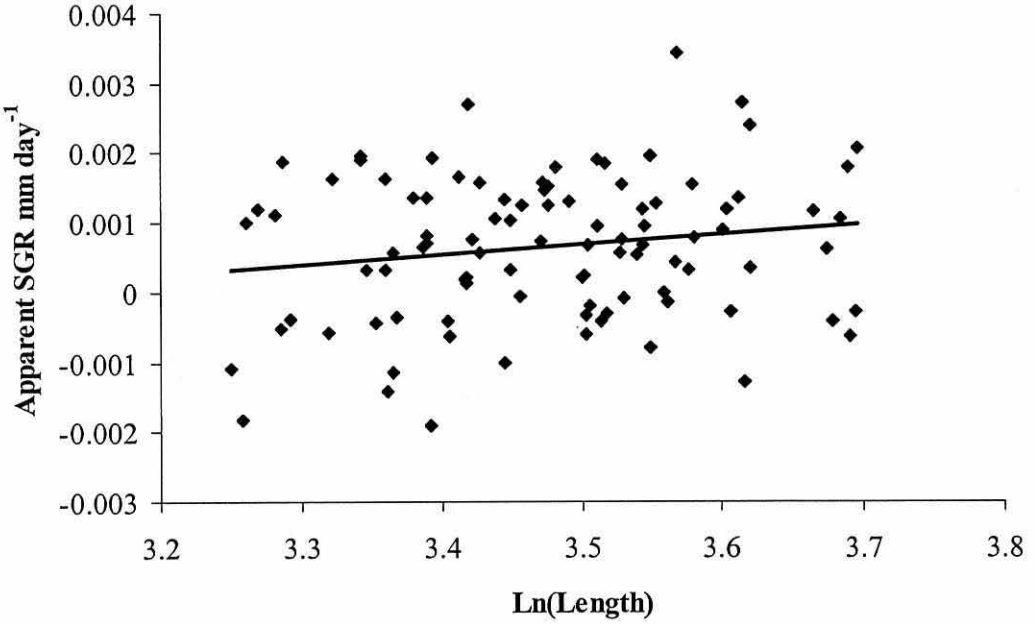

Fig. 3.6. Caged Site. Apparent mussel length SGR over the 'winter' growth period for mussels grown at four initial seeding densities (15, 7.5, 5 and 2 kg m^{-2}) and six shore heights (70, 100, 130, 160, 190, 210 mean minutes exposure at low water springs). Solid line indicates linear fit to data from all treatments.

c. Complete experimental time period

The caged site SGR models for the 'summer' and 'winter' period were used to predict mussel length over the whole time period for the four initial seeding densities, and six shore heights using the same prediction dates as for the main site (summer: beginning of March – mid September, winter: mid September – beginning of March). In order to demonstrate the fit of the predictive model to the observed data combinations of the highest and lowest experimental values of initial density and shore height were used (Fig. 3.7). The best fit of the model to the observed data was fairly consistently found at the lowest shore level (SH=70) for each density, and for the highest initial density (15 kg m^{-2}) at each shore level (Table 3.9). The r^2 values for the goodness of fit of the model to the individual treatment combination were all greater than 0.71, with the average value of 0.88. At the low initial seeding density treatment at the lowest shore level growth is under-predicted over the winter period resulting in growth being under-predicted for the following 'summer' growth period. At the very high initial density treatment (15 kg m^{-2}) at the lowest shore level the extent of growth over the 'summer' period is over-predicted and hence compensates for the under-prediction of growth during the winter period. At the highest shore level the 'summer' season for both very high (15 kg m^{-2}) and low (2 kg m^{-2}) initial density appears to be of the right duration. However, the growth is again under-predicted for the lowest (2 kg m^{-2}) initial density over the winter period.

Table 3.9. Least squares goodness of fit (r^2) for caged site length model predictions to each observed cages treatment (shore height 70, 100, 130, 160, 190 and 210 minutes exposed at mean low water springs, initial density Low 2, Medium 5, High 7.5 and Very High 15 kg m^{-2}) for full experimental time period.

Shore Height	Initial Density			
	Low	Medium	High	Very High
70	0.909	0.960	0.923	0.956
100	0.811	0.820	0.919	0.952
130	0.804	0.899	0.939	0.870
160	0.771	0.927	0.920	0.949
190	0.708	0.886	0.912	0.911
210	0.862	0.896	0.790	0.851

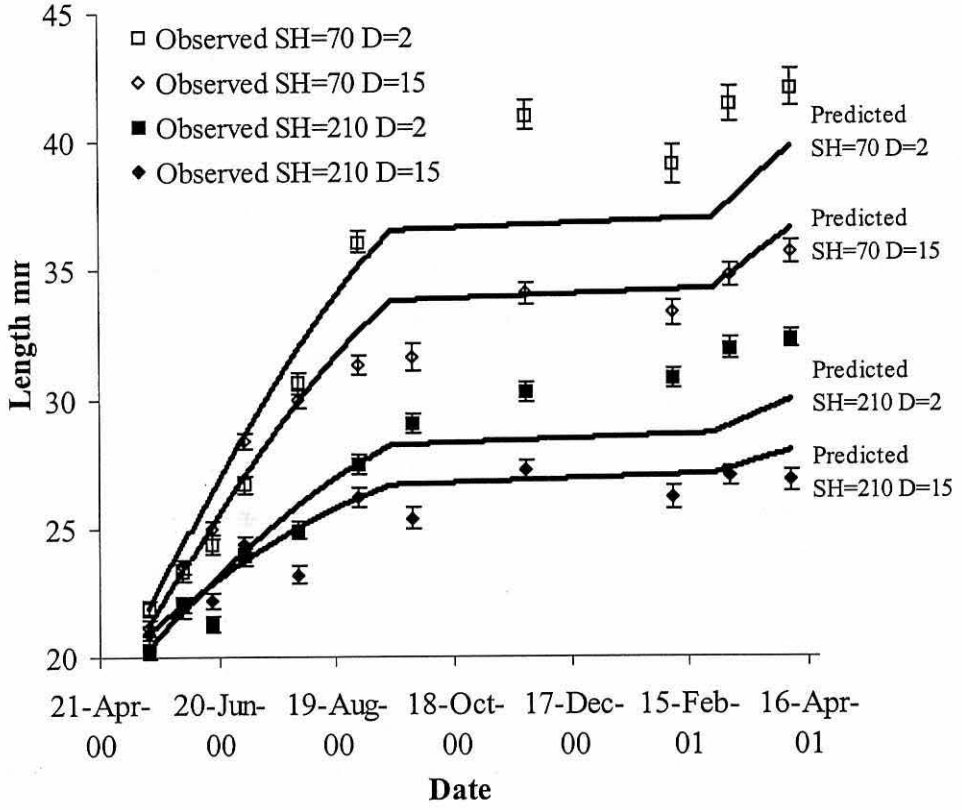

Fig. 3.7. Caged Site. Predicted and observed mean shell length (± SE) of mussels grown at highest (SH=210) and lowest (SH=70) shore heights and highest (D=15) and lowest (D=2) initial seeding densities. Shore height measured in mean minutes exposure at low water springs. Density as initial seeding density in kg m^{-2}.

3. Combined data sets

a. 'Summer' growth period

The two data sets from the main site and caged site were combined together. It was therefore necessary to establish the shore height at the main site. This was determined from observation to be 115 minutes mean exposure at low water springs. The combined main site and caged mussel data sets were used in a single model (as Equation 2). The single model (Combined sites summer length model) did not fit the observed data significantly worse than the two separate models (Table 3.10 and 3.11) ($F_{3,331}$=0.313 p=0.816).

Table 3.10. Main Site and Caged Site. 'Summer' growth period. Analysis of goodness of fit of individual regression models for each site (Main site summer length model and Caged site summer length model) and regression models of the combined data set (Combined sites summer length model).

Source	df	Sum of squares	Mean Square	F value	P	r^2
Main site summer length model						
Within (explained by length, density)	2	0.000401	0.00020037	109.03	<0.0001	0.537
Unexplained	188	0.000345	0.00000184			
Total (Main site)	190	0.000746				
Caged site summer length model						
Within (explained by length, density, shore height)	3	0.000311	0.00010368	20.31	<0.0001	0.303
Unexplained	140	0.000715	0.00000510			
Total (Cages)	143	0.001030				
Combined sites summer length model						
(Main site + cages data)						
Separate Models						
Within separate models	5	0.000712	0.00014324	44.04	<0.0001	0.398
Between sites (separate models)	1	0.000014	0.00001377	4.260	0.0398	0.008
Total explained by separate sites and models	6	0.000726	0.00012092	37.41	<0.0001	0.405
Total unexplained by separate models	328	0.001060	0.00000323			
Single model (Equation 2)						
Within (explained by length, density and shore height)	3	0.000723	0.00024093	75.02	<0.0001	0.405
Unexplained by single model	331	0.001060	0.00000321			
Total (All data)	334	0.001790				

Table 3.11. Main Site and Caged Site 'Summer'. Parameter estimates for Combined sites summer length single model (using Equation 2)

SGR = a + b(Initial Density) + c.Ln(Length) + d(Shore Height)

Parameter	Estimate	SE
a	0.0346	0.0021
b	-0.0000804	0.0000260
c	-0.00841	0.000592
d	-0.0000224	0.00000293

b. 'Winter' growth period

Over the winter period an average SGR value of 0.0008 $mmday^{-1}$ was assumed.

c. Complete experimental time period

Not surprisingly the model based on the combined data set did not have as good a fit to the observed main site data as the model calculated solely for the main site. However the difference in the r^2 values was only slight (combined data set model for lowest to highest density (main site only model in brackets) r^2=0.9571 (0.9574), 0.9931 (0.9932), 0.9804 (0.9805), 0.9908 (0.9908). The model fit equally well to the caged mussel data as the individual caged mussel model, and the r^2 values were exactly the same.

Dry Weight Data

1. Main Site

Significant regression relationships between Ln(Length) and Ln(DW) were found for each initial density treatment on each sampling date (in regression analysis all $p<0.0001$). A clear pattern in the length/DW relationship was demonstrated over the yearly cycle for each density treatment and this is illustrated by the change in the slope and the intercept of the linear regressions for each date (Fig. 3.8 and 3.9). A regression model was developed for each initial density treatment using a cosine function to model the change in slope and intercept over the yearly cycle.

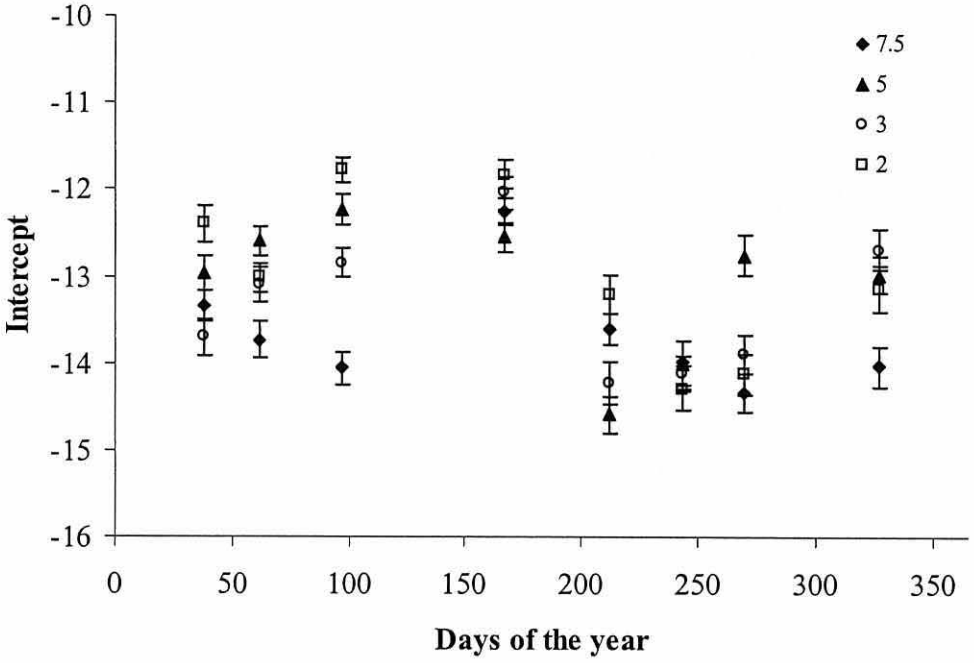

Fig. 3.8. Main Site. Relationship of the intercept (± SE) over a yearly cycle of the linear regression between Ln(Length) and Ln(Dry Weight) for the 4 initial seeding densities (7.5, 5, 3 and 2 kg m^{-2}).

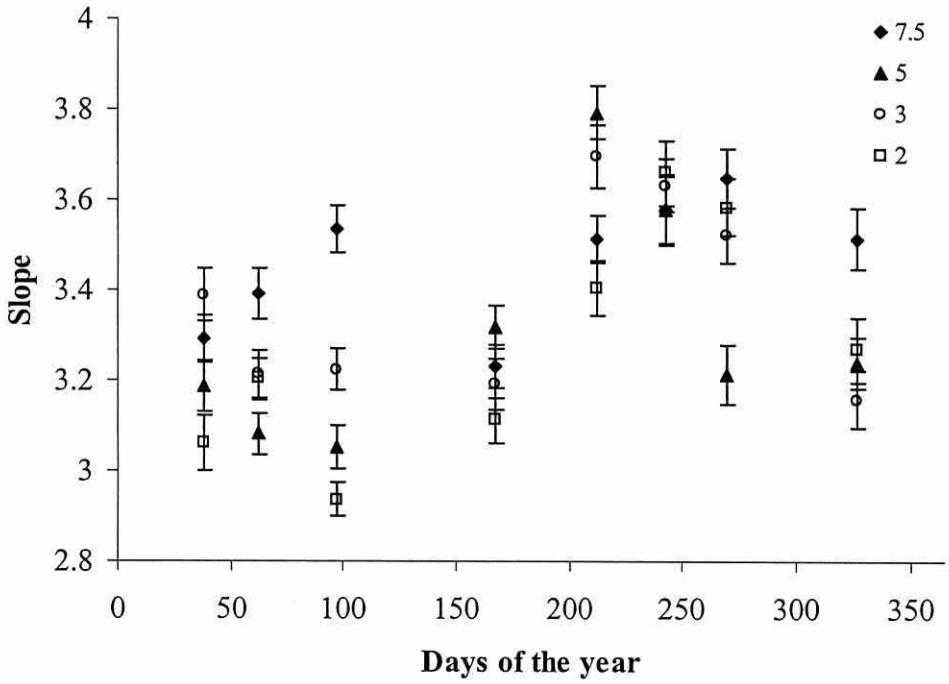

Fig. 3.9. Main Site. Relationship of the slope (± SE) over a yearly cycle of the linear regression between Ln(Length) and Ln(Dry Weight) for the 4 initial seeding densities (7.5, 5, 3 and 2 kg m^{-2}).

Main site seasonal DW model

Ln(Dry Weight) =Intercept + Slope.Ln(Length) Equation 3

Where:

Intercept = $0.5(a+b+(a-b)\cos(2\pi)((Days/365)-(c/365)))$

Slope = $(0.5(d+e+(d-e)\cos(2\pi)((Days/365)-(f/365)))))$

Where a, b, c, d, e and f are fitted parameters. Days represent the day of the year where January 1st= day 1.

For each initial density treatment the regression model had a highly significant fit to the data (Table 3.12).

To support further development of the Main Site Seasonal DW Model an ANCOVA was carried out on each date to test the effect of initial seeding density on DW, with length as a covariate. Initial density had a significant effect on each of the dates, except for day 243 (Table 3.14). A single regression model was developed for the entire data set to demonstrate this effect of initial seeding density by the addition of an extra term to Equation 3 to represent the effect of the initial density treatment (Table 3.12 and 3.13).

Main site seasonal DW model with density

Ln(Dry Weight) =Intercept + Slope.Ln(Length) + g(Initial Density) Equation 4

Where: Intercept = $0.5(a+b+(a-b)\cos(2\pi)((Days/365)-(c/365)))$

Slope = $(0.5(d+e+(d-e)\cos(2\pi)((Days/365)-(f/365)))))$

and where a, b, c, d, e, f and g are fitted parameters.

The single model 'Main site seasonal DW model with density' had a significantly worse fit to the data than the combined 'Main site seasonal DW models' of each initial density treatment ($F_{17,27862}$=16.4 $p<0.0001$) (Table 3.12 and 3.13). The single model did not fit the observed data equally well for each initial density treatment, and the worst fit occurred between the model predictions and the observed Medium-Low density treatment (Low, Medium-Low, Medium, High initial densities respectively r^2=0.767, 0.435, 0.688, 0.616) (Fig. 3.10). However, the single model still maintained a significantly good fit to the data, and reduced the number of model parameters by 16 (Table 3.12).

Table 3.12. Main Site. Analysis of goodness of fit of regression models of i) Ln(DW) to Ln(length) for each initial seeding density (Main site seasonal DW models, Equation 3) and ii) Ln(DW) to Ln(length) and initial seeding density. Initial seeding densities Low (2 kg m^{-2}), Medium-Low (3 kg m^{-2}), Medium (5 kg m^{-2}), and High (7.5 kg m^{-2}).

Source	df	Sum of squares	Mean Square	F value	P	r^2
Low Density						
Within (explained by length)	6	13932.3	2322.1	36794	<0.0001	0.967
Unexplained	7447	470.0	0.0631			
Uncorrected Total	7453	14402.3				
Total	7452	1986.5				
Medium-Low Density						
Within (explained by length)	6	14858.6	2.476.4	33729	<0.0001	0.965
Unexplained	7420	544.8	0.0734			
Uncorrected Total	7426	15403.4				
Total	7425	2161.8				
Medium Density						
Within (explained by length)	6	16529.8	263.9	39690	<0.0001	0.969
Unexplained	7531	522.7	0.0694			
Uncorrected Total	7537	17052.5				
Total	7536	2106.0				
High Density						
Within (explained by length)	6	18197.6	3032.9	42516	<0.0001	0.972
Unexplained	7460	532.2	0.0713			
Uncorrected Total	7466	18729.8				
Total	7465	2265.5				
Main site seasonal DW model with density (combined data sets of all densities)						
Separate Models						
Within separate models	20	6450.1	322.51	4653	<0.0001	0.743
Between sites (separate models)	3	162.6	54.200	782	<0.0001	0.019
Total explained by separate sites and models	23	6612.7	287.51	4148	<0.0001	0.762
Total unexplained by separate models	29862	2069.7	0.0693			
Single model (Equation 4)						
Within (explained by density and length)	7	63499	9071.3	129730	<0.0001	0.968
Unexplained by	29875	2089	0.0699			
Uncorrected total	29882	65588				
Total (All data)	29881	8682.4				

Table 3.13. Main Site. Parameter estimates for Main site seasonal DW model with density single model (Equation 4).

Ln(Dry Weight) =Intercept + Slope.Ln(Length) + g(Initial Density)

Where: Intercept = $0.5(a+b+(a-b)\cos(2\pi)((Days/365)-(c/365)))$

Slope = $(0.5(d+e+(d-e)\cos(2\pi)((Days/365)-(f/365)))))$

Parameter	Estimate	SE
a	-15.3	0.076
b	-9.87	0.0512
c	-42.9314	1.0664
d	3.875	0.0211
e	2.46	0.0147
f	-48.1	1.16
g	-0.00794	0.000734

Table 3.14. Main Site. ANCOVAs on each sampling day to test the effect of initial density on DW with Ln(Length) as covariate. Initial seeding densities Low (2 kg m^{-2}), Medium-Low (3 kg m^{-2}), Medium (5 kg m^{-2}), and High (7.5 kg m^{-2}).

Source	df	F value	P	Source	df	F value	P
Day 38				**Day 212**			
Length	1	12925	<0.0001	Length	1	14079	<0.0001
Density	3	6.56	0.0002	Density	3	8.68	<0.0001
Density*Length	3	5.53	0.0009	Density*Length	3	8.47	<0.0001
Error	3557			Error	3738		
Corrected Total	3564			Corrected Total	3745		
Day 62				**Day 243**			
Length	1	15756	<0.0001	Length	1	10500	<0.0001
Density	3	6.51	0.0002	Density	3	0.26	0.8507
Density*Length	3	6.27	0.0003	Density*Length	3	0.30	0.8226
Error	3770			Error	3649		
Corrected Total	3777			Corrected Total	3656		
Day 97				**Day 270**			
Length	1	19038	<0.0001	Length	1	12053	<0.0001
Density	3	35.29	<0.0001	Density	3	9.26	<0.0001
Density*Length	3	32.85	<0.0001	Density*Length	3	8.83	<0.0001
Error	3770			Error	3785		
Corrected Total	3777			Corrected Total	3792		
Day 167				**Day 327**			
Length	1	15600	<0.0001	Length	1	10180	<0.0001
Density	3	3.46	0.0158	Density	3	6.39	0.0003
Density*Length	3	2.93	0.3250	Density*Length	3	5.81	0.0006
Error	3760			Error	3789		
Corrected Total	3767			Corrected Total	3796		

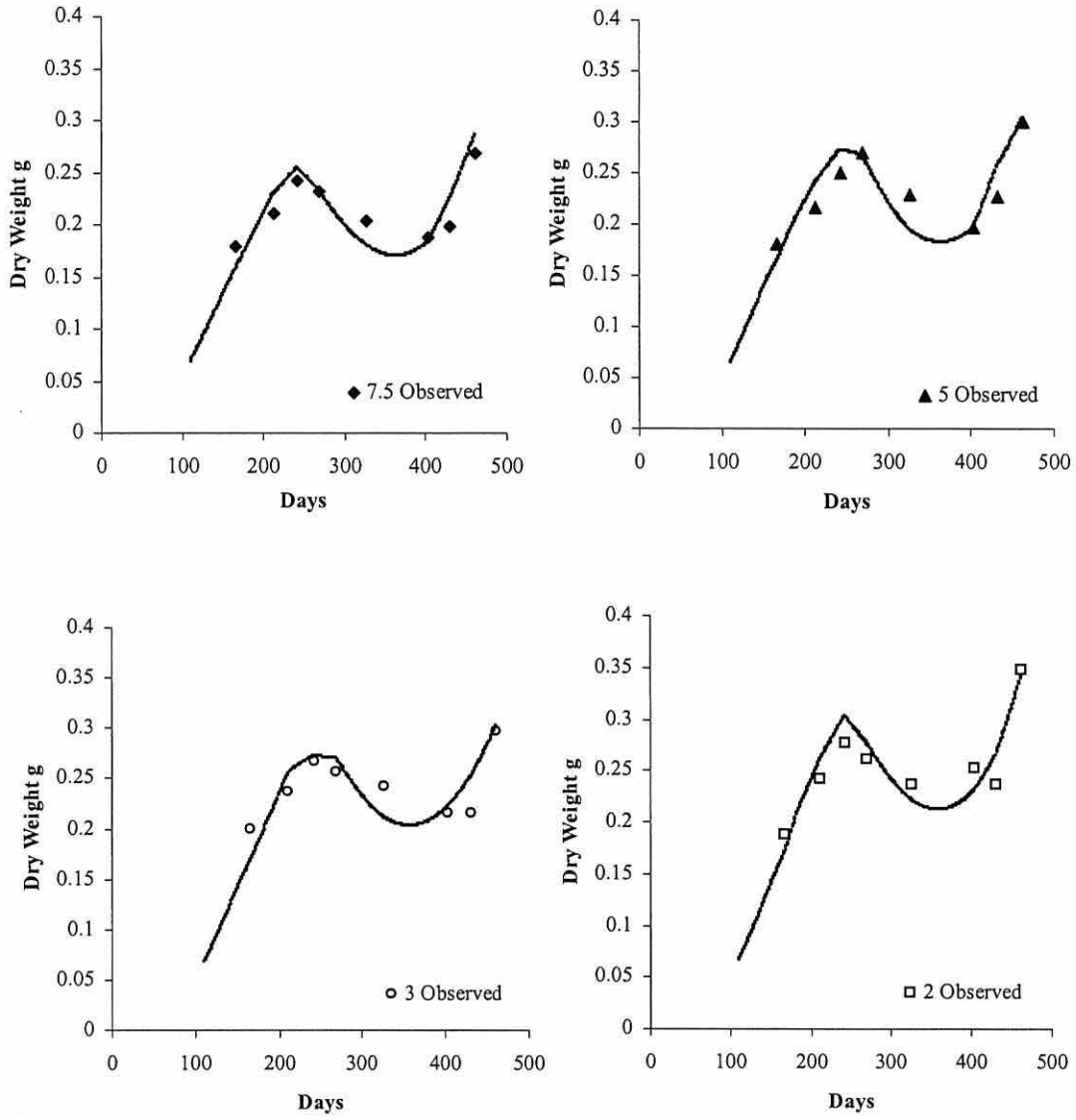

Fig. 3.10. Main Site. Predicted (solid line) and observed dry weight of mussels grown at four initial seeding densities (7.5, 5, 3 and 2 kg m^{-2}) using the Main site seasonal DW model with density (Equation 4). Where day 1 is 1st January 2000.

2. Caged mussel site

Significant regression relationships between Ln(Length) and Ln(DW) were found for each initial density, and at each shore height on each sampling date (for all regression analyses in all cases $p<0.0001$). To test the effect of shore height and initial density on mussel DW ANCOVAs were carried out on each date, with length as a covariate. Significant effects of shore height and density were found on each of the dates except for shore height on day 38, and 243 and initial mussel density on day 243 (Table 3.15).

Table 3.15. Caged Site. ANCOVAs on each sampling day to test the effect of shore height (SH) and initial seeding density on DW with Ln(Length) as covariate (shore height 70, 100, 130, 160, 190 and 210 minutes exposed at mean low water springs, initial density Low 2, Medium 5, High 7.5 and Very High 15 kg m^{-2}).

Source	df	F value	P	Source	df	F value	P
Day 38				**Day 212**			
Length	1	2084	<0.0001	Length	1	1567	<0.0001
Density	3	8.69	<0.0001	Density	3	5.98	0.0005
SH	5	1.74	0.1233	SH	5	99.03	<0.0001
Density*Length	3	8.39	<0.0001	Density*Length	3	7.10	0.0001
SH*Length	5	1.62	0.1532	SH*Length	5	96.50	<0.0001
Error	668			Error	675		
Corrected Total	685			Corrected Total	692		
Day 97				**Day 243**			
Length	1	4798	<0.0001	Length	1	4088	<0.0001
Density	3	10.47	<0.0001	Density	3	1.27	0.2851
SH	5	11.79	<0.0001	SH	5	3.62	0.0030
Density*Length	3	8.21	<0.0001	Density*Length	3	0.98	0.4007
SH*Length	5	9.44	<0.0001	SH*Length	5	3.38	0.0050
Error	700			Error	693		
Corrected Total	717			Corrected Total	710		
Day 167				**Day 270**			
Length	1	2433	<0.0001	Length	595	915.8	<0.0001
Density	3	54.33	<0.0001	Density	3	21.53	<0.0001
SH	5	56.65	<0.0001	SH	5	56.25	<0.0001
Density*Length	3	65.64	<0.0001	Density*Length	35	21.63	<0.0001
SH*Length	5	56.16	<0.0001	SH*Length	1	54.76	<0.0001
Error	700			Error	612		
Corrected Total	717			Corrected Total			
Day 184				**Day 327**			
Length	1	5521	<0.0001	Length	1	4375	<0.0001
Density	3	5.12	0.0017	Density	3	2.82	0.0382
SH	5	3.31	0.0058	SH	5	5.74	<0.0001
Density*Length	3	5.52	0.0010	Density*Length	3	2.90	0.0344
SH*Length	5	3.39	0.0049	SH*Length	5	6.05	<0.0001
Error	689			Error	698		
Corrected Total	715			Corrected Total	715		

To demonstrate the effects of initial density on mussel DW a linear regression model was formulated for each shore height as for the 'Main site seasonal DW model with density' (Equation 4). The models provided a significant fit to the data at each shore level, although the fit was not found to be as good for the data of the lowest shore height (SH=70) compared to the other shore heights (Table 3.16).

To demonstrate the effect of both initial seeding density and shore height on mussel DW the regression model was developed further incorporating all initial densities and shore heights (Table 3.17 and 3.18).

Caged site seasonal DW model with density and shore height Equation 5

$$\text{Ln(Dry Weight)} = \text{Intercept} + \text{Slope}.\text{Ln(Length)} + g(\text{Initial Density}) + h(\text{Shore Height})$$

Where: $\text{Intercept} = 0.5(a+b+(a-b)\cos(2\pi)((\text{Days}/365)-(c/365))))$

$\text{Slope} = (0.5(d+e+(d-e)\cos(2\pi)((\text{Days}/365)-(f/365)))))$

Where a, b, c, d, e, f, g and h are fitted parameters.

The single model (Caged site seasonal DW model with density and shore height) fit the data significantly worse than the combined separate models for each of the shore heights ($F_{33,5529}=489$ $p<0.0001$). The single model did not fit equally well to all the shore heights and initial density treatments (Table 3.18, Fig. 3.11 and Fig. 3.12). The best model fits to the observed data were found at the lowest initial densities and lowest shore heights, while the worst fits occurred at the highest initial density and highest shore heights. At the highest initial density and shore height there is a less distinct seasonal trend in the observed DW compared to that of the lower initial density and shore height treatments (Fig. 3.11). Nonetheless, the single model does provide a significantly good fit to the data, with a reduction of 33 parameters.

Table 3.16. Caged Site. Analysis of goodness of fit of regression models of i) Ln(DW) to Ln(length) and density for each shore height (Main site seasonal DW models with density, Equation 4), and ii) Ln(DW) to Ln(length), density and shore height (Equation 5). Initial seeding densities 2, 5, 7.5 and 15 kg m^{-2}, and shore heights 70, 100, 130, 160, 190 and 210 minutes exposed at mean low water springs.

Source	df	Sum of squares	Mean Square	F value	P	r^2
SH = 70						
Within (length and density)	7	2100.2	300.0	1278	<0.0001	0.402
Unexplained	922	216.4	0.2347			
Uncorrected Total	929	2316.6				
Total	928	360.8				
SH = 100						
Within (length and density)	7	2249.7	7126	7126	<0.0001	0.866
Unexplained	942	42.5	0.0451			
Uncorrected Total	949	2292.1				
Total	948	318.0				
SH = 130						
Within (length and density)	7	2815.6	402.2	6819	<0.0001	0.836
Unexplained	886	52.3	0.0590			
Uncorrected Total	893	2867.9				
Total	892	319.4				
SH = 160						
Within (length and density)	7	3271.0	467.3	5665	<0.0001	0.786
Unexplained	917	75.6	0.0825			
Uncorrected Total	924	3346.6				
Total	923	354.1				
SH = 190						
Within (length and density)	7	3872.8	553.3	731	<0.0001	0.822
Unexplained	949	69.1	0.0728			
Uncorrected Total	956	3941.9				
Total	955	388.6				
SH = 210						
Within (length and density)	7	4380.6	625.8	6325	<0.0001	0.766
Unexplained	913	90.3	0.0989			
Uncorrected Total	920	4471.0				
Total	919	385.7				
Caged site seasonal DW model with density and shore height (all SH) Equation 5						
Separate Models						
Within separate models	36	1580.4	43.9	444	<0.0001	0.646
Between sites (separate models)	5	325.1	65.0	658	<0.0001	0.132
Total explained by separate sites and models	41	1905.5	46.5	470	<0.0001	0.777
Total unexplained by separate models	5529	546.2	0.0988			
Single model (Equation 5)						
Within (explained by length density and shore height)	8	18413.2	2301.6	15560.2	<0.0001	0.664
Unexplained by single model	5563	822.9	0.1479			
Uncorrected total	5571	19236.1				
Total (All data)	5570	2451.7				

Table 3.17. Caged Site. Parameter estimation for Caged site seasonal DW model with density and shore height (Equation 5)

Ln(Dry Weight) =Intercept + Slope.Ln(Length) + g(Initial Density) + h(Shore Height) Where:

Intercept = $0.5(a+b+(a-b)\cos(2\pi)((Days/365)-(c/365)))$

Slope = $(0.5(d+e+(d-e)\cos(2\pi)((Days/365)-(f/365)))))$

Parameter	**Estimate**	**SE**
a	-7.488	0.126
b	-12.330	0.199
c	-157.3	2.78
d	1.83	0.0366
e	3.09	0.0548
f	-153	0.0548
g	-0.0122	0.00109
h	-0.00158	0.000111

Table 3.18. Caged Site. Least squares goodness of fit (r^2) of Caged Site Seasonal DW Model with Density and Shore Height predictions to observed dry weight for each treatment (shore height 70, 100, 130, 160, 190 and 210 minutes exposed at mean low water springs, initial density Low 2, Medium 5, High 7.5 and Very High 15 kg m^{-2}).

Shore Height	Initial Density			
	Low	Medium	High	Very High
70	0.879	0.667	0.893	0.598
100	0.891	0.833	0.724	0.636
130	0.903	0.838	0.710	0.300
160	0.842	0.677	0.166	0.150
190	0.691	0.544	0	0.016
210	0.553	0.435	0	0

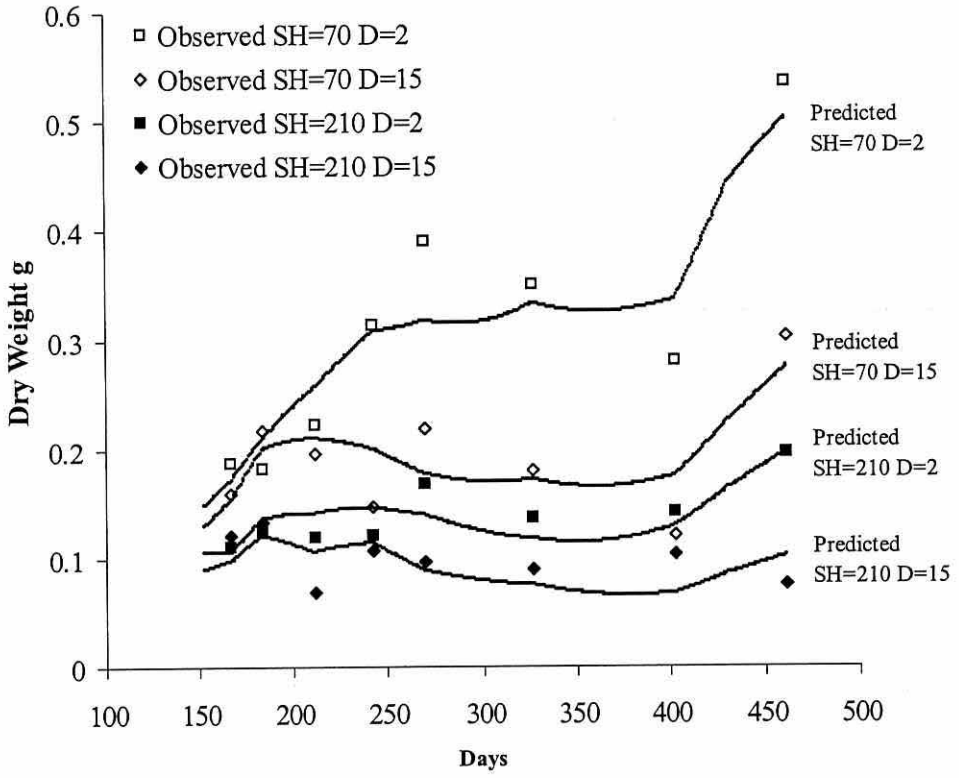

Fig. 3.11. Caged Site. Predicted and observed dry weight of mussels grown at highest (SH=210) and lowest (SH=70) shore heights and highest (D=15) and lowest (D=2) initial densities using the Caged site seasonal DW model with density and shore height (Equation 5). Shore height measured in mean minutes exposure at low water springs. Density as initial seeding density in kg m^{-2}.

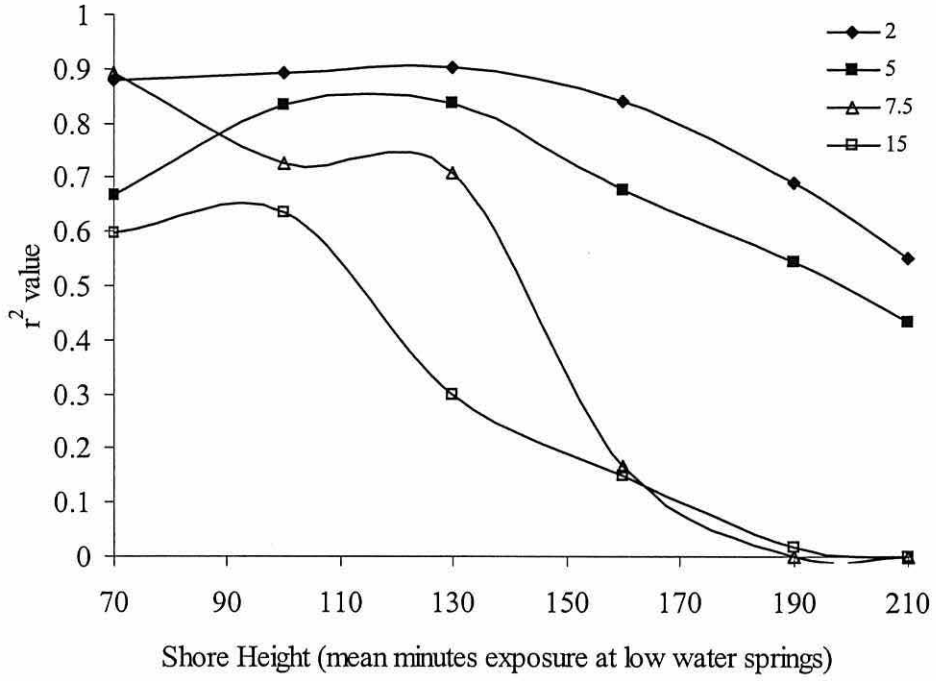

Fig. 3.12. Caged Site. Goodness of fit (r^2 value) of predicted (using the Caged site seasonal DW model with density and shore height Equation 5) to observed dry weight of mussels grown in cages at four initial seeding densities (15, 7.5, 5 and 2 kg m^{-2}) and six shore heights (70, 100, 130, 160, 190, 210 mean minutes exposure at low water springs).

DISCUSSION

Mussel shell length

The rate of increase in mussel shell length at the main site decreased with increasing mussel density. High mussel density can cause reduced growth rate by both physical interference (Okamura 1986; Fréchette *et al.* 1992), and/or by localised food depletion (Bertness and Grosholz 1985; Fréchette and Bourget 1985a and b). Through the use of a linear regression model for SGR that incorporated density effects, mussel shell length was predicted with high precision for the four initial seeding densities at the main site. However over the 'winter' period significant differences in growth rate were not found between the different initial density treatments (Fig 3.5). This might be due to the limited number of sampling occasions used to detect differences in a relatively small amount of growth over this period. During the colder winter months, although reduced growth rate is expected as a result of reduced food supply (Seed 1969), density dependent effects may have continued to have an effect within the mussel populations. Hence the increasing discrepancy over the winter months between predicted and observed mussel shell length growth (Fig. 3.5) with decreasing density in the Complete experimental time period length model, is likely to be a result of the constant growth rate within the model for all of the mussel densities.

The caged site summer length model did not have as good a fit to the observed data in comparison to the main site summer length model over the 'summer' growth period (Table 3.10). This may be due to the lower sampling effort and replication at the caged mussel site compared to the main site. However, significant effects of shore height and initial seeding density were found for the caged mussels. The shore height effect was very clear with pronounced differences between the lowest and highest shore levels (Table 3.6). The effect of shore height is related to the time available for feeding, hence those mussels lower down the shore have longer to feed and therefore the potential to attain high growth rates (Sukhotin and Maximovich 1994; Baird 1966). When the separate density treatments were considered individually for the effect of shore height a significant effect was only found in only one of the density treatments. For the high initial density treatment (7 kg m^{-2}) there was no significant relationship of SGR with length, and for this reason a significant effect of shore height may not have been detected in the pairwise tests. However, when the other initial density treatments were considered a clearer pattern was found with a greater effect of shore height at the higher densities (Table 3.7). Over the experimental period the amount of space available in the cages would have been reduced due to increase in total biomass and this would occur at a relatively faster rate in the higher density

treatments due to the greater number of individuals present. At these higher densities there may therefore be a greater negative effect on mussel growth rate due to physical interference (Fréchette *et al.* 1992). The effect of density at the caged mussel site was not as marked as the effect of shore height and no significant differences were found between initial seeding densities when the shore heights were analysed separately. When the data were split into the separate densities there was no significant relationship for SGR with length in the high density treatment. This may have been the result of a large amount of variability in the data and could have subsequently effected the density data set such that the likelihood of establishing a density effect was reduced.

Over the 'winter' growth period in the caged mussel site, as for the main site, there was no significant effect of initial density or shore height on mussel shell growth rate. Again this is likely to be due to the reduced number of sampling occasions over which a relatively small growth increment was measured. Nonetheless, the complete experimental time period model for the caged mussels provided a good fit to the observed data sets (Table 3.10). The model did not fit equally well at all the initial seeding densities and shore heights, with the best fits observed at the highest initial densities and lowest shore level (Table 3.9). On examination of the predicted against the observed data the variation in the model fit appears to be as a result of two main factors. Firstly, the constant SGR over the winter period had an important effect. The observed data indicated that there had been an effect of both shore height and initial density over the 'winter' period as demonstrated in the 'summer' growth period, even though these effects were not detected with statistical significance in this experiment. This would result in higher growth rates at the lowest shore levels and initial densities compared to the higher initial densities and shore heights. The second factor was the timing and number of days in each of the growth seasons. At the highest initial density the growth rate of the mussels decreased earlier in the year than at the low initial densities. It is likely that this was a food limited response since the decreasing food supply over this period would be exhausted by mussels at a high density at a faster rate than a low density. The effect was also more apparent at the lower shore heights were the mussels were larger and therefore each mussel would remove a relatively larger amount of the food resource (Jørgensen 1990). The effect of over-predicting the shell length of mussels during the 'summer' growth period at the high initial densities also meant that the mussels were predicted to be larger by the start of the 'winter' period than was observed, and hence this compensated for the effect of under-predicting 'winter' growth rate at the lower shore heights. The number of

days used in the model of the 'summer' growing season may have had further repercussions in the accuracy of the model predictions as difference in the time period of each growing season as a result of shore height was not a factor that was included in the development of the SGR models.

Using the combination of the main site and caged mussel site data sets in generating a single model of the effect of initial density and shore height on mussel growth is viewed with caution. For example the cages will have had an effect on the hydrodynamic regime influencing food availability as demonstrated by Virnstein (1978), and due to being at different sites the caged and main site may have had different substrates, shore gradients and general hydrodynamic regime which could have influenced mussel growth rate. However, when the data sets were combined to produce a single model there was no a significant change in the fit to the observed data (over the 'summer' growth period). The advantage of this combined model is that it would allow prediction of mussel growth rate for a range of both shore heights and initial densities, as used in this experiment. The final combined dataset model provided good fits to the observed data and thus provides a useful tool in the determination of seabed cultivated mussel shell growth for a range of initial seeding densities and shore heights.

Mussel flesh dry weight

The regression models developed for mussel flesh dry weight represent a seasonal pattern through modelling the change in the linear relationship between Ln(dry weight) and Ln(length) over time. Food scarcity and the metabolic requirements of the mussel gametogenic cycle govern the seasonal change in the relationship between length and dry weight over the yearly cycle (Smaal and Vonckk 1997; Hawkins and Bayne 1985; Dare and Edwards 1975). In temperate zones dry weight increases from April/May to September, and then declines in autumn and winter, which has been attributed to food scarcity (Dare and Edwards 1975; Pieters *et al.* 1979; Smaal and Vonckk 1997). Additionally the utilisation of reserves for gonad development in the late autumn and winter can cause weight loss at a time of reduced food availability (Dare and Edwards 1975). Dry weight then reaches a minimum in spring following spawning (Dare and Edwards 1975).

A significant affect of initial density on the mussel DW/Length relationship was demonstrated for every date except one. Mussel density affects growth through localised food depletion (Okamura 1986; Fréchette and Lefaivre 1990) and physical

interference (Bertness and Grosholz 1985; Fréchette and Bourget 1985a, b) and this is likely to have similar consequences for dry weight as for shell growth. The impact of density-dependent effects on dry weight, even though they are complicated by the gametogenic cycle, would also be more apparent than in measurements of shell length as body weight can be lost as well as gained. The model developed for DW for the main site (Main site seasonal DW model with density) provided a good fit to the observed data for each initial seeding density treatment (Table 3.12), although the fit was not as good for the medium-low initial density (Fig. 3.10). The initial model developed solely for the medium-low density gave a good fit to the data hence the cyclic relationship was well represented (Table 3.12). The Main site seasonal DW model (Equation 3) provided a good fit to the observed dry weight data for the density treatments both above and below this density treatment, thus the assumption of a linear relationship for density in the Single Model Main Site Seasonal DW Model with Density (Equation 4) was valid. It is therefore unclear why the model did not provide as good a fit to the observed medium-low density dry weight. Nonetheless overall the single model provided a good fit to the main site observed dry weight data.

At the caged mussel site there was evidence of the effect of both density and shore height on the mussel DW/Length relationship (Table 3.15). Some bivalve species display increased clearance rates, or absorption efficiency at higher tidal levels to compensate for reduced feeding time (e.g. *Perna canaliculus*, Marsden and Weatherhead 1999; *Mytilus californicus*, Segal *et al.* 1953). *Mytilus edulis* does not demonstrate either of these adaptations (Jorgensen 1975, Widdows and Shick 1985), however, it is able to adapt to intertidal conditions by maximising the energy available for growth, primarily by conserving energy during air exposure (Famme *et al.* 1981; Widdows and Shick 1985) and anaerobic metabolism (Gillmor 1982; de Zwaan 1977). In this experiment the effect of shore height was still significant. Therefore adaptation by the mussels was not able to fully compensation for the effects of a reduced and intermittent feeding regime found at higher shore levels.

The Caged site seasonal DW model with density and shore height (equation 5) fit well to the dataset. However, the model did not fit equally well to the observed data of all the individual initial seeing densities and shore heights. The best model fits were observed at the lowest density (2 kg m^{-2}) and lowest shore level (70 minutes mean exposure low water springs) (Table 3.18). In the mussel shell length model, even though there were differences in the goodness of fit, the r^2 value was consistently above 0.70. In the dry weight model the r^2 values range from zero to

0.90, clearly displaying a greater variation in the fit to the model. The individual shore height models of mussel flesh dry weight, which combined the initial seeding density treatments, provided good fits to the data. Hence there was a good linear relationship between the density treatments on mussel dry weight and this concurs with the findings on the main site. The low r^2 values displayed in the combined shore height and density model may therefore occur as a result of the inclusion of shore height. This does not mean that shore height does not have an effect but that the effect is non-linear and hence is not well represented by the model. The r^2 value is lowest for the highest initial densities at the highest shore levels and this is the most stressful environment of all mussel treatments, with the greatest emersion times and crowding. It is possible that under these conditions the mussels did not display the characteristic seasonal cyclic pattern of DW to the same extent as at the other treatments. Energy partitioning may also be different in these treatments with greater resources supplied to shell growth rather than flesh weight (Seed 1973).

The shore height model did not provide a good fit for all of the shore height treatments and for this reason the caged mussel data set was not combined with the main site data set in the same way as for the mussel shell length analysis. The main site model provides a good representation of the dry weight/length relationship for mussel cultivation at approximately 115 minutes mean water exposure at low water springs. The full caged mussel model (shore height and density) is not appropriate for all of the shore height treatments of the experiment but still provided good estimations within 70-130 minutes mean water exposure time at low water springs.

Management options

The mussel shell length and dry weight models can be used as a management tool to predict mussel production for a variety of different cultivation strategies. The growth models predict 'apparent specific growth rate', not actual specific growth rate. This means that size specific mortality is included within the model and hence the apparent growth rate results not only from mussel growth but also from change in mean mussel size as a result of mortality. While this method means that actual mussel growth rates are not predicted, it provides a more precise management tool since it will reflect actual mussel production not potential mussel production without mortality.

The statistical model developed will enable mussel shell length to be predicted with a high degree of accuracy over the full range of intertidal conditions used for mussel cultivation in the Menai Strait. The high r^2 values (all >0.70) reflect the confidence

that can be placed in these predictions over the various shore heights, initial seeding densities and season. The dry weight models will be of most value in determining time of harvest to ensure maximal flesh weight. In the final growth period before harvest the mussels are likely to have been moved to the areas of fastest growth rate and hence lower down the shore, and this is the region in which the model predictions are most accurate. Consequently, the models predict well in the most appropriate shore height range for management purposes.

This study has therefore provided a valuable management tool for intertidal mussel cultivation through the development of a predictive statistical growth model integrating length, shore height, initial seeding density and season.

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Chapter 4

The mortality of mussels in large scale beds

ABSTRACT

The population dynamics within mussel beds are strongly influenced by mussel mortality. In order to provide a better understanding of mussel population dynamics and to aid shellfish management it is therefore necessary to determine the factors that result in mussel mortality and the relative magnitude of these causes of mortality. A field experiment was undertaken to ascertain the seasonal mortality of mussels grown over a range of initial seeding densities and shore heights. The results indicated that there was no significant difference between the rates of mortality at the different initial seeding densities and shore heights, and that on the main experimental site mortality was significantly higher over the summer than the winter months. Crab predation on the main experimental site was low over the winter and increased over the spring to a peak in the summer. Seasonal statistical models were developed that described total mussel mortality and mortality due to crab predation. Using these models crab predation was found to account for only a small proportion of the total mussel mortality. The uses of these models in shellfish management to determine optimal initial mussel seeding densities is discussed with a view to reducing the total amount of seed mussels harvested and hence provide a more sustainable approach to mussel cultivation.

INTRODUCTION

In both commercial and natural situations, the population dynamics within mussel beds are strongly influenced by mussel mortality. The processes that influence mortality rate are of interest to mussel cultivators as they are confronted with losses associated with both predation (Seed 1993) and from competition for food and space between mussels (Guinez and Castilla 1999). Therefore in order to provide a better understanding of mussel population dynamics, and develop improved accurate management predictions, it is necessary to determine both the factors that result in mussel mortality and the relative magnitude of the importance of these causes of mortality.

Mussels in the intertidal zone are susceptible to a wide range of predators that include birds, fishes, crabs and starfishes (Seed 1993). The pressure exerted by the various predatory species will vary according to the position of the mussel bed on the shore, with the size of the mussels, the state of tidal inundation and with time of year. In Northern Europe, the two most important predators of mussels located in the intertidal zone are birds (e.g. oystercatchers *Haematopus ostralegus*) and crabs (e.g. *Carcinus maenas*) (Dare and Edwards 1976). Starfish are important, but these are mainly confined to the area of the shore adjacent to extreme low water spring tides. Crab predation pressure is strongly seasonal and generally highest in the spring and summer (Hunter and Naylor 1993; Aagaard et al. 1995), whereas consumption of mussels by oystercatchers is greatest in the winter when large flocks gather in the coastal zones of Northern Europe (Seed and Suchanek 1992). Size-selective predation can impact on the size structure of mussel populations. Oystercatchers preferentially consume larger mussels from 25-55 mm in shell length (Meire 1993), while *Carcinus maenas* predate upon mussels from a few mm in length up to approximately 40 mm in length (Davies 1966). The smallest mussels suffer disproportionately high losses from crabs, since all size ranges of crabs can crush small sized prey (Seed 1976). For a given size of crab (*Carcinus maenas)*, handling time increases as a power function with increasing mussel (*Mytilus edulis*) shell length (Elner and Hughes 1978). In addition prey density can affect mortality rate as crabs have been shown to preferentially forage in areas of higher prey density (Boulding and Hay 1984). Handling times for mussels presented as part of a group also tends to be shorter than for mussels presented singly, which may result in higher mussel losses per unit time at high densities compared to mussels that are more sparsely distributed (Burch and Seed 2000).

Mussel density also influences the intrinsic mortality rate within a mussel bed. At high population densities self-thinning occurs with an observed negative relationship between individuals per unit area and average individual mass (Hughes and Griffiths 1988). Density dependence in aggregations of mussels can have adverse effects on mussel growth and reproductive output and has been suggested to occur as a result of some property of live adjacent individuals (Svane and Ompi 1993; Okamura 1986). The effect of physical pressure on a mussel shell from neighbouring mussels can result in reduced valve gape that may restrict the diameter of the mussel's siphons and hence filtration rate, leading to reduced growth and ultimately death (Fréchette et al. 1992). Food availability can be affected at high mussel densities as a result of food depletion immediately above mussel populations and can lead to the mussels becoming food limited (Frechette and Bourget 1985a, 1985b). Such food depletion at high mussel densities can cause a reduction in individual growth rate and hence may lead to mussel mortality (Bertness and Groshoz 1985).

The rate of mortality in mussel populations is of particular interest to cultivators of mussels on the seabed, where mortality can be so great that the weight return ratio is only 1:1 for mussels laid as seed (approximately 20 mm) and harvested 18 – 36 months later (i.e. one tonne of seed mussels yield only one tonne of harvestable mussels) (Dare and Edwards 1976). This study was conducted on an intertidal site and at a scale large enough to provide data relevant to mussel cultivators on mussel mortality rates under different stocking regimes. The study has focused upon total mussel mortality and mortality due to the predatory shore crab *Carcinus maenas* as the small size of the mussels present on experimental plots during the study period meant that they were unlikely to be of interest to oystercatchers (Meire 1993, Beadman *et al.* in press). Therefore, the aim of this study was to determine seasonal rates of mortality for mussels cultivated over a range of initial seeding densities, and to interpret these for evidence of density-dependence and crab predation. A better understanding of the relative importance of different sources of mortality within mussel beds would allow more informed decisions to be made with respect to the sustainable management of cultivated mussels through optimisation of the limited mussel seed resource.

METHODS

Total mortality – Main experimental site

The study site was located on an intertidal mudflat adjacent to Bangor Pier in the Menai Strait, North Wales, at approximately low water spring tide level (Fig. 4.1). In April 2000 two square areas each composed of 16 cells 20 m x 20 m, were seeded with mussels approximately 20 mm in length at one of four different stocking levels (7.5, 5, 3, 2 kg m^{-2}) using a Latin square design. At the time of seeding the mussels were of similar sizes hence the stocking treatments in biomass can be referred to as density treatments. These stocking levels were chosen to represent a range greater than that normally used in commercial mussel cultivation (mussels at this site have been laid at approximately 5 kg m^{-2} until recently). Each Latin square was marked with buoys and the mussels scattered over each plot from a boat. Due to the effects of tidal currents and inaccuracies of boat positioning, it was not possible to lay the mussels in precise squares; however an *a posteriori* examination of the experimental site revealed that distribution of mussels at the designated densities had occurred sufficient for the purposes of the experiment.

The experimental site was sampled at the time of seeding and on a further 10 occasions over the following year until April 2001. Sampling was carried out more frequently over the period of greatest mussel growth (May-July). On each sampling occasion four quadrats of 0.25 m x 0.25 m were taken per cell in areas of mussel cover. The contents of each quadrat were placed in a plastic bag, labelled and taken back to the laboratory where the number of mussels in each quadrat was counted.

Total mortality – Caged mussel experimental site

In addition an extra site was established at which the density of mussels in cages designed to exclude predators was examined. This site had a steeper gradient than the mudflat at the main site. The caged site was set up in close proximity to the main site on the island of Ynys Faelog in the Menai Strait, North Wales. Cages of dimension 0.5 m (wide) x 0.75 m (long) x 0.25 m (high) were constructed from wooden frames with plastic mesh (5 mm square) sides. The cages were supported on metal frames approximately 0.5 m above the seabed to prevent smothering of the mussels by accumulated sediments.

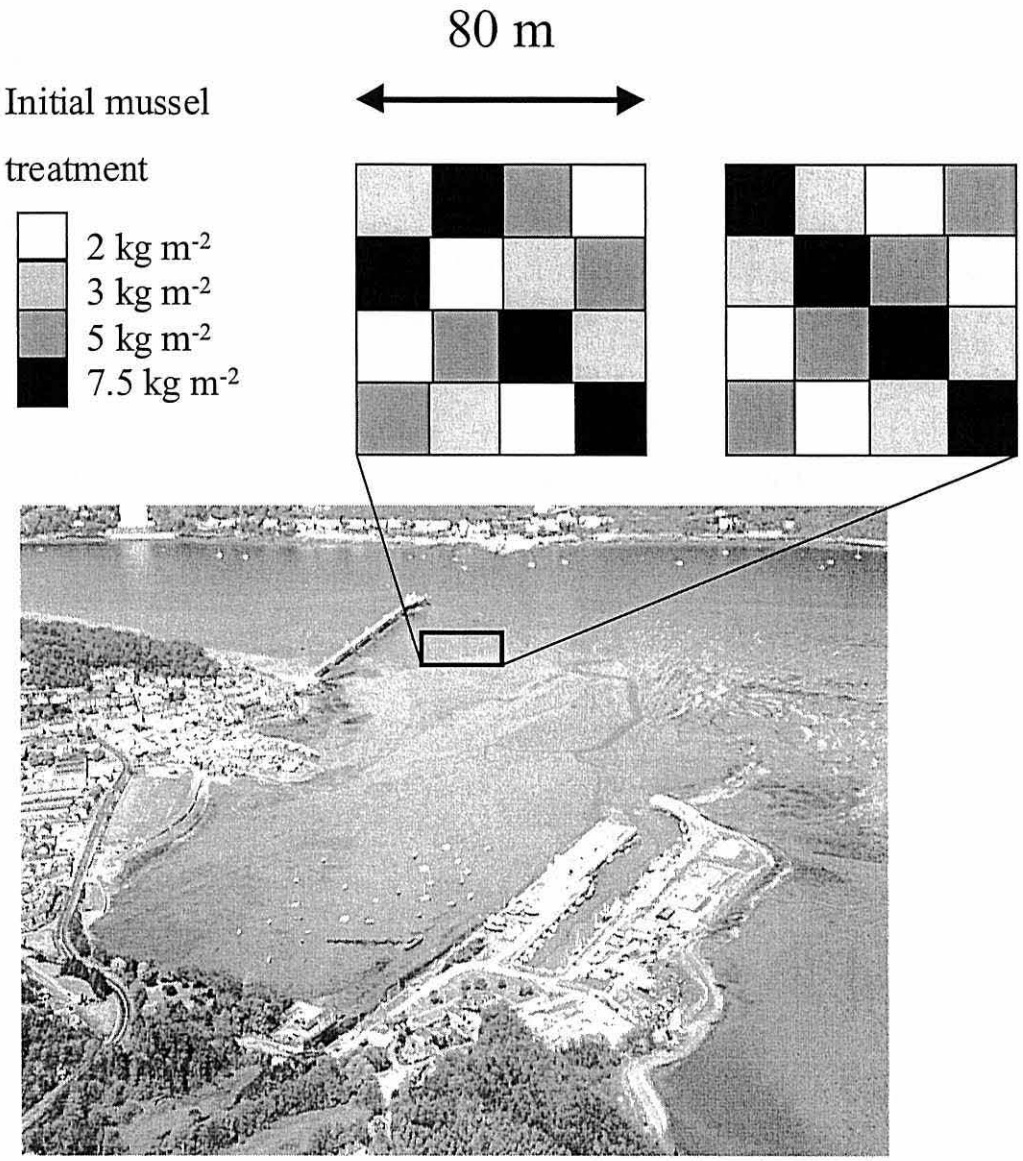

Fig. 4.1. Main site experimental set-up. Adjacent to Bangor Pier in the Menai Strait, North Wales.

Four initial mussel stocking treatments of 2, 5, 7.5 and 15 kg m^{-2} were deployed in the cages at six shore heights spaced down the shore at regular intervals spanning approximately 70 - 210 minutes mean exposure at low water springs. A total of 24 cages were deployed on the shore. The cages were seeded with mussels in May 2000, and were first sampled in June and a further 9 times over the following year until April 2001. On each sampling occasion 120 mussels from each cage were randomly selected and placed in a 2 litre plastic beaker to provide a volumetric measurement and then put back into the cages to maintain the density within the cage. The density in each cage was then determined by volumetrically measuring the amount of mussels present in the cage and converting this to actual numbers using the volume of the 120 mussel subsample as a conversion factor. A volumetric technique was used to minimise the amount of time that the mussels were exposed to air while being counted in the laboratory.

Statistical analyses for total mortality

Prior to analysis, at the main site, for each cell the number of mussels counted in the four samples were pooled. The mean density for each cell on each date was calculated, and the density for each cell or cage was standardised to give the density per m^2. To determine the change in mortality rate with season, mean mussel density was plotted against time.

For each mortality period Ln(mussel density) was plotted against number of days from the start of the experiment. Regression analysis was conducted for each site and for each initial density treatment (main site and caged site) and shore height (caged site). Where possible, regression models were formulated to describe mussel mortality.

An ANCOVA was used to examine each treatment where the covariate was days and the response was initial seeding density (for main site and caged site) and shore height (for caged site). Least-square means pairwise tests (LSM) were conducted to investigate the existence of significant differences between each treatment.

Full experimental time period models were tested for goodness of fit to the observed data using the least squares method in the software package ModelMaker3 (Cherwell Scientific 1997). All other statistical analyses were carried out using SAS version 8.2 (SAS Institute Incorporated 1999-2001).

Mortality due to crab (*Carcinus maenas*) predation

Sampling of the crab population was conducted on the main experimental site at high tide from a boat sited over one of the Latin squares (Fig. 4.1). Each cell (n=16) was marked out with a surface marker buoy to permit accurate positioning of the boat. A square metal frame (1 m x 1 m) was constructed and completely covered with a sheet of nylon mesh (5 cm x 5 cm) to form a flat net of dimension $1m^2$. On each sampling occasion the net was lowered onto the seabed, within a cell, and left for 10 minutes before raising the net. Crabs retained on the net were collected, sexed and maximum carapace width measured with Vernier callipers to the nearest mm. This process was repeated three times in each cell. Since the net was not baited this method provided a quantitative method to determine the number of crabs moving across the seabed per m^2. Sampling was first carried out in July 2000 and then a further eight times over the following year until July 2001.

Statistical analyses of losses due to crab predation

It was assumed that all crabs sampled over the mussel beds were feeding on mussels and were not feeding on alternative prey. In addition the crab feeding rate was estimated for a 'summer' temperature hence the calculations were of the maximum possible loss of mussels from crab predation. The feeding rate of crabs on mussels, in KJ $m^{-2}day^{-1}$, was estimated for each sampled crab according to Elner (1980) where:

For males Feeding rate = -17.56 + 4.88(carapace width, cm)

For females Feeding rate = -6.61 + 2.18(carapace width, cm)

From these estimates total potential mussel consumption was calculated for each sample taken in each cell. Kruskal-Wallis (K-W) tests were carried out on each date to determine if there was an effect of initial seeding density on crab predation pressure (4 density replicates, 3 samples per cell).

The mean feeding rate in KJ $m^{-2}day^{-1}$ (n=48 per sampling date) was calculated for each date and plotted against sampling date. A quadratic curve was fitted to the data with date as number of days where January 1st 2001 was day 1. The number of mussels lost to crab predation per day for each of the initial seeding density treatments was calculated for each of the sampling dates used in the main site total mortality experiment. This was estimated by converting the loss of mussels in KJ $m^{-2}day^{-1}$ into the number of mussels actually consumed using the formulae in Elner (1978):

Ln(Mussel energy content) = 3.03 + 0.09*Ln(mussel length, cm) – 2.34

Mussel energy content would have varied with season but this variable has not been included in the analysis for simplicity. Mussel size was taken from mean length measurements recorded in Chapter 3. Total mussel losses $m^{-2}day^{-1}$ for each sampling date in the main site total mortality experiment were calculated using the mortality model for the main site and compared to potential mussel losses from crab predation.

All statistical analyses were carried out using SAS version 8.2 (SAS Institute Incorporated 1999-2001).

RESULTS

Total mortality on main site

The density of mussels on the main site decreased over the experimental period (Fig. 4.2). The initial stocking levels relate to biomass hence it should be noted that the increments between treatments in terms of density of mussels were not linear. Over the summer months (April to September) there was a rapid decrease in numbers, which slowed over the winter (September to March). The numbers of mussels appeared to increase from March to April although the values are generally within the standard error of the previous sampling date. The first 6 sampling dates from April until the end of August 2000 were designated as the 'summer' mortality period, with dates from the end of August 2000 to the beginning of March 2001 designated as the 'winter' mortality period. The last sampling date has not been included in the analysis.

a. 'Summer' mortality period

Ln(Mussel density) displayed a significant negative relationship with time (in days from the start of the experiment - 24.04.01) for the whole data set and each initial density treatment (Table 4.1).

There was a significant effect of initial seeding density on the mussel mortality relationship (Table 4.2). There was no significant difference between the slopes of the regression relationships of the initial seeding density treatments (interaction term of the ANCOVA), but significant differences were found between the intercept values of the initial density treatments. Since the slopes of the regression relationships for each initial density treatment were not significantly different this implies that there was no significant difference in the rate of mortality between the treatments.

b. 'Winter' mortality period

Ln(Mussel density) displayed a significant negative relationship with time (in days from the start of the experiment) for the whole winter data set and for each initial density treatment (Table 4.3).

Initial mussel seeding density had a significant effect on the mussel mortality relationship (Table 4.4). Again this effect was found in the intercept and there was no significant difference between the slopes of the initial seeding density treatment regression relationships (number of mussels against time).

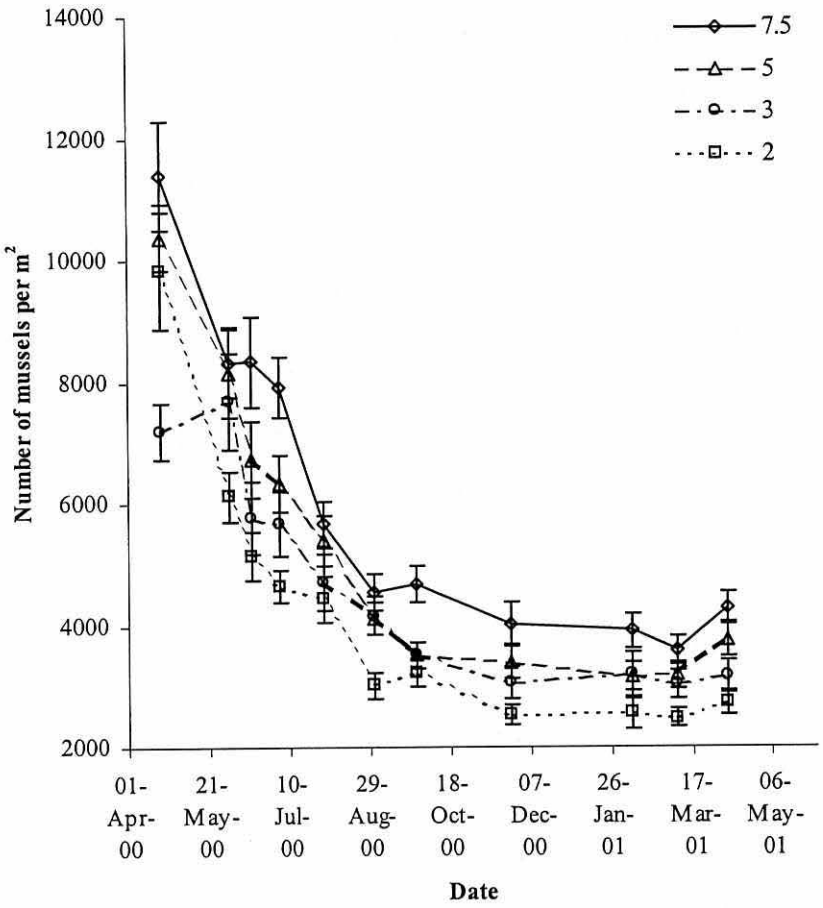

Fig. 4.2. Main Site. Mussel density from four initial density treatments (7.5, 5, 3 and 2 kg m^{-2}) (±SE mean) over experimental period from April 2000 to April 2001.

Table 4.1. Main Site. Summer. Analysis of goodness for fit of regression models of Ln(mussel density) on time (days from start of the experiment) for all data and each initial density treatment (2, 3, 5 and 7.5 kg m^{-2}).

Source	df	Sum of squares	Mean Square	F value	P	r^2
Low Density						
Within (explained by days)	1	5.3514	5.35142	26.8	<0.0001	0.368
Unexplained	46	9.1762	0.19948			
Total	47	14.528				
Medium-Low Density						
Within (explained by days)	1	1.9200	1.92000	15.1	<0.0001	0.248
Unexplained	46	5.8200	0.12652			
Total	47	7.7400				
Medium Density						
Within (explained by days)	1	3.9457	3.94571	58.8	<0.0001	0.561
Unexplained	46	3.0882	0.06713			
Total	47	7.0339				
High Density						
Within (explained by days)	1	3.8454	3.84543	64.9	<0.0001	0.585
Unexplained	46	2.7276	0.05930			
Total	47	6.5731				
Summer mortality model (all data)						
Within (explained by days)	1	14.617	14.61652	106	<0.0001	0.360
Unexplained	190	26.004	0.13686			
Total (All data)	191	40.620				

Parameter values for summer mortality model where:

Ln (mussel density) = a + b (days)

Parameter	Value	SE
a	9.12	0.0507
b	-0.00649	0.000628

Table 4.2. Main Site. Summer. ANCOVA of the effect of initial mussel seeding density on Ln(mussel density) against time (days from start of the experiment). Interaction term not significant ($F_{3,184}$=1.31 p=0.227)

Source	df	Seq SS	Adj SS	Adj MS	F	P
Day	1	14.617	14.617	14.6165	129	<0.0001
Density	3	4.746	4.746	1.5820	13.9	<0.0001
Error	187	21.258	21.258	0.1137		
Total	191	40.620				

Table 4.3. Main Site. Winter. Analysis of goodness of fit for regression models of Ln(mussel density) on time (days from start of the experiment) for all data and each initial density treatment (2, 3, 5 and 7.5 kg m^{-2})

Source	df	Sum of squares	Mean Square	F value	P	r^2
Low Density						
Within (explained by days)	1	0.3989	0.39886	4.25	0.0464	0.103
Unexplained	37	3.4762	0.09395			
Total	38	3.8751				
Medium-Low Density						
Within (explained by days)	1	0.4290	0.42898	4.37	0.0432	0.103
Unexplained	38	3.7271	0.09808			
Total	39	4.1561				
Medium Density						
Within (explained by days)	1	0.2949	0.29487	6.05	0.0185	0.137
Unexplained	38	1.8514	0.04872			
Total	39	2.1463				
High Density						
Within (explained by days)	1	0.3307	0.33068	7.74	0.0084	0.169
Unexplained	38	1.6244	0.04275			
Total	39	1.9550				
Winter mortality model (all data)						
Within (explained by days)	1	1.4050	1.40498	15.0	0.0002	0.087
Unexplained	157	14.665	0.09341			
Total (All data)	158	16.067				

Parameter values for winter mortality model where:

Ln (mussel density) = a + b (days)

Parameter	Value	SE
a	8.39	0.0787
b	-0.00128	0.000331

Table 4.4. Main Site. Winter. ANCOVA of the effect of initial mussel seeding density on Ln(mussel density) against time (days from start of the experiment).

Interaction term not significant ($F_{3,151}$=0.04 p=0.990)

Source	df	Seq SS	Adj SS	Adj MS	F	P
Day	1	1.405	1.4451	1.4451	20.8	<0.0001
Density	3	3.978	3.9776	1.3259	19.1	<0.0001
Error	154	10.687	10.687	0.0694		
Total	158	16.070				

c. Complete experimental time period

For both the summer and winter there was no significant effect of initial seeding density on the slope of the regression relationship between Ln(mussel density) and time. There was a significant difference between the slopes (rate of mortality) of the winter and summer periods (Table 4.5). Therefore, the slopes of both of the regression relationships of the data sets for each time period (i.e. slope of summer mortality model Table 4.1, and slope of winter mortality model Table 4.3) have been used as the rates of mortality (Ln(number of mussels) per day) to model mussel density over the full experimental time period. For the production of the mortality models the dates for the two mortality periods were limited by the sampling dates. However, in order to make predictions of mussel density using these models, the mortality periods have been defined as 'summer': from the beginning of March to half way through September, and 'winter': from half way through September to the beginning of March. This model provided a good fit to the observed data, with the best fits at the highest initial mussel density treatments (r^2 values 2, 3, 5, 7.5 kg m^{-2} initial seeding treatments respectively 0.759, 0.528, 0.987, 0.974) (Fig. 4.3).

Table 4.5. Main Site. ANCOVA of the effect of season (summer or winter) on Ln(mussel density) against time (days from start of the experiment).

Source	df	Seq SS	Adj SS	Adj MS	F	P
Day	1	16.60	14.89	14.885	127	<0.0001
Season	1	21.71	23.17	23.170	198	<0.0001
Season*Day	1	6.657	6.657	6.657	56.8	<0.0001
Error	347	40.67	40.67	0.117		
Total	350	85.64				

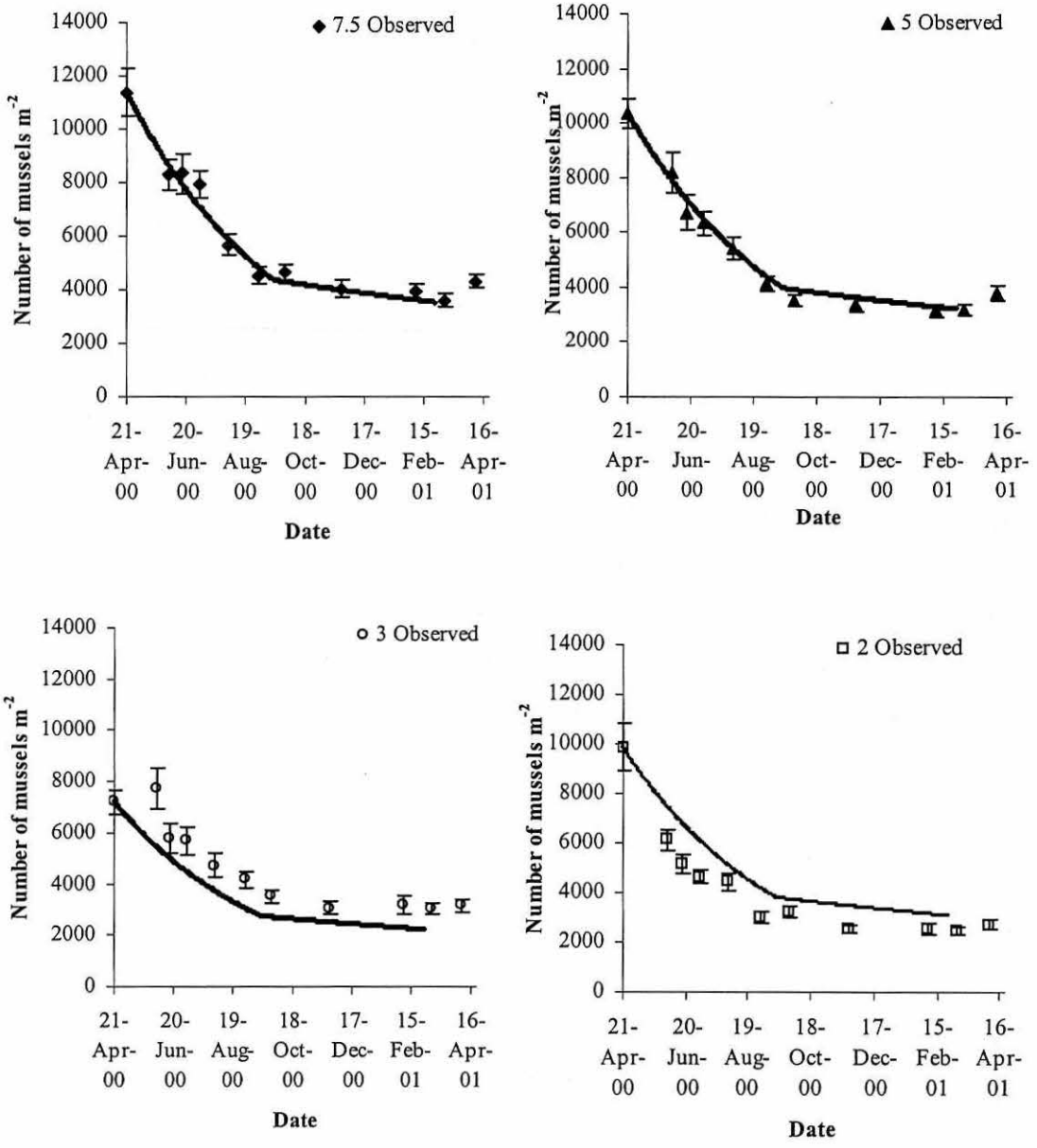

Fig. 4.3. Main Site. Modelled (solid lines) and observed mussel density (± SE) of mussels grown at four initial seeding densities (7.5, 5, 3 and 2 kg m^{-2}).

Caged mussel experimental site

The same sampling time periods used on the main site for 'summer' and 'winter' mortality were maintained for the analysis of the caged mussel data.

a. 'Summer' mortality period

There was no significant regression relationship of Ln(mussel density) against time for either the full data set or for the individual initial seeding density treatments (all $p>0.05$).

b. 'Winter' mortality period

There was no significant regression relationship of Ln(mussel density) against time for the full data set or for the individual initial seeding density treatments 3, and 7.5 kg m^{-2} (all >0.05). Significant regression relationships were found for the initial seeding density treatments 5 and 15 kg m^{-2} (respectively $F_{1,29}=5.17$ $p<0.05$; $F_{1,29}=12.49$ $p<0.05$).

c. Complete experimental time period

There was no significant regression relationship of Ln(mussel density) against time for the full data set ($p>0.05$). However, there was a highly significant negative regression relationship of Ln(mussel density) against time in days for all of the individual initial seeding density treatments, apart from the lowest density treatment 2 kg m^{-2} (Table 4.6). Since there was no significant reduction in mussel density over the experimental time period for the lowest initial seeding density treatment it was excluded from further analysis.

There was a significant regression relationship between Ln(mussel density) and time in the combined data of the three highest initial seeding density treatments (Table 4.6). To demonstrate the effect of shore height and initial density treatment on the relationship between mussel density and time a three variable regression model of time (in days from the start of the experiment), shore height and initial seeding density was formulated (Table 4.6). Such a model would provide a prediction of the actual mussel density rather than a mortality rate as in the main site mortality model. This type of model would have been inappropriate for the main site since the mortality rate changed between the summer and winter and two models would have been required with one for each season. The summer model could have been formulated since the number of mussel at the beginning of the season could be determined. However, the number of mussels at the beginning of the winter season

would depend on number of days from seeding. Hence the winter model could only be used in future applications if the number of days from seeding were the same as used in the present experiment. The model could not be used if mussels were seeded earlier or later in the year, clearly limiting its applicability.

Caged site mortality model

Ln(mussel density) = a + b(Initial Density) + cLn(Days) + d(Shore Height)

Where a, b, c and d are fitted parameters.

The model provided a significantly better fit to the data set than the one variable model of length ($F_{2,177}$=624 $p<0.0001$). However, the model did not fit equally well to all of the shore heights and initial density treatments (Table 4.7).

To support the development of the caged site mortality model an ANCOVA was carried out to test the effect of shore height on mussel density, with time in days as a covariate. Shore height had a significant effect on mussel density (ANCOVA covariate days $F_{1,171}$=83.8 $p<0.0001$, initial density $F_{2,171}$=498 $p<0.0001$, shore height $F_{5,171}$=6.35 $p<0.0001$). To establish between which shore heights significant differences existed, pairwise LSM tests were conducted between all combinations of shore heights. There was no consistent pattern in the differences between pairs of shore-heights although the highest shore height was significantly different to all others except the shore height that equated to 130 minutes mean exposure at low water springs (Table 4.8). Additionally, to establish if shore height had a significant effect on mussel density at all of the initial seeding densities, each set of initial density treatment data was analysed separately by ANCOVA, with time in days as a covariate. In this analysis shore height had a significant effect on mussel density at each initial seeding density (ANCOVA for 5, 7.5 and 15 kg m^{-2} respectively, covariate days $F_{1,53}$=27.9 $p<0.001$, $F_{1,53}$=34.7 $p<0.001$, $F_{1,53}$=46.5 $p<0.001$; shore height effect $F_{5,53}$=9.81 $p<0.001$, $F_{5,53}$=5.58 $p<0.001$, $F_{5,53}$=5.52 $p<0.001$). In LSM pairwise tests there were some significant differences between shore heights for each of the initial density treatments, but there was no clear pattern in these differences (Table 4.9).

Table 4.6. Caged Site. Complete experimental time period. Analysis of goodness of fit for regression models of i) Ln(mussel density) on days for each initial density treatment and ii) Ln(mussel density) on days, shore height and initial seeding density. Initial seeding densities Low 2, Medium 5, High 7.5 and Very High 15 kg m^{-2}. Shore heights 70, 100, 130, 160, 190 and 210 minutes exposed at mean low water springs.

Source	df	Sum of squares	Mean Square	F value	P	r^2
Low Density						
Within (explained by days)	1	0.0291	0.02906	0.43	0.5159	0.007
Unexplained	58	3.9442	0.06800			
Total	59	3.9732				
Medium Density						
Within (explained by days)	1	0.5078	0.50783	15.9	0.0002	0.215
Unexplained	58	1.8563	0.03201			
Total	59	2.3642				
High Density						
Within (explained by days)	1	0.8621	0.86211	24.8	<0.0001	0.30
Unexplained	58	2.0130	0.03471			
Total	59	2.8752				
Very High Density						
Within (explained by days)	1	1.0983	1.09826	33.4	<0.0001	0.366
Unexplained	58	1.9049	0.03284			
Total	59	3.0032				
***Caged site mortality model – highest density treatments (not Low, 2 kg m^{-2})**						
Within (explained by days)	1	2.4104	2.41042	12.4	0.0005	0.065
Unexplained	178	34.482	0.19372			
Total	179	36.893				
Caged site complete time period mortality model (all data except low density)						
Within (explained by days shore height and denisty)	3	29.311	9.77028	227	<0.0001	0.795
Unexplained	176	7.5818	0.04308			
Total (All data)	179	36.893				

Parameter values for *Caged site mortality model – highest density treatments, where:
Ln (mussel density) = a + b (days)

Parameter	Value	SE
a	9.41	0.0521
b	-0.00106	0.000301

Table 4.7. Caged site complete experimental time period. Least squares goodness of fit (r^2) for cages mortality model prediction to each observed cages treatment (shore height 70, 100, 130, 160, 190 and 210 minutes exposed at mean low water springs, initial density Low 2, Medium 5, High 7.5 and Very High 15 kg m^{-2}) for full experimental time period.

Shore Height	Initial Density		
	Medium	High	Very High
70	0	0	0.030
100	0.186	0.363	0.398
130	0	0.414	0
160	0.523	0	0.431
190	0	0	0.175
210	0.369	0	0.429

Table 4.8. Caged Site. Complete experimental time period. Pairwise tests – Least square means for the effect of Shore Height on mussel initial seeding density with covariate days for HO: LSMean (i) = LSMean (j). (Shore heights 70, 100, 130, 160, 190 and 210 minutes exposed at mean low water springs).

Bold print indicates significance $p<0.05$.

	Shore Height (minutes exposure)				
i/j	70	100	130	160	190
100	0.374				
130	**0.017**	**0.001**			
160	0.912	0.436	**0.012**		
190	0.182	**0.027**	0.281	0.149	
210	**<0.001**	**<0.001**	0.162	**<0.001**	**0.014**

Table 4.9. Caged Site Complete experimental time period. Pairwise tests – Least square means for the effect of Shore Height on mussel density for each initial density (Low 2, Medium 5, High 7.5 and Very High 15 kg m^{-2}) with the covariate days for HO: LSMean (i) = LSMean (j). Shore heights 70, 100, 130, 160, 190 and 210 minutes exposed at mean low water springs.

Bold print indicates significance $p<0.05$.

Shore Heights Compared		Initial Density		
i	j	Medium	High	Very High
70	100	**<0.001**	0.967	**0.036**
	130	0.793	0.523	**<0.001**
	160	0.661	0.486	0.374
	190	**0.023**	0.178	**0.062**
	210	0.480	**0.001**	**<0.001**
100	130	**<0.001**	0.551	0.120
	160	**<0.001**	0.460	0.214
	190	**<0.001**	0.165	0.805
	210	**<0.001**	**0.001**	**0.029**
130	160	0.484	0.184	**0.006**
	190	**0.043**	**0.050**	**0.073**
	210	0.334	**0.007**	0.512
160	190	**0.008**	0.510	0.317
	210	0.788	**<0.001**	**0.001**
190	210	**0.004**	**<0.001**	**0.016**

Initial mussel seeding density had a significant effect on mussel density (ANCOVA covariate days $F_{1,171}=83.8$ $p<0.0001$, initial density $F_{2,171}=498$ $p<0.0001$, shore height $F_{5,171}=6.35$ $p<0.0001$), and in LSM pairwise tests, there was a significant difference between each initial density treatment compared with every other density treatment (all $p<0.0001$). Analysis of the data within each shore height revealed that there was a significant effect of initial seeding density on mussel density at all of the shore heights (Table 4.10). In LSM pairwise tests within each shore level each initial seeding density treatment was significantly different from all others (all $p<0.0001$).

Table 4.10. Caged Site. Complete experimental time period. ANCOVA of the effect of initial mussel seeding density (for 3 highest initial seeding densities) on Ln(mussel density) against time in days for each shore height. Initial seeding densities Medium 5, High 7.5 and Very High 15 kg m^{-2}. Shore heights 70, 100, 130, 160, 190 and 210 minutes exposed at mean low water springs. (Interaction terms were not significant).

Source	df	Seq SS	Adj SS	Adj MS	F	p
SH=70						
Day	1	0.651	0.651	0.6508	27.0	<0.0001
Density	2	3.184	3.184	1.5922	66.1	<0.0001
Error	26	0.626	0.626	0.0241		
Total	29	4.461				
SH=100						
Day	1	0.354	0.354	0.3535	13.2	0.001
Density	2	7.427	7.427	3.7135	138	<0.0001
Error	26	0.698	0.698	0.0269		
Total	29	8.479				
SH=130						
Day	1	0.499	0.499	0.4981	29.3	<0.0001
Density	2	5.409	5.409	2.7044	159	<0.0001
Error	26	0.442	0.442	0.0170		
Total	29	6.349				
SH=160						
Day	1	0.361	0.361	0.3612	35.8	<0.0001
Density	2	3.927	3.927	0.19635	65.8	<0.0001
Error	26	0.262	0.262	0.0101		
Total	29	4.551				
SH=190						
Day	1	0.556	0.556	0.5560	21.8	<0.0001
Density	2	3.362	3.362	1.6811	65.8	<0.0001
Error	26	0.664	0.664	0.0255		
Total	29	4.582				
SH=210						
Day	1	0.122	0.122	0.1220	4.12	0.053
Density	2	6.667	6.667	3.3334	113	<0.0001
Error	26	0.770	0.770	0.0296		
Total	29	0.756				

Mortality due to crab predation

There was no significant effect of initial mussel seeding density on crab predation pressure on any of the sampling dates (K-W all $p>0.05$). Estimated predation pressure by crabs (using mean potential loss of mussels in $KJm^{-2}day^{-1}$ over the whole experimental site) was at a maximum over the summer decreasing to zero from November to March and then increasing from March to a maximum in July (Fig. 4.4).

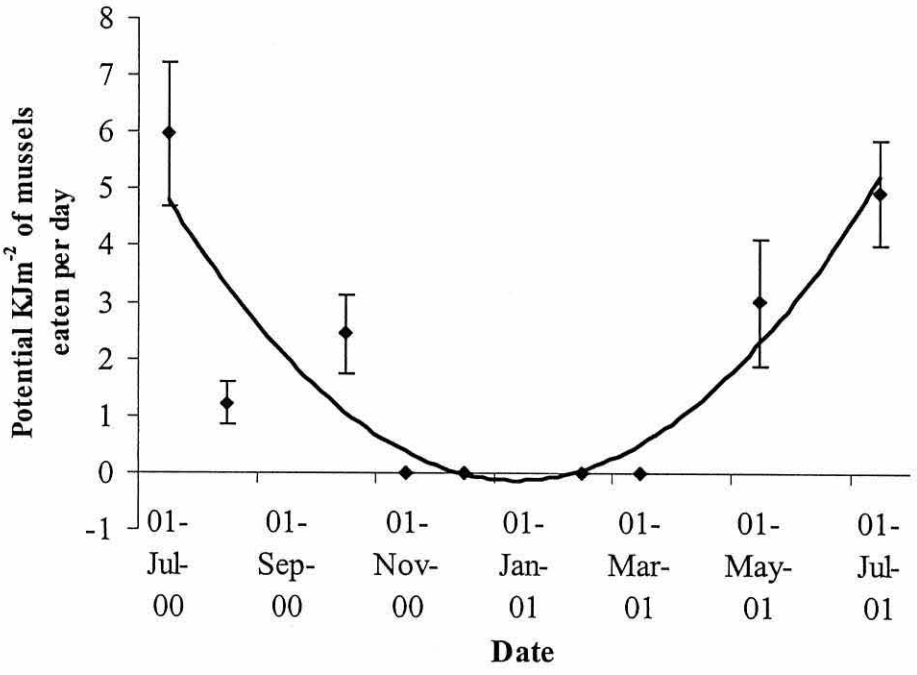

Fig. 4.4. Main Site. Potential loss of mussels in KJ $m^{-2}day^{-1}$ (± SE) due to crab predation on the main site between July 2000 and July 2001.

A quadratic function was fitted to the data to allow predictions to be made of mussel consumption in KJ $m^{-2}day^{-1}$.

Crab predation model

KJ eaten $m^{-2}day^{-1} = 0.0002(day)^2 - 0.00048(day) - 0.1938$ ($r^2 = 0.807$).

where day is number of days and January 1st 2001 was day 1.

In order to compare the mussel losses due to crab predation to total mortality the loss of mussels in $KJm^{-2}day^{-1}$ was converted to the number of mussels that died $m^{-2}day^{-1}$ according to Elner (1980). The number of mussels lost to crab predation was calculated for each of the sampling dates used to determine mussel density on the main site. The numbers of mussels eaten by crabs on the main site were very low compared to the total number of mussel lost through mortality (calculated from main site mortality model) (Table 4.11). The loss of mussels as a result of crab predation relative to other sources of mortality varied over the year, increasing over the summer, reaching a peak in October, before decreasing over the winter months (Fig. 4.5).

Table 4.11. Main Site. Estimated Loss of mussels for each sampling date for each initial seeding density calculated i) as total loss using main site mortality model and ii) losses to crabs using crab mortality model. All values represent number of mussels lost $m^{-2}day^{-1}$.

Date	**Initial seeding density**							
	Low		**Medium**		**Medium-Low**		**High**	
	Total loss	Crab loss	Total loss	Crab loss	Total loss	Crab loss	Total loss	Crab loss
21/04/00	73.6	1.1191	67.1	1.1188	46.5	1.1189	63.7	1.1188
02/06/00	56.1	2.2323	51.1	2.2325	35.4	2.2325	48.5	2.2323
16/06/00	51.2	2.6833	46.7	2.6835	32.3	2.6825	44.3	2.6835
03/07/00	45.8	3.2949	41.8	3.2854	29.0	3.2855	39.8	3.2859
31/07/00	38.2	2.3113	34.8	2.3115	24.1	2.3119	33.1	2.3119
31/08/00	31.3	1.4409	28.5	1.4411	19.7	1.4410	27.1	1.4414
27/09/00	5.49	0.8402	5.01	0.8405	3.47	0.8405	4.75	0.8405
24/11/00	5.10	0.0496	4.65	0.0496	3.35	0.0496	4.42	0.0496
07/02/01	4.63	0.0389	4.22	0.0389	2.93	0.0389	4.01	0.0390

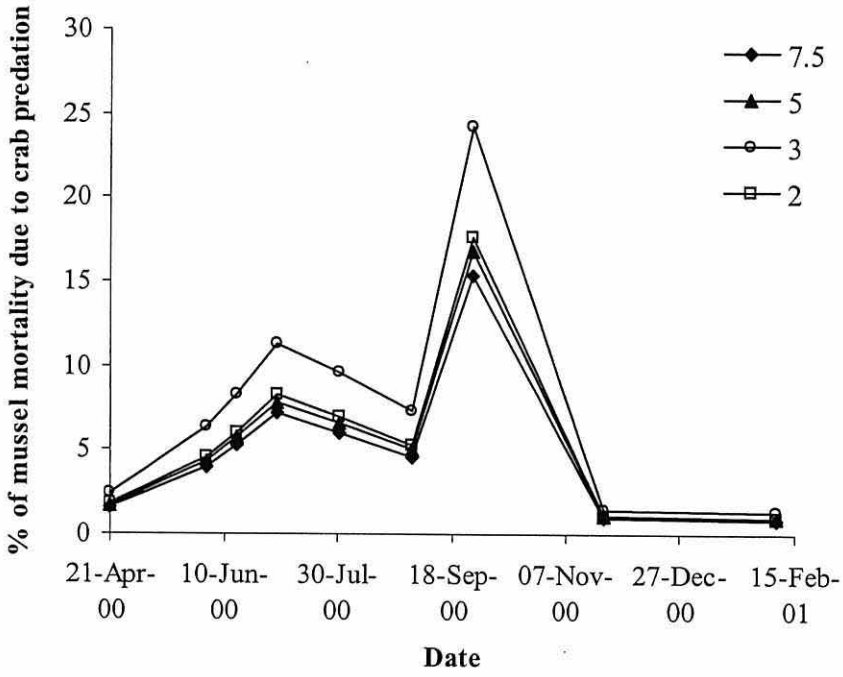

Fig. 4.5. Main Site. Predicted percentage of total mussel mortality due to crab predation for mussels grown at four initial seeding densities (7.5, 5, 3 and 2 kg m^{-2}).

DISCUSSION

On the main site there was no significant effect of initial mussel seeding density on the rate of mortality for either the summer or winter period (Table 4.2 and 4.4). However, the regression models were formulated with Ln(mussel density) against time which indicates that the actual number of mussels lost per day was greatest when mussel density was at its highest for all of the initial seeding density treatments. At high mussel densities reduced growth rate caused by physical interference (Okamura 1986, Fréchette *et al.* 1992), and/or by localised food depletion (Bertness and Groshoz 1985, Fréchette and Bourget 1985a and b) can ultimately result in death. Therefore at high densities these density-dependant effects may have occurred and resulted in the observed relationships of Ln(mussel density) over time. The density of mussels on the main site was modelled over the complete experimental time period, using the slope of the regression relationships from the summer and winter periods to provide a rate of mortality. This model gave good representations of mussel density for all of the initial mussel seeding densities on the main site (Fig. 4.3).

There was a significant seasonal effect on the mortality rate at the main site, and this difference in mortality between the summer and winter periods could have been the result of two main factors. Firstly, differing growth rates over the year could have resulted in different intensities of density dependent effects and secondly, varying levels of predation pressure over the different times of year could have resulted in different mortality rates. Over the summer months, growth rate is expected to be higher than during the food depleted winter months (Seed 1969). Furthermore, at this cultivation site, recent research has demonstrated lower growth rates during the winter than the summer (Chapter 3). As the mussels become larger in size crowding will increase and result in greater physical interference between individual mussels. Physical interference may reduce growth rate by restricting valve gape (Fréchette *et al.* 1992), and it is likely that other effects operate within the mussel bed, such as smothering, where mussels are pushed down into the mussel mud as a result of the growth of conspecifics. When the mussels were growing faster over the summer months these negative impacts would have occurred at a faster rate resulting in a higher rate of mortality. In comparison, when the mussels grew more slowly over the winter months the crowding effects would be less intense.

Predation pressure could also have affected the mortality rate on the main site. On this intertidal, soft sediment site the main predators are the oystercatcher *Haematopus ostralegus* and the crab *Carcinus maenas* (Dare and Edwards 1976). These predators

are seasonal in their abundance and hence predatory activity varies concordantly. Therefore, the difference in mortality rates may be partly as a result of the crabs inflicting higher mortalities on the mussels in the summer compared to the oystercatchers over the winter. The prey size preference of these predators lends support to this hypothesis since the mussels during the experimental period were 20 - 38 mm, which is well within the range of the size range preferred by the crabs encountered at this site (Elner and Hughes 1978; Dare and Edwards 1976) but at the very lower end of the size range taken by oystercatchers (Meire 1993). At this site mortality due to oystercatcher predation between September 2000 and March 2001 was estimated to remove only 1% of the mussel stock (R Caldow pers comm). However to establish whether crab predation was a significant factor in the mortality observed during the summer months the main site experiment needs to be compared with an area without predation; the caged mussel site.

At the caged mussel site there was no significant seasonal pattern of mussel mortality. This may indicate that the seasonal effect found on the main site was a result of predators, which were excluded from the caged site. A significant relationship between Ln(mussel density) was only established over the complete experimental time period for the three highest density treatments. This suggests that mortality over the whole study period was low, but the large amount of variability within the data set may have made it more difficult to detect any trend in the decrease in mussel density over time. Both shore height and initial mussel seeding density had a significant effect on the relationship between Ln(mussel density) and time. A three variable model using shore height, initial seeding density and time described changes in mussel density within the caged mussel site. Although the model was a good fit to the entire data set, it did not fit the individual treatments equally well (Table 4.7), and it is possible that this is also a result of the large amount of variability within the data set. The densities of mussels on the caged mussel site were not counted directly and the use of the volumetric method may have introduced additional variability into the data.

Although shore height and initial density had a significant effect at the caged mussel site on the relationship between Ln(mussel density) and time the difference was not found in the slope (rate of mortality) but in the intercept. Therefore the slope of the regression relationship for the data for all of the shore heights and the three highest densities could be used as an estimate of mussel mortality rate at the caged mussel site (since the lowest mussel density treatment did not have a significant regression

relationship it has not been used). This provides a direct method of comparing the mortality rates of the main and caged sites. However, it was not possible to test if there was a statistically significant difference between the rates of mortality at the different sites due to non-homogeneity of variance in the data set. Direct comparison of the values of the slopes (as an indication of mortality rate) of the regression relationships for the caged mussel site and the main site over the summer, revealed that the mortality rate was approximately 5 times higher on the main site than the caged site. However, the overall mortality rates for the caged mussel site and winter mortality rates on the main site were very similar. Predation pressure on the main site was at its lowest over the winter period and therefore the similarity in the mortality rates between the caged and main site over this period may reflect the similar conditions regarding the amount of predation pressure (low or absent). In the summer, when predation pressure was much greater at the main site, the increased predation pressure may have been reflected in the higher mortality rate compared to that experienced at the caged site where the mussels were protected from predation.

Crab predation pressure on the main site reflected the findings of other studies with low levels of predation in the winter that increase over the spring to a peak in summer (Hunter and Naylor 1993; Aagaard et al. 1995) (Fig. 4.4). There was no significant relationship between the initial seeding density on crab predation pressure, although the experimental cells may have been too close together to detect a significant effect. Moreover, even at the lowest initial seeding density the mussels were still very abundant, so the range of mussel densities studied may not have been sufficient to effect a response to prey density by feeding crabs as has been shown elsewhere (Boulding and Hay 1984).

Shore crabs have an important role as predators on the benthos in shallow coastal waters (Reise 1985) and in particular on juvenile bivalves such as mussels (Walne and Dean 1972). Crab predation can be the major factor that restricts mussel production by causing mortality levels of 70-85% in the first year of mussel growth (mussel length <45mm) (Dare and Edwards 1976). In this study the predation pressure due to crabs did not appear to be of the same magnitude as reported elsewhere (Fig. 4.5). The highest percentage of total mussel mortality as a result of crab predation occurred in October. This is an interesting result as it is expected that crab predation pressure would be relatively greater when crab numbers are highest. However, since the total mortality rate is significantly lower by October crab

predation pressure was of greater importance in relative terms. Nevertheless, crab predation still accounted for only a quarter of the total mortality.

It is possible that the number of mussels eaten over the experimental period could have been higher since mean mussel size on each sampling occasion was used in the conversion of crab predation pressure from KJ to mussel numbers. The results may therefore be misleading if the smallest mussels in the population, rather than the mean size, were consistently eaten. The smallest mussel sizes suffer disproportionately high losses since all size ranges of crabs can eat them (Seed 1969) and with reduced handling times (Elner and Hughes 1978). If a smaller mussel size had been used in the calculation then the results would have indicated that more mussels $m^{-2}day^{-1}$ might have been consumed. However, mussel size only makes a very slight difference, so that even though mean mussel length was significantly different between the initial density treatments on the main site the difference in the number of mussels taken is only noticeable at the third and fourth decimal place (Table 4.11). The average crab carapace width over the experimental period was 2.66 cm and this would also suggest that the crabs would preferentially eat mussels smaller than the mean sizes (20-37mm) (Elner 1980). Nonetheless, this would not have increased mussel losses to the high levels that have been recorded elsewhere (Dare and Edwards 1976).

The vulnerability of a particular bivalve population to predation will depend on shell size, shape and thickness and also on the availability of alternative prey species (Dare *et al.* 1983). In a cultivated mussel bed, where there is an abundant supply of mussels and the sizes are very similar, crabs may be able to consume more mussels per unit time due to reduced handling and searching times. The effect of reduced handling times of mussels presented as part of a group compared to mussels presented singly has been demonstrated by Burch and Seed (2000). Hence the actual number of mussels consumed on a cultivated mussel bed may be greater than has been suggested by laboratory experiments. However, this will be countered by interference between crabs and kleptoparasitism that have been reported from field observations (Dare and Edwards 1980), both of these factors have not been considered in laboratory studies of crab feeding behaviour.

The present study has demonstrated a seasonal effect on mussel mortality with higher mortality rates over the summer than in the winter on a cultivated mussel bed in the intertidal zone. The results from the caged mussel site, from which predators were excluded and at which mortality rates were much lower compared to the summer on

the main site, suggested that the higher mortality rates on the main site resulted from high crab predation pressure. However, crab predation accounted for only a small proportion of the total mortality on the main site. Other factors such as density dependent effects, as a result of the high growth rates that occurred over the summer, would have contributed to the high mortality rate on the main site, although it is not clear why this did not occur to a similar extent at the caged mussel site. It is possible that the sides of the cages may have provided extra substratum for the mussel to attach and hence reduced the severity of crowding within the cage compared to the mussels on the mud flat. Although this experiment has not explicitly indicated the cause of mussel mortality it has provided a useful management tool, and indicated that crab predation may not be responsible for as large a proportion of the mortality on mussel beds as might be suspected by intuition.

Management Options

A seasonal model of mortality rate has been formulated for the main site. This is a useful tool for mussel cultivators that will enable predictions to be made of mussel mortality during the first year of mussel growth over a range of initial seeding densities. Since the caged experiment indicated that shore height did not significantly affect the rate of mussel mortality the model from the main site could be used with caution over a range of shore heights. The relationship between Ln(mussel density) and time also provided evidence that the loss of mussel numbers is greater at higher densities, which would support a more conservative use of seed mussels. Mussel yield in terms of flesh weight, comparing initial seeded mussels to the mussels at the end of the experiment on the main site (mussel density per m^2 * flesh dry weight of mussel of mean length), using the seasonal dry weight model from Chapter 3 estimated that the best return was obtained from initial seeding densities between 3 and 5 kg m^{-2} (flesh weight return for initial seeding densities 2, 3, 5, 7.5 $kg.m^{-2}$ respectively 1:1.4, 1:2.0, 1:1.7, 1:1.6). Hence by using a lower initial seeding density a higher return in terms of mussel biomass can be achieved as a result of reduced mussel mortality and the remaining mussels achieving larger sizes. Establishing an optimum mussel seeding density, over which negative impacts on mussel yield are demonstrated, allows better utilisation of the natural mussel seed stocks. Additionally, when the cultivated mussel lays have been covered with seed mussel up to an optimum initial density there will be no incentive to continue to harvest wild seed, and hence may reduced the pressure on this ephemeral resource.

Chapter 5

Self-thinning in mussel populations: applications in the sustainable development of mussel cultivation

ABSTRACT

Mussels in both natural and cultivated conditions are found in dense beds where density dependent effects on survival and growth are expected. This study was conducted in the Menai Strait, North Wales to investigate the seasonal density-dependent relationships of mussels cultivated on the seabed at a commercial scale. A large-scale field experiment was carried out and mussel samples collected to obtain density and length measurements over a twelve month period. From the data collected the relationship between mussel mean weight and density over time were examined using statistical models of varying complexity in order to model the self-thinning relationship over time. The relationship between mussel mean weight and density changed rapidly over the summer months in comparison to the winter months. The differences in the change of the relationship appeared to be related to seasonal growth rates and predation pressure. The results indicated that a self-thinning line had not been reached over the duration of the experiment by all of the mussel populations on the site. Evidence of density dependence and self-thinning in the experimental mussel populations are discussed and related to possible applications in the improvement of the management of seabed mussel cultivation through reduction of initial seeding densities providing a more sustainable approach to mussel cultivation.

INTRODUCTION

Under natural conditions mussels are found in dense beds covering intertidal and subtidal areas on a range of substrata (Seed 1976). In these dense assemblages density dependent effects on survival and growth are expected that result in self-thinning (Guinez and Castilla 1999). Self-thinning describes the negative relationship that is observed between individual mean size and mean population density in a cohort of growing organisms (Westoby 1984). The process of self-thinning has been a subject of interest for plant ecologists during the past three decades (e.g. Yoda *et al.* 1963; White 1980; Westoby 1984; Weller 1987). This research has pointed to a general ecological rule or relationship that describes plant population structure that results from competition in stands of plants of an even age. This relationship is also known as the '-3/2 power law' (Yoda *et al.* 1963) because mean weight (W) is related to mean density (N) by the power function $W=kN^{-3/2}$ (where k is a fitted parameter). The relationship of the observed rule is based on the assumption that there is total (100%) occupation of the substratum and that growth is isometric. In this case the substratum surface (S) occupied by an individual is proportional to 1/N, and to the square of a linear dimension (L). It is then assumed that the weight is proportional to the cube of the linear dimension hence:

$1/N \propto S \propto L^2 \propto (L^3)^{2/3} \propto W^{2/3}$ so that $W=kN^{-3/2}$ where k is a fitted parameter.
When Log W is plotted against Log N a straight line of slope –3/2 is observed in the range of densities where self-thinning is assumed to occur.

Plant ecologists have therefore assumed from the relationship between mean weight and mean density that self-thinning occurs through competition for space. While this may not necessarily have application for mobile animals (Begon *et al.* 1986; Latto 1994; Elliott 1993), the concept of space as a limiting factor has been adapted for sedentary animals by Hughes and Griffiths (1988) who described a geometry of packing that leads to the observed self-thinning. Again an exponent of –3/2 is derived relating mean individual mass to population density, while allometric growth and multi-layered packing are used to explain deviations from this exponent. The concept of multi-layered packing is of less relevance in botany where plants are unlikely to grow one upon the other. In contrast, many sedentary marine organisms are capable of adhering to and growing upon conspecifics such that a multi-layered structure can result. Fréchette and Lefaivre (1990) have included these effects of isometric growth and multi-layered packing of mussels together with the additional criterion of substratum roughness in the relationship:

$$W=kN^{\frac{1-\frac{3}{2}(1-\alpha)}{(1-\varepsilon)(1-\delta)}}$$

Where α accounts for deviations from isometric growth.

ε represents the effect of multi-layer packing and has a positive value smaller than 1

δ represents the roughness of the surface substratum.

Guinez and Castilla (1999) proposed a 3-dimensional self-thinning model that encompasses the previous 2-dimensional models and specifically addressed multi-layered packing of intertidal mussels. This model suggested that density dependence could be more frequent than has previously been indicated by the 2-dimensional models. However, Fréchette and Lefaivre (1990) have suggested that for benthic suspension feeders food may also regulate self-thinning, and have suggested a food regulated self-thinning exponent of –1.33 derived from energetic considerations, although this exponent will vary dependant upon environmental conditions and water column mixing.

Self-thinning in dense cohorts is potentially a key component in predicting population productivity, and is therefore a particularly important consideration for the commercial cultivation of mussels on the seabed. Precise knowledge of the relationship between mean mussel biomass and population density over time would have the potential to determine optimal initial mussel seeding densities and would allow better utilisation of the finite natural mussel seed resource. Furthermore, the use of these density–dependent relationships coupled with predictions of mussel growth would enable the evaluation of mussel production under a range of management scenarios. The present study was carried out on a commercial site and at a commercial scale to investigate density dependence in a seabed cultivated cohort of mussels to establish the relationship between mean individual biomass and density over time. In addition a caged mussel experiment, in close proximity to the main experiment, was run concurrently to examine mussel density-biomass relationships in the absence of the effects of predation. The aims of this study were therefore to determine the relationship between mussel growth and density and to support the development of statistical models of seasonal co-variation such that mussel farmers could better assess the point at which self-thinning might occur, and thereby avoid wasteful over-stocking of their mussel beds. The findings are discussed in the context

of their application for improving the management of commercially cultivated mussels on the seabed in light of the new emphasis on the need for the sustainable management of marine resources.

METHODS

Main Site

The study site was located on an intertidal mudflat adjacent to Bangor Pier within the Menai Strait, North Wales, at approximately low water spring tide level. Mussels have been cultivated in this area by laying mussel seed directly onto the substratum since the 1960s (Dare 1980), however the actual experimental site had not been used for this purpose prior to April 2000 (K. Mould personal communication).

In April 2000 two experimental areas were divided into 16 (4 x 4) cells, each 20 m x 20 m, and these were seeded with mussels approximately 20 mm in length at one of four different stocking levels (7.5, 5, 3, 2 kgm^{-2}) using a Latin square experimental design (Fig. 5.1). Each Latin square was marked with buoys and the mussels scattered over each plot from a boat. Due to the effects of tidal currents and inaccuracies of boat positioning, it was not possible to lay the mussels accurately in the Latin squares. However an *a posteriori* examination of the experimental site revealed that a relatively even initial distribution of mussels at the designated levels had occurred.

The experimental site was sampled at the time of seeding and a further 10 times over the following year until April 2001. Sampling was carried out most frequently during the times of greatest mussel growth (May - July). On each sampling occasion four quadrats of 0.25 m x 0.25 m were taken randomly per cell in areas of mussel cover. The contents of each quadrat were placed in a plastic bag, labelled and taken back to the laboratory. In the laboratory the number of mussels in each quadrat were counted, and 120 randomly selected mussels from each sample measured for their length to the nearest mm from the umbone to the edge of the posterior margin of the shell using Vernier calipers.

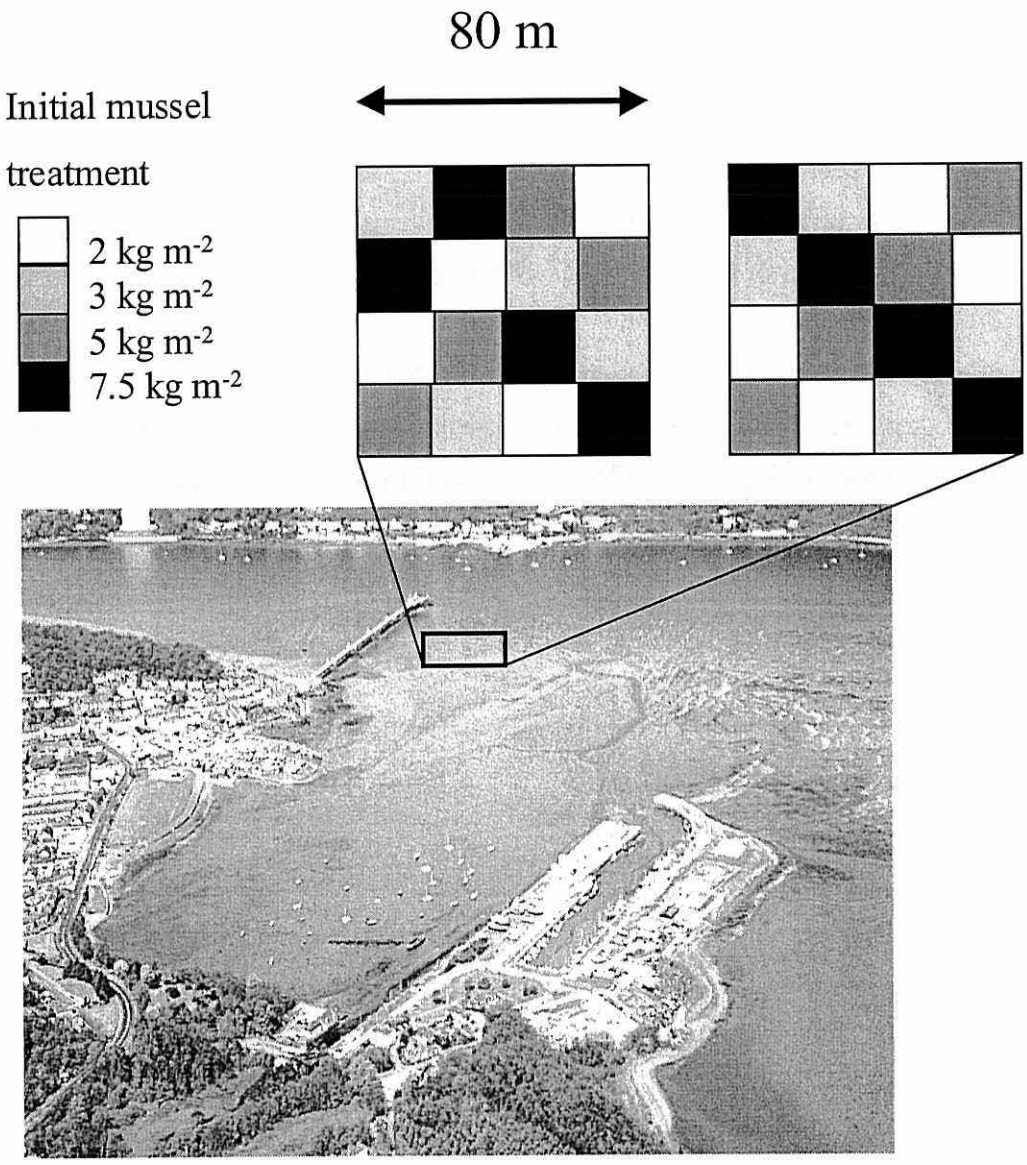

Fig. 5.1. Main site experimental set-up. Adjacent to Bangor Pier in the Menai Strait, North Wales.

Caged mussel experimental site

The caged experimental site was established in close proximity to the main site on the island of Ynys Faelog in the Menai Strait, North Wales. This island is the private property of the University and hence the likelihood of vandalism of the cages was reduced. Cages of dimension 0.5 m (wide) x 0.75 m (long) x 0.25 m (high) were constructed from wooden frames with plastic mesh (5 mm square) sides. The cages were supported on metal frames approximately 0.5 m above the seabed to prevent sedimentation and smothering of the mussels.

Four initial mussel stocking densities of 2, 5, 7.5 and 15 kgm^{-2} were deployed in the cages at six shore heights at regular intervals spanning approximately 70 - 210 minutes mean exposure on low water springs. A total of 24 cages were set up. The cages were seeded with mussels in April 2000, but were first sampled in June 2000 and were then sampled a further 9 times during the following year until April 2001. On each sampling occasion 120 mussels from each cage were randomly selected and length measured to the nearest mm from their umbone to the edge of the posterior margin of the shell using Vernier calipers. The mussels were placed in a 2 litre plastic beaker to provide a volumetric measurement of the 120 mussels and then put back into the cages to maintain the density within the cage. The density in each cage was then determined by volumetrically measuring the amount of mussels present in the cage and converting this to actual numbers using the volume of the 120 mussel subsample as a conversion factor.

Statistical analyses

All statistical analyses were carried out using SAS Version 8.2 (SAS Institute Incorporated 1999-2001). Prior to any statistical analysis the four samples from within each cell (replicate) from the main site were pooled. For each data set a W-N (see below) diagram was created (as in Westoby 1981) to initially establish evidence of self-thinning.

In all analyses:

W = The cube of length was used as a proxy for weight (W) since with isometric growth body volume and therefore individual mass are related to a standard linear dimension of the body (L) such that W is proportional to L^3 (Hughes and Griffiths 1988). L was determined as the mean value based on the four samples from each cell in the Latin square on each sampling occasion.

N = density, represented by mean Ln(Density) based on four samples from each cell in the Latin square on each sampling occasion.

Four statistical models of varying complexity were used to analyse the temporal relationship between W and N over the 11 sampling occasions of the experimental period. This allowed the density dependent effects on the cultivated mussel populations over time, towards a possible 'self-thinning line', to be analysed. The models were compared to test their ability to explain the observed data. The significance of the improvement of the model fit to the data were determined through calculation of an F value from comparison of the model explained sum of squares.

To support the model development ANCOVAs, that compared the effect of sampling date with mean density as the covariant and mean shell length as the response, were carried out on the main site and caged site data sets. Least-square means pairwise tests were also conducted to test for significant differences between each sampling date.

Model development

Model A: Single self-thinning line

$W\{N\} = a + b.N$

a and b are fitted parameters.

Regression analysis was conducted on the entire data set for all dates of Ln(Length^3) against Ln(Density), to provide a single linear relationship between W and N for the whole sampling time period.

Model B: Date-dependant self-thinning lines

$W\{N,date\} = |a|_{date} + |b|_{date}.N_{date}$

Regression analysis was conducted on the data from each individual sampling date of Ln(Length^3) against Ln(Density). Thus the intercept (a) and slope (b) varied for each date. The results of the separate regression analyses were then combined to illustrate the effectiveness of the individual regression relationships in describing the data.

Model C: Self-thinning line with date-specific intercepts

$W\{N, date\} = a_{date} + b.N$

A single model was developed with a common slope term (b) for each sample date, but with an individual date specific value for the intercept (a).

Model D: Self-thinning line with time-varying exponent

$W\{N, date\} = a_{date} + m*(1-exp(-k*(Date-z)))*N$

Where m, l, k and z are fitted parameters.

Model C was developed further in Model D so that the self-thinning was defined as a continuous function of time to imitate the change in the slope of the regression relationships from Model B, with an individual date specific intercept calculated for each date.

RESULTS

Main Site

A clear pattern emerged for the relationship between mean mussel weight (W) and density (N) through time (Fig. 5.2). It should be noted that there was no visible recruitment to the site over the duration of the experiment. Details of the statistical fits of the models to the data and the comparison of model fits are all given in Table 5.1, and parameter values are detailed in Table 5.2. A good relationship between mean weight and density ($F_{1,348}$=675 $p<0.001$ r^2=0.66) for the entire data set is represented by Model A, which is a single linear regression of the data over the whole experimental period (Table 5.1). To establish whether this relationship between mean mussel weight and density changed over time, Model B was developed whereby each date was considered individually with separate regression models. This model provided a significantly better fit to the data than Model A ($F_{21,349}$=802 $p<0.001$ r^2=0.98) (model comparison: A to B $F_{20,339}$=275 $p<0.001$ r^2=0.32) (Table 5.1) indicating that the relationship between mean mussel weight and density had varied over time. This variation in the relationship over time is illustrated by a change in the slope and intercept values of the regression equation between mean weight and density for each of the eleven sampling dates (Fig. 5.3 and 5.4). The slope of the regression relationship increases (although they are negative numbers this simply indicates the direction of the slope) over the first five dates (25/04/00 to 31/07/00) where the values for the remaining six dates (31/08/00 to 07/04/01) appear to be similar (Fig 5.3). Similarly the intercept increases over the first five dates, and the remaining six dates appear to be similar in value (Fig 5.4). There was a good correlation between the date specific slopes and intercepts (Pearson correlation = -0.99 $p<0.0001$).

To examine whether a self-thinning model with a common exponent (slope) could adequately describe the observed data Model C was developed. This model does not provide as good a fit to the data as Model B ($F_{10,339}$=4.62 $p<0.001$ r^2=0.003), but does reduce the number of model parameters by ten (i.e. is more parsimonious), and is still a significantly better fit to the data that Model A ($F_{10,339}$=478 $p<0.001$ r^2=0.32) (Table 5.1). However, although Model C reflected the constant slope of the final six dates it does not incorporate the increasing slope of the first 5 dates to reach this asymptote.

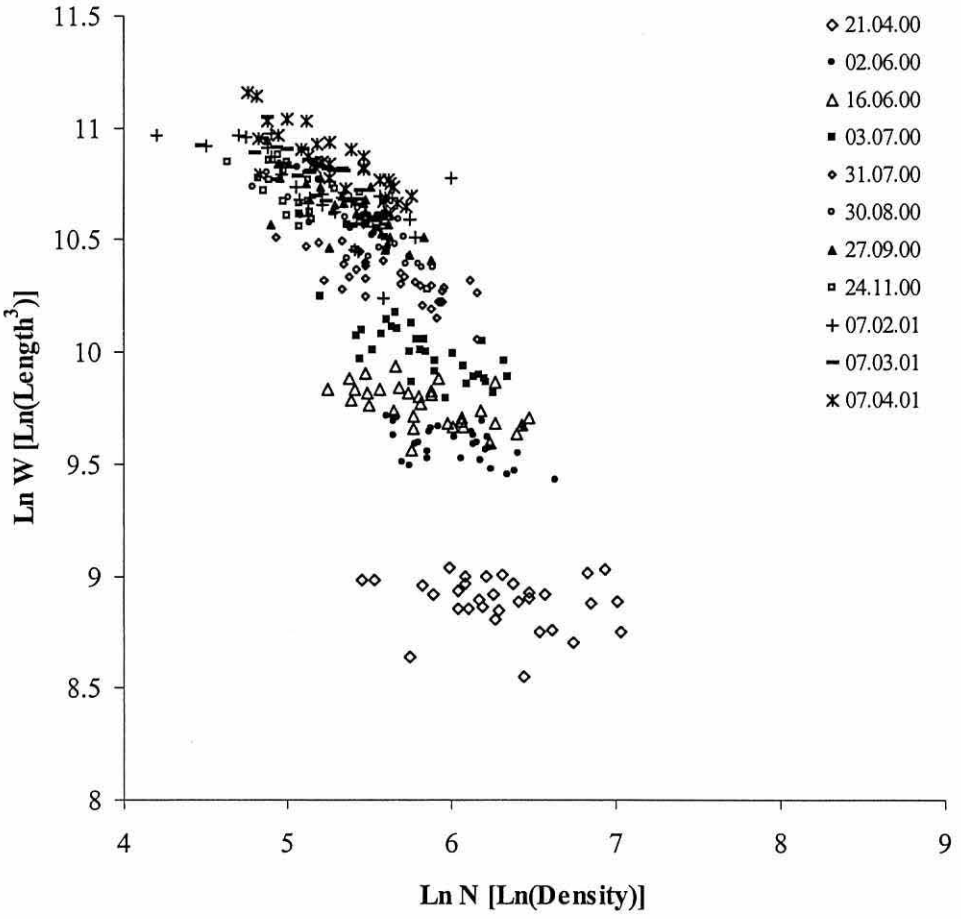

Fig. 5.2. Main Site. W-N [Ln(Length^3) - Ln(Density)] Diagram of mussels sampled from Main Site April 2000 to April 2001.

Table 5.1. Main Site. Analysis of goodness-of-fit between the Models A-D and the experimental data. Models C and D were calculated using a non-linear procedure hence the regression model show n not n-1 for df. The df are corrected in the total. Model comparison was calculated by comparing the explained mean squares of two models:

((Model 2 SS – Model 1 SS)/(Model 2 df – Model 1 df))/Model 2 residual SS/Model 2 residual df)

where Model 2 SS > Model 1 SS

Source of Variation	df	SS	MS	F	p	r^2
Model A $W\{N\} = a + b.N$						
Model	1	84.7287	84.7287	675	<0.0001	0.660
Residual	348	43.6511	0.12543			
Corrected Total	349	128.380				
Model B $W\{N, date\} = \|a\|_{date} + \|b\|_{date}.N_{date}$						
Within separate models	11	2.63645	0.23968	32.1	<0.0001	0.021
Between dates (separate models)	10	123.276	12.3276	1650	<0.0001	0.960
Total explained by separate dates and model	21	125.913	5.99585	802	<0.0001	0.981
Residual	328	2.45320	0.00748			
Corrected total	349	128.400				
Model comparison: A to B	20	41.184	2.05922	275	<0.0001	0.321
Model C $W\{N, date\} = a_{date} + b.N$						
Model	12	16877.4	3073.1	1340	<0.0001	
Residual	338	2.8810	0.00852			
Uncorrected total	350	26880.3				
Corrected total	349	128.400				
Model comparison: A to C	10	40.790	4.0790	478	<0.0001	0.318
Model comparison: C to B	10	0.3940	0.0394	4.62	<0.0001	0.003
Model D $W\{N,date\} = a_{date} + m*(1-exp(-k*(Date-z)))*N$						
Model	14	36876.6	2634.0	881	<0.0001	
Residual	336	3.6595	0.0109			
Uncorrected total	350	36880.3				
Corrected total	349	128.400				
Model comparison: A to D	12	40.012	3.3343	305	<0.0001	0.312
Model comparison: D to B	8	1.1725	0.1466	19.6	<0.0001	0.009
Model comparison: D to C	2	0.7785	0.3893	45.7	<0.0001	0.006

Table 5.2. Main Site. Parameter estimations for Models A-D (see text for full model descriptions).

Model	Parameter	Date										
		All dates	**21/04/00**	**02/06/00**	**16/06/00**	**03/07/00**	**31/07/00**	**30/08/00**	**27/09/00**	**24/11/00**	**07/02/01**	**07/03/01**	**07/04/01**
A	**a**	15.99										
	SE	0.222										
	b	-1.03										
	SE	0.040										
B	**a**		9.240	10.52	10.67	11.58	11.72	12.51	12.56	12.43	12.34	12.79	12.89
	SE		0.326	0.277	0.252	0.286	0.212	0.246	0.299	0.276	0.302	0.274	0.243
	b		-0.056	-0.154	-0.156	-0.271	-0.248	-0.359	-0.357	-0.339	-0.314	-0.389	-0.386
	SE		0.052	0.046	0.043	0.049	0.038	0.045	0.056	0.053	0.058	0.053	0.046
C	**a**		10.51	11.14	11.27	11.50	11.77	11.96	12.03	12.00	12.04	12.11	12.21
	SE		0.102	0.097	0.94	0.094	0.091	0.088	0.87	0.085	0.085	0.084	0.086
	b	-0.257										
	SE	0.016										
D	**a**		9.26	10.23	10.48	10.83	11.31	11.71	11.95	12.27	12.77	12.99	13.30
	SE		0.249	0.151	0.136	0.135	0.143	0.155	0.163	0.154	0.148	0.175	0.241
	k	-4.53										
	SE	51.33										
	m	0.0002										
	SE	0.0031										
	z	-49.81										
	SE	61.61										

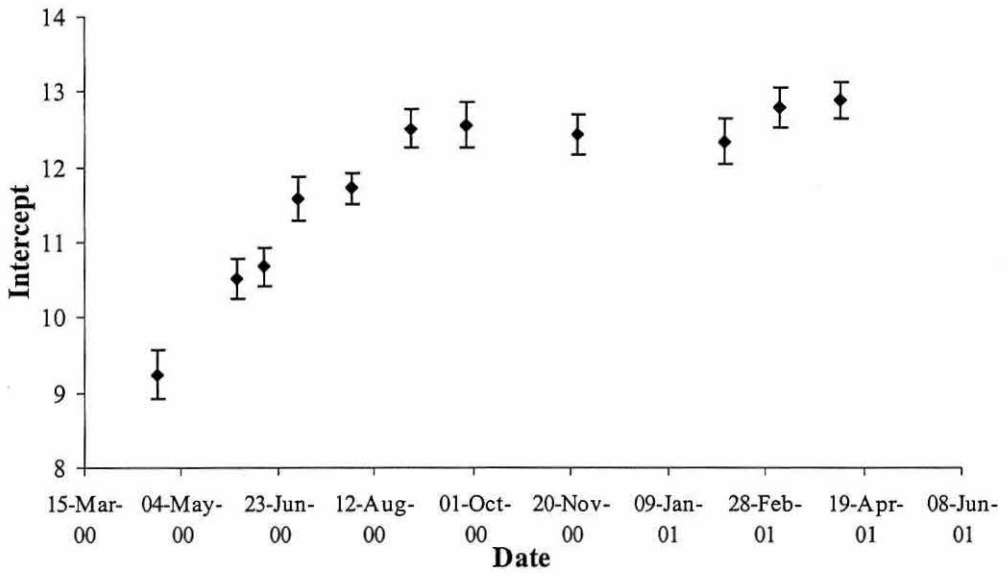

Fig. 5.3. Main Site. Intercept (± SE) of regression relationship between mussel W [Ln(Length^3)] and N [Ln(Density)] for each sampling occasion between April 2000 and April 2001.

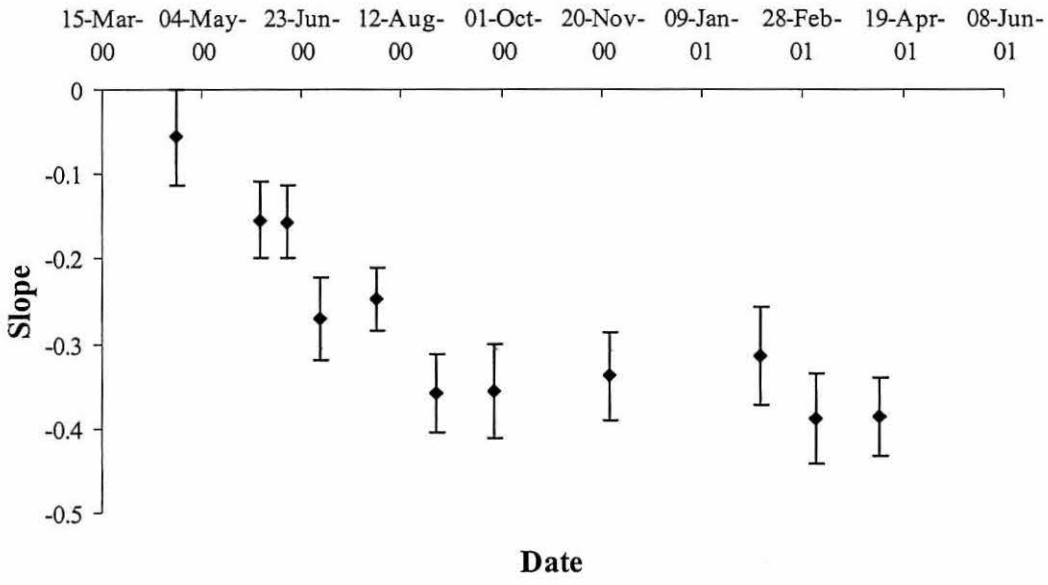

Fig. 5.4. Main Site. Slope (± SE) of regression relationship between mussel W [Ln(Length^3)] and N [Ln(Density)] for each sampling occasion between April 2000 and April 2001.

There was a significant effect of sampling date on the relationship between W and N (date*density terms of the ANCOVA) illustrating that the slope of the relationship changed over time (Table 5.3). However, since this was an interaction term it is not possible to do *post hoc* tests to establish where the significant differences are in the data set. To support the assumptions of the model development it was necessary to establish whether there were significant differences in the last six dates. The data for the last six dates were therefore compared using ANCOVA (Table 5.4). There was no significant difference in the slope of the regression relationships over time, though the intercept was found to change significantly over time. In particular, among the last six dates, the two final sampling occasions were significantly different to all the others (Table 5.5).

Table 5.3. Main Site. ANCOVA of mussel Ln(Length^3) against Ln(Density) comparing all sampling dates. Adjusted SS used for tests.

Source of Variation	df	Seq SS	Adj SS	MS	F	p
Density	1	84.73	2.386	2.3857	319	<0.0001
Date	10	40.77	1.423	0.1423	19.0	<0.0001
Density*Date	10	0.428	0.428	0.4278	5.72	<0.0001
Error	338	2.453	2.453	0.0075		
Corrected total	349	128.4				

Table 5.4. Main Site. ANCOVA of mussel Ln(Length^3) against Ln(Density) comparing last 6 sampling dates. Adjusted SS used for tests.

(No interaction term as no significant difference between slopes $F_{5,179}$=0.34 P=0.8886)

Source of Variation	df	Seq SS	Adj SS	MS	F	p
Density	1	2.570	2.108	2.1084	276.4	<0.0001
Date	5	1.143	1.143	0.2287	29.97	<0.0001
Error	184	1.404	1.404	0.0076		
Corrected total	190	5.117				

Table 5.5. Main Site. Pairwise tests – Least square means for effect Date P>t for HO: LSMean (i) = LSMean (j) of mussel Ln(Length^3) against Ln(Density) comparing last 6 sampling dates.

i/j	31/08/00	27/09/00	24/11/00	07/02/01	07/03/01
27/09/00	0.005				
24/11/00	0.249	0.100			
07/02/01	0.004	0.855	0.067		
07/03/01	<0.0001	0.003	<0.0001	0.001	
07/04/01	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

Model D was developed to represent the change in the regression relationship between mean weight and density over time to reach an asymptotic slope for the final dates. This model explained a statistically significant part of the observed variance in the data and provided a better fit than Model A ($F_{8,341}$=19.6 $p<0.001$ r^2=0.009) (Table 5.1). However, the model fit the data significantly worse than the other model developments B and C (respectively $F_{8,341}$=19.6 $p<0.001$ r^2=0.009; $F_{2,347}$=45.7 $p<0.001$ r^2=0.006). The models B and C demonstrated that there was significant temporal variation in the self-thinning line. Model D explicitly demonstrated that the exponent (slope) became significantly more negative with time. Therefore although Model D explained slightly less of the observed variance in the data it provided a greater understanding about the nature of the variation.

Caged mussel experimental site

The W-N diagram for the mussels from the caged experiment does not show a clear relationship between mean weight (W) and density (N) (Fig. 5.5). However the data for all of the sampling dates showed a significant regression using Model A (Table 5.6). Parameter values are given in Table 5.7. When data from each sampling date were regressed separately, only the regression models for the last five dates were significant (27/09/00-07/04/01), therefore, it was not considered appropriate to formulate more sophisticated models for the full data set or continue along the same modelling lines as for the Main Site.

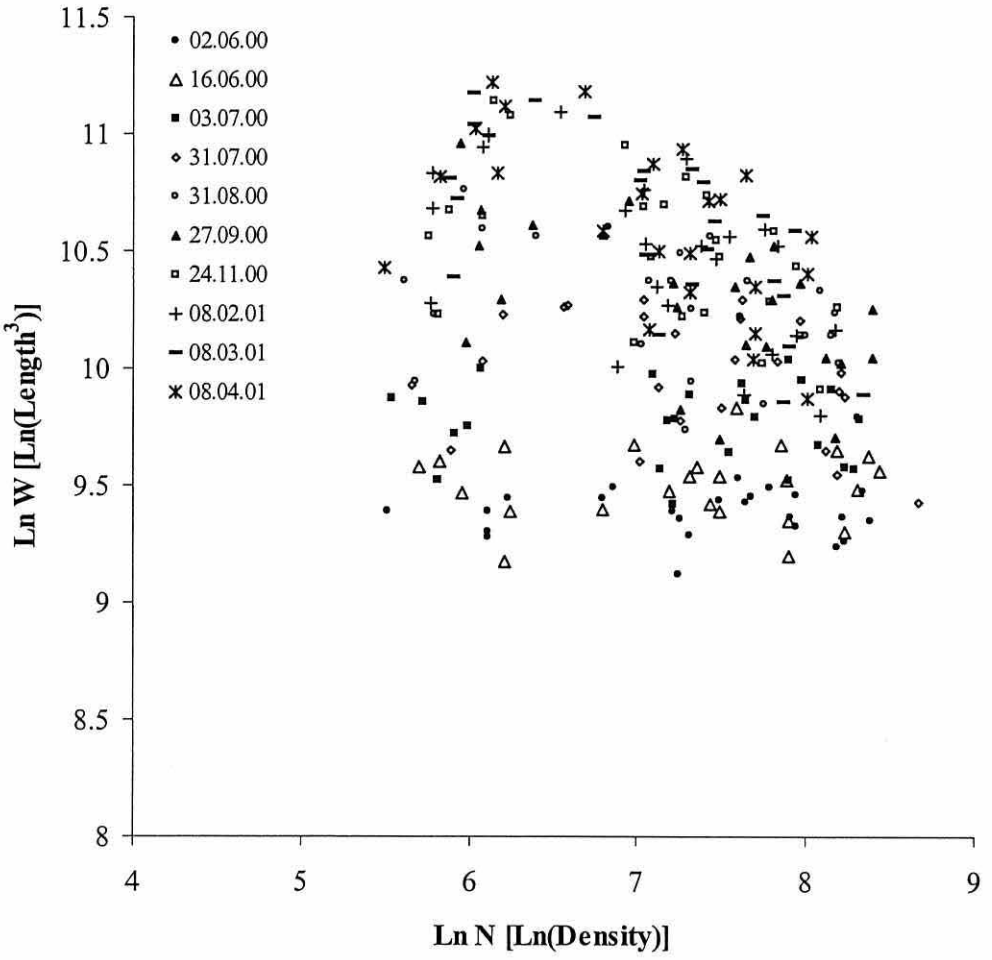

Fig. 5.5. Caged Site. W-N [Ln(Length^3) - Ln(Density)] Diagram of mussels sampled from Main Site June 2000 to April 2001.

Table 5.6. Caged Site. Analysis of goodness-of-fit of Model A and the experimental data.

Source of Variation		df	SS	MS	F	p	r^2
Model A	$W\{N\} = a + b.N$						
Model		1	5.84210	5.8421	24.05	<0.0001	0.092
Error		238	57.8125	0.2429			
Corrected Total		239	63.6546				

Table 5.7. Caged Site. Parameter estimations for Model A (see text for full model description).

Model	Parameter	All Dates
A	a	11.54
	SE	0.287
	b	-0.195
	SE	0.040

Not surprisingly, there was a significant effect of sampling date on the full data set (Table 5.8). The last five dates were then considered separately since they had significant regression relationships between mean weight and density. Significant differences occurred between the last five dates (Table 5.9). The slopes of the regression relationships did not differ significantly, and the difference between sampling dates resulted from changes in the intercept of the regression relationships (Table 5.10).

Table 5.8. Caged Site. ANCOVA of mussel Ln(Length^3) against Ln(Density) comparing all sampling dates. Adjusted SS used for tests.

Source of Variation	df	Seq SS	Adj SS	MS	F	p
Density	1	5.842	3.458	3.4584	55.5	<0.0001
Date	9	42.02	4.496	0.4995	8.02	<0.0001
Density*Date	9	2.081	2.081	0.2312	3.71	<0.0001
Error	110	13.71	13.71	0.0623		
Corrected total	119	63.65				

Table 5.9. Caged Site. ANCOVA of mussel Ln(Length^3) against Ln(Density) comparing last 5 sampling dates. Adjusted SS used for tests.

(No interaction term as no significant difference between slopes $F_{4,110}$=0.33 P=0.8574)

Source of Variation	df	Seq SS	Adj SS	MS	F	p
Density	1	5.021	4.493	4.4929	54.07	<0.0001
Date	4	1.071	1.071	0.2677	3.22	<0.0001
Error	114	9.473	9.473	0.0831		
Corrected total	119	15.57				

Table 5.10. Caged Site. Pairwise tests – Least square means for effect Date P>t for HO: LSMean (i) = LSMean (j) of mussel Ln(Length^3) against Ln(Density) comparing last 5 sampling dates.

Bold text indicates significant difference of p<0.05.

i/j	27/09/00	24/11/00	07/02/01	07/03/01
24/11/00	0.049			
07/02/01	0.072	0.863		
07/03/01	0.004	0.340	0.261	
07/04/01	0.002	0.213	0.156	0.767

DISCUSSION

For the main site a clear relationship developed between mean mussel weight (measured as Length^3) and density over the experimental period. As the mean size of the cohort increased this linear relationship became increasingly negative (Fig. 5.4), implying that at the higher densities the mussels were becoming more restricted in their growth and hence displayed density dependence. The cohorts may have experienced size dependent mortality over the experimental period therefore are not strictly independent over time and it is accepted that this may have confounded the relationship between mean mussel weight and density. Nonetheless, the method used in this study has allowed examination of the change in the mussel weight-density relationship over time. The significant correlation between the date specific slopes and intercepts also mean that analysis of the significance of the variations in the self-thinning lines between dates becomes more difficult, as it implies that the slope and intercept change over time together. The variation in the relationship between mussel mean mussel weight and density was illustrated through the better fit of Model B to the data set, which allowed for change in the relationship over time, as compared to Model A that provided a constant relationship. An apparent asymptote in the slope of the regression relationship between mean mussel weight and density indicated that a possible self-thinning line might have been reached. This would mean that as the biomass of the mussels increased, so the mussel density would decrease along the self-thinning line with a slope defined by Model D.

The exponent that Model D predicts for a self-thinning line of the mussel populations for the last six dates ranges from –0.2 to -0.4. For single layered mussels, with isometric growth this exponent would be expected to be –3/2 (Hughes and Griffiths 1988). The mussels at this site were multi-layered (personal observations), and were able to maintain a high level of multi-layering due to the low wave exposure of the mud-flat, where risk of dislodgement is small. This multi-layering can alter the self-thinning line, and is likely to decrease the self-thinning exponent (Guinez and Castilla 1999). Additionally, the degree of layering may have been quite variable due to clumping/aggregation of the mussels. Hence the data for a cell may reflect a combination of areas with above average density, high levels of layering (with possible strong self-thinning) and areas of below average density, low levels of layering (that do not display self-thinning) increasing the variability of the samples taken. Nonetheless, this situation realistically represents the commercial situation given the size of the plots and the fact that the industry laid the mussels. Allometric growth of the mussels will also have influenced the self-thinning line, although in

many cases the effect is small (Fréchette and Lefaivre 1990). However, even with the combined effect of multi-layering and allometric growth, it is unlikely that these factors would be sufficient to cause such a drastic reduction in the self-thinning exponent.

Model D gave a very good statistical fit to the data; however, since the model predicted a variable exponent for the last six dates this model does not accurately represent the temporal relationship between mean mussel weight and density. The slope (apparent self-thinning exponent) of the regression relationships did not differ significantly over the last six dates, but the intercept did increase with time (Fig. 5.3). This implies that the regression line on each date was moving higher up the W axis i.e. that as the mean weight of the cohort increased the apparent self-thinning line was also moving. If a self-thinning line had been reached both the slope and intercept would not have differed significantly over time, hence it must be concluded that a self-thinning line had not in fact been reached.

The dates over which there was no significant difference in the slope of the regression relationship between mean mussel weight and density coincide with the autumn and winter sampling dates. It is possible that the apparent self-thinning line is therefore due to reduced growth over the colder, food-scarce months as the mussels grow less rapidly and therefore incur less density dependent effects. This would concur with the finding that the last dates had intercepts that were significantly different to all others, as by this date (March - April) food will have become more abundant and hence the mussels will start to resume growth at a faster rate. Over this period (March-April) it is likely that the growth of mussels caused the intercept of the regression line to increase. However, the growth rate was probably still relatively low compared to the summer months and the populations at the highest densities would therefore not incur the same extent of density dependent effects and hence the slope of the regression line did not significantly differ over this period. The data from the caged mussel experiment also displayed a similar pattern with a constant slope having been achieved while the intercepts changed significantly with time (Table 5.9). It may also be possible that by spring the growth space available to the mussels would have increased due to non-density dependent mortality over the winter.

It may be expected that as the mussels start to grow at a faster rate over the summer months subsequent to this experiment the slope of the regression relationship might again increase until the actual self-thinning line is reached. Although the mussels in

all of the cells of the main experiment had not reached the self-thinning line, this does not mean that density dependent effects did not occur in the mussel populations. In both the main site and caged mussel experiments a decrease was evident in the highest densities sampled over time (Fig. 5.2 and 5.5). On the main site this could be explained by crab predation over the summer months, as in temperate climates crab numbers are highest over this period (Hunter and Naylor 1993; Aagaard *et al.* 1995). The smallest mussels would have been the most susceptible to crab predation, since all size ranges of crabs can crush small sized prey (Seed 1976) and with a reduced handling time compared with that required for larger mussels (Elner and Hughes 1978). Over the summer months this would have resulted in a higher mortality rate for the smallest mussels compared with the larger sized mussels. The smallest mussels were consistently found at the highest densities so this may have additionally confounded the relationship between mean mussel weight and density. In the winter months crab numbers are greatly reduced as they move into deeper water, and the other major predators of mussels in the intertidal zone, oystercatchers (*Haematopus ostralegus*), are unlikely to be interested in the small sized mussels used in the present study (Meire 1993; Beadman *et al.* in press). Hence, over the winter months there will have been less size selective mussel mortality due to predation.

The size dependent mortality over the summer months could have partially been responsible for the seasonal change in the relationship between mussel biomass and density. However, it is unlikely that crab predation pressure alone would have been sufficient to produce the observed seasonal change in the relationship. The crab predation pressure in winter would have been focussed on the smallest mussels and the consistently good regression relationships between biomass and density over the entire size range of mussels implies that other factors contributed to these relationships. For example, mussel density can influence growth rates through space limitation whereby the effect of physical pressure on a mussel shell from neighbouring mussels results in reduced valve gape and hence filtration rate, leading to reduced growth (Fréchette *et al.* 1992). Furthermore, Okamura (1986) found that mussels at higher densities displayed lower reproductive output than mussels found at relatively low densities. Depletion of food at high mussel densities has been shown also to significantly affect mussel growth (Fréchette and Bourget 1985; Peterson and Black 1987). It seems likely therefore that density dependent effects were apparent in the mussel populations resulting in the observed relationships between mussel biomass and density. Unfortunately due to the variation in the caged mussel

experiment data it was not possible to directly compare the differences between the main site and the cages designed to exclude predation.

Although a self-thinning line was not reached within the duration of this experiment this study has demonstrated at a large-scale how the relationship between mussel biomass and density changes over time as a result of mussel growth. In particular it has highlighted the impact of seasonal variation on density dependent effects in mussel populations. The model development demonstrated how the relationship between mean mussel weight and density changed rapidly over the periods of fast growth in the summer months, and remained relatively constant over the food depleted winter months. The findings of the study are therefore directly relevant to the commercial cultivation of mussels on the seabed, and the potential impact of mortality and reduced growth rate on mussel populations due to density dependent effects.

Management Options

At present, in the commercial cultivation of mussel seed on the seabed, mussels are laid down at the highest densities that can be obtained from the limited natural seed resource. The establishment of a self-thinning line would provide mussel growers with guidance as to the density above which they will incur density dependant mortalities for a given mussel size. Although the self-thinning line was not reached by the whole of the experimental mussel population this does not mean that it would be advisable to continue to lay the mussels at the highest densities. There has been some evidence of density dependence at these high densities and as the mussels grow larger this effect will become more pronounced. Over the experimental period the 'self-thinning line' became steeper which illustrates the increasing impact of density dependent effects on the mussel population. This implies that by initially seeding at lower densities unnecessary losses due to density dependent effects over the cultivation period could be avoided. Thus, through optimising the use of the natural seed resource by reducing the amount of natural seed mussels that need to be removed from the environment this would provide a more sustainable approach to mussel cultivation.

The results of the study also indicate that the time of the year, and therefore growth rate (which may also be affected by position on the shore) affect the relationship

between mean mussel weight and density and will therefore be an important factor in determining stocking density. Hence in the management of mussel stocks, when stocks are being relocated both shore height and season should be taken into consideration. At higher shore levels and over the colder food depleted months the mussel populations could be stocked at higher densities with reduced density dependent effects compared to higher growth areas over the faster growth season.

Mortality and reduced growth rate due to high stocking densities also lends support to the management option of seed 'banking' (Beadman *et al.* in press). This involves 'banking' seed mussel on high shore areas in times of abundant natural mussel settlement and in subsequent years, when natural settlement is low and the supply of wild seed is limited, transferring them down shore or subtidally to enhance growth to marketable size. By using mussels for 'banking' and stocking at a reduced density on the main cultivation plots this will not only reduce the density dependent effects on the main growing areas, but also even out the unpredictable supply of seed mussel for on-growing.

Chapter 6

Density-dependent changes in invertebrate assemblages associated with mussel cultivation

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ABSTRACT

Mussel beds alter the infaunal benthic community of the adjacent and interstitial sediments through provision of a complex habitat, input of organically rich material and larval removal through filter feeding. This study was carried out at a site of commercial seabed mussel cultivation to determine the effect of mussels on the infaunal community structure of an intertidal mudflat. The presence of mussels resulted in a change in both the composition of species of the infaunal community, and also the number of individuals and number of species. The infaunal communities of plots with mussels were less abundant, in terms of both individuals and numbers of species, than the control areas at all but the lowest areas of mussel cover. Negative trends of species numbers and abundance of individuals with increased area of mussel cover were also demonstrated. Although the species composition and abundance of individual invertebrate species was altered by the presence of mussels, the distribution of individuals among species remained relatively unchanged.

INTRODUCTION

Mussels (Bivalvia: Mytilidae) are distributed globally and are a conspicuous feature of many intertidal habitats on both hard and soft substrata (Seed 1976). They form a key component of many marine communities and often are the dominant organisms in terms of their biomass (Seed 1976; Herman 1993). Mussels also create a secondary habitat, composed of layers of mussels with accumulated sediment, faeces, pseudofaeces and shell debris, which also has been shown to support its own highly diverse community (e.g. Tsuchiya and Nishihira 1985; 1986, Svane and Setyobudiandi 1993; Ragnarsson and Raffaelli 1999). Differences in the faunal community associated with mussel beds compared to that of the surrounding sediments have been demonstrated (e.g. Dittman 1990; Guenther 1996; Commito 1987; Ragnarsson and Raffaelli 1999). In terms of physical habitat structure, mussels provide a complex habitat capable of harbouring a diverse assemblage of associated flora and fauna (Seed and Suchanek 1992). Biologically, the mussels provide an input of sediment and organic matter in the form of faeces and pseudofaeces (Tsuchiya 1980; Kautsky and Evans 1987), and remove fine particulate matter and some larvae of benthic invertebrates through their filter-feeding activities (Cowden 1984 *et al.*; Morgan 1992; Wahl 2001). Consequently, mussel communities have the capacity to either enhance or degrade the infaunal assemblage.

Mussels occur in naturally settled beds in the intertidal and subtidal zones. Alternatively, they can be laid in 'artificial' beds for the purposes of cultivation. In seabed cultivation small 'seed' mussels (up to 25 mm in shell length) are dredged from their site of natural settlement and transferred to a cultivation site where there are good conditions for mussel growth. The mussel cultivator will lay mussels at different densities and at different tidal heights so as to realise the greatest financial return when they are harvested. At high mussel densities mutli-layering is likely to occur that will increase mussel bed complexity; however, the accumulation of large amounts of sediment from biodeposition can produce a reducing environment that will affect the density or diversity of the associated animals (Tsuchiya and Nishihira 1985; Asmus 1987). At low mussel densities patches of mussels interspersed with bare substratum may be produced as the mussels clump together, and patch size has been shown to have an effect on species richness and number of individuals of associated species (Tsuchiya and Nishihira 1985).

In past studies the effects of mussel density on invertebrate assemblages and other environmental parameters has been related to the mussel density encountered at the

time of sampling (e.g. Dittman 1990; Commito 1987). However, the mussel density encountered within a bed at the time of sampling requires careful consideration in view of the fact that the mussel bed will change dynamically due to mussel growth and mortality (predation and density dependant effects). As a result the infaunal assemblages encountered at the time of sampling may reflect not only the mussel density at the time of sampling but also the initial mussel stocking density. The latter may have a long-term influence in terms of the biodeposition that has occurred prior to the collection of invertebrate samples.

The need to be able to determine the effects of various activities within the coastal zone such as mussel cultivation has arisen due to growing environmental awareness and the resulting legislation. It is of particular importance to the mussels industry since the areas that are used for seabed cultivation, such as intertidal mudflats and sandflats, are specifically covered under European Habitat Conservation Regulations (Council Directive 92/43/EEC Annex I). If the area becomes designated as a Special Area of Conservation under these features it must undergo an appropriate assessment. Therefore, with the growth of the UK mussel industry it is important that the impact of expanding the areas of subtidal and intertidal mudflat on which mussels are laid can be established.

The present study was carried out at a site of commercial mussel cultivation and formed part of an extensive mussel growth experiment. The aims of the experiment were to determine:

1) The differences, if any, in the infaunal community structure between areas of bare mud and areas on which mussels were grown before and 18 months after mussels were laid.
2) Whether the infaunal community encountered at the time of sampling was related to the original density at which mussels were laid or more closely to the mussel density at the time of sampling.

METHODS

The study site was located on an intertidal mudflat adjacent to Bangor Pier on the Menai Strait, North Wales, at approximately low water spring tide level. Mussels have been cultivated in this area by laying directly onto the substratum since the 1960s (Dare 1980), however the actual experimental site had not been used for this purpose before April 2000 (K. Mould personal communication).

Infaunal and sediment sampling

The experiment was conducted as a part of a large-scale mussel growth experiment, which was set up in October 1999. This consisted of a 4 x 4 Latin square that comprised of 16 individual plots (20 x 20 m). Initially in October 1999, the infaunal community was sampled by taking five cylindrical cores (15 cm diameter x 15 cm deep) at random from within four of the plots that were distributed across the site (A3, B4, C2, D5) (Fig. 6.1). These have been termed the 1999 controls in the present experiment. A sediment sample was taken in each plot using a cylindrical core (5 cm diameter x 5 cm deep) and stored frozen until analysed.

In April 2000 each of the plots was seeded with mussels at one of four different stocking treatments (7.5, 5, 3, 2 kgm^{-2}) which meant that approximately 27 tonnes of mussels were laid in total. The Latin square was marked with buoys and the mussels scattered over each plot from a boat. Due to the effects of tidal currents and boat positioning, it was not possible to lay the mussels in precise squares, however an *a posteriori* examination of the experimental site revealed that a relatively even initial distribution of mussels at the designated densities had occurred.

In October 2001, 18 months after seeding, the site was resampled. Five cores were taken randomly within each plot in areas covered with mussels. Since the mussels had clumped together it was possible to take an extra set of samples in the lowest mussel treatment plots on the extensive areas of bare mud where no mussels had grown at any point. These have been termed the 2001 controls for this experiment. Again a sediment sample was taken in each plot, after first removing the layer of mussels covering the substratum.

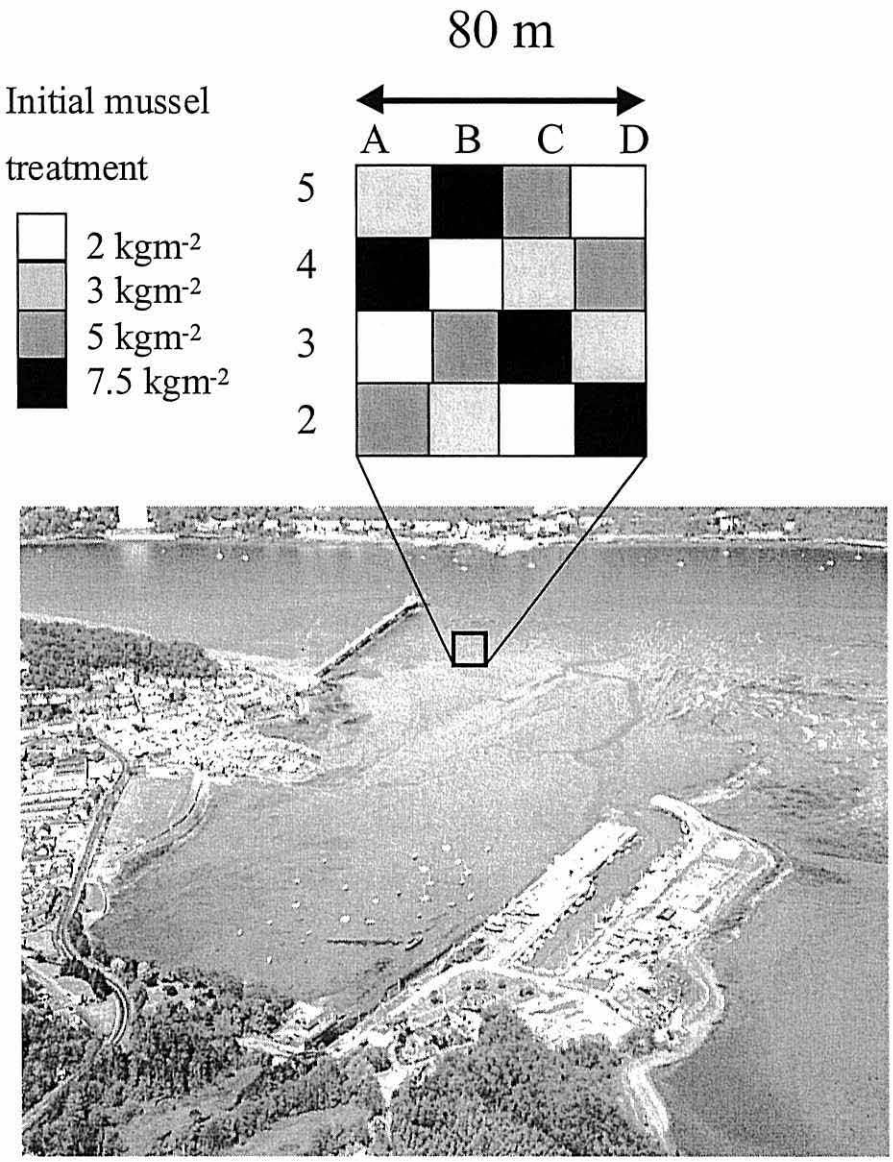

Fig. 6.1. Experimental set-up. Adjacent to Bangor Pier in the Menai Strait, North Wales.

The infaunal samples were washed over a 0.5 mm mesh and the residue preserved in 4% formalin. Animals were identified to the lowest taxonomic level whenever possible. The total number of individuals and the total number of species for each sample were counted, however, when they occurred, the mussels within each core were excluded from these counts.

Mussels in each sample were counted separately and their length established by measuring the distance between the umbone and the edge of the posterior margin of the shell using Vernier calipers. Total mussel surface area ($length^2$), mussel volume ($length^3$) and dry weight were estimated for each of the plots. Mussel flesh dry weight was determined by drying in an oven at 90°C for 12 h. The sediment samples were analysed for organic content by drying the sediment at 90°C for 12 hours and then incinerating a known weight of dry sediment at 550°C for 6 hours. The percentage organic content was determined from the loss of weight on ignition (Holme and MacIntyre 1984).

Statistical treatment

The data from the five cores collected from each plot were pooled prior to undertaking further analyses. The data were analysed in two ways:

1. Grouped by presence or absence of mussels

Initially the data were grouped according to the presence or absence of mussels creating 3 groups 1) With mussels; 2) Control 1999 and 3) Control 2001. The PRIMER ecological statistical software package (Clarke and Warwick 1994) was used to perform multivariate analyses of the data. Cluster analyses on the community data were performed using the Bray-Curtis index of similarity on fourth root transformed data followed by multi-dimensional scaling (MDS). The overall percentage contribution made by each species to the average dissimilarity between two groups was ascertained using the SIMPER programme. Differences between treatments were tested using an *a priori* one-way analysis of similarities (ANOSIM) test. Ranked species abundance plots (dominance plots) were constructed to analyse changes in community structure.

Mann-Whitney pair-wise tests were used to test for differences in the median number of individuals, median number of species, and numbers of individuals per species between treatments. Differences in the median organic content of the sediment samples at each treatment were also tested using Mann-Whitney pair-wise tests.

Non-parametric tests were used, as the data were not normally distributed (Anderson-Darling test).

2. Infaunal community associated with the mussel bed

The control data were excluded from this analysis in order to specifically analyse the effects of mussel density upon the associated infaunal community within the mussel bed.

a. Original seeding treatment

The data were grouped according to the four original seeding treatments. The PRIMER ecological statistical software package (Clarke and Warwick 1994) was used to perform multivariate analyses of the data. Cluster analyses on the community data were performed using the Bray-Curtis index of similarity on fourth root transformed data followed by multi-dimensional scaling (MDS). Significant differences between treatments were determined using an *a priori* one-way ANOSIM test.

Kruskal-Wallis tests were used to test for significant differences in the median number of individuals and median number of species between treatments. Differences in the median organic content of the sediment samples at each treatment were also tested for using a Kruskal-Wallis test. Non-parametric tests were used, as the data was not normally distributed (Anderson-Darling test).

b. Mussel density at time of sampling

The mussel density at the time of sampling was not grouped *post hoc*. The data have been analysed according to actual number of mussels in each plot. Counts of mussels were excluded from the multivariate community analyses and hence were treated as a variable against which the community relationships could be compared. The relationship between the environmental factors, in terms of mussel presence (numbers, area, volume, dry weight) and sediment organic content, and the benthic community were investigated using BIOENV (Clarke and Warwick 1994) and supported by the RELATE test (Clarke and Warwick 1994).

Regression analysis was used to determine whether significant relationships occurred between mussel area and total number of species, total abundance and abundance of individual species.

RESULTS

1. Grouped according to presence or absence of mussels

a. Infaunal community associated with mussel beds and control areas

There was a significant difference between the infaunal communities of the control areas (1999 and 2001) and areas on which mussels were present. (ANOSIM R=0.959 $p<0.001$, R=0.839 $p<0.001$ respectively) (Fig. 6.2). This difference was reflected in fewer numbers of animals per sample in the plots with mussels compared with either of the controls (Mann-Whitney Mussels vs 1999 Control W=142.0 $p<0.05$, Mussels vs 2001 Control W=216.0 $p<0.05$) (Fig. 6.3). The median number of species was also significantly lower in the plots with mussels than the 1999 control (Mann-Whitney W=139.0 $p<0.05$). There was no significant difference between the plots with mussels and the 2001 control (Mann-Whitney W=148.0 $p=0.0654$) (Fig. 6.4). However, it should be noted that although the median number of species in plots with mussels was not significantly different from the 2001 Control, the identity of some of the species recorded were different between the two treatments (Table 6.1). There was no clear difference in community structure between the treatments in terms of dominance by rank species abundance (Fig. 6.5).

An analysis of the individual species that contributed to the major difference between the controls (1999 and 2001) and plots with mussels illustrated the differences in the infaunal communities. Some species were specific to either the mussels or control treatment plots. The species *Corophium multisetosum, Polydora antennata* and *Pygospio elegans* (only one individual was present in the lowest density mussel sample) were only present in the control plots (1999 and 2001). Conversely, *Carcinus maenas* and *Scololepis squamata* were only found within the plots with mussels (respectively mean = 8.56 SE = 1.22; mean = 0.94 SE = 0.87). Other species showed either increased (Cirratulidae, *Corophium volutator, Nephtys hombergi, Notomastus latericeus*) or decreased (*Melita palmata, Tubificoides benedeni*) numbers of individuals, in both the 1999 and 2001 control plots compared to the plots with mussels (Fig. 6.6, Table 6.2).

Organic content was significantly higher in the plots with mussels than in either the 1999 or 2001 controls plots (Mann-Whitney W=200 $p<0.05$ in both cases).

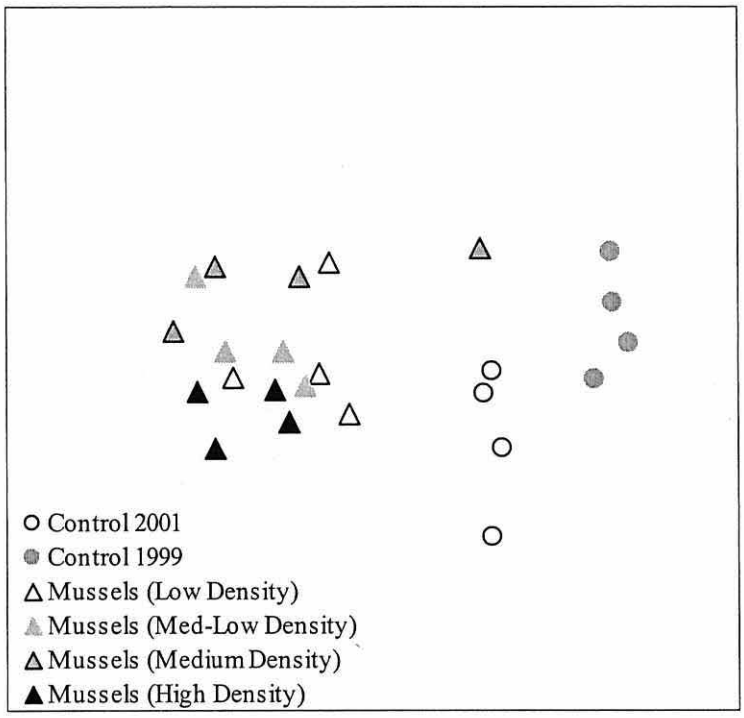

Fig. 6.2. Two dimensional MDS ordination of community data found in the control and plots with mussels 2001 (stress = 0.1).

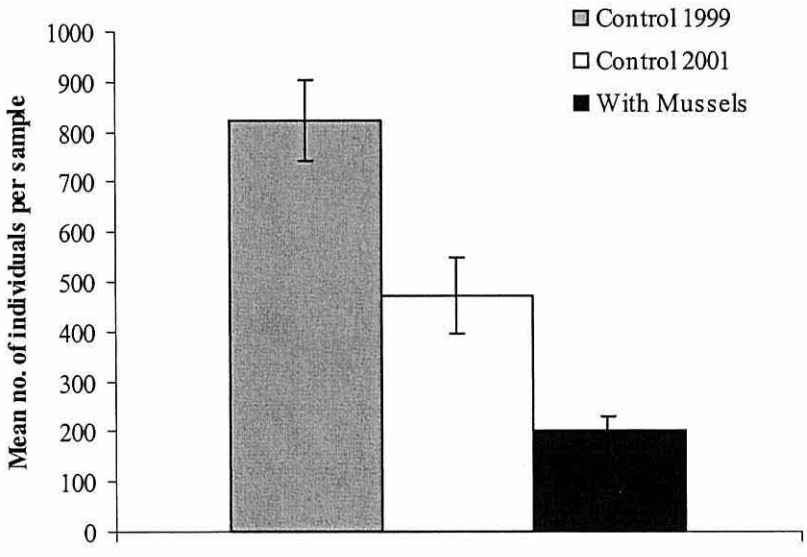

Fig. 6.3. Mean abundance of infaunal animals in 1999 Control (before mussels were laid), 2001 Control (18 months after mussels were laid) and plots with mussels (±SE). Means and SE are shown for clarity rather than median values.

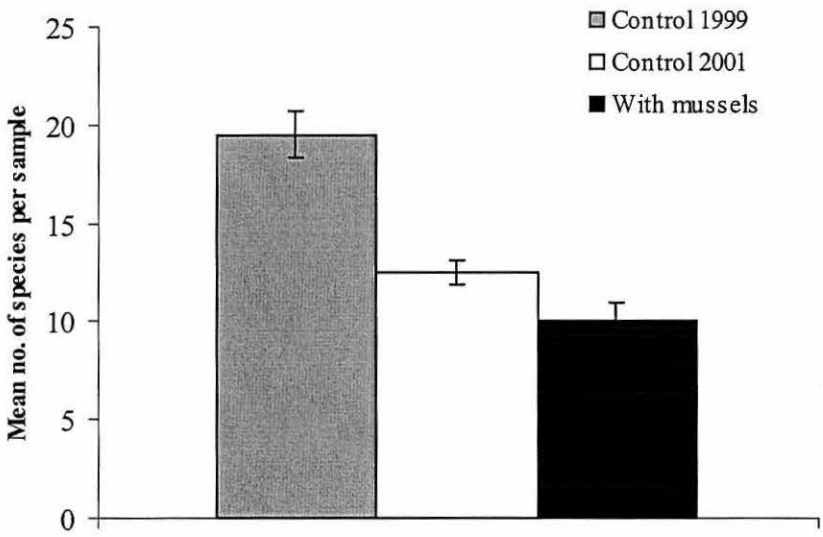

Fig. 6.4. Mean number of species of infaunal animals in 1999 Control (before mussels were laid), 2001 Control (18 months after mussels were laid) and plots with mussels (± SE). Means and SE are shown for clarity rather than median values.

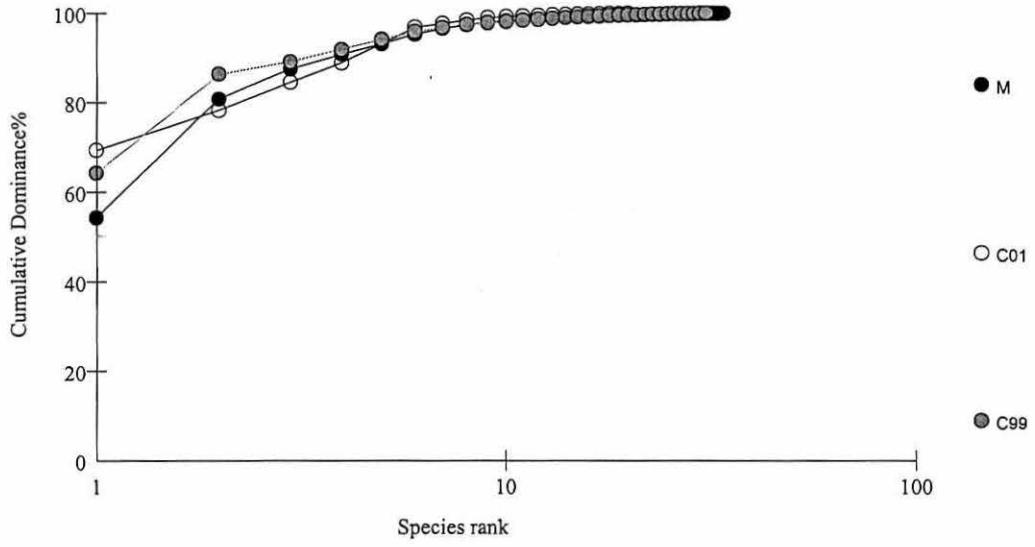

Fig. 6.5. Dominance plot of cumulative species abundance against ranked species for 1999 Control (C99) (before mussels were laid), 2001 Control (C01) (18 months after mussels were laid) and plots with mussels (M).

Table 6.1. Species recorded within the mussels plots, in the 2001 controls, and 1999 controls (Sampling effort respectively n=16, n=4, n=4).

Class: Anthozoa (A), Bivalvia (B), Gastropoda (G), Malacostraca (M), Oligochaeta (O), Ophiuroidea (Op), Polychaeta (P). *Phylum Nemertea (N).

Species	**Class**	**Mussel Plots**	**2001 Control**	**1999 Control** (before mussels laid)
Anemone spp.	A	+		
Amphicteis gunneri	P	+		
Amphipholis squamata	Op	+		
Carcinus maenas	M	+		
Gammarus locusta	M	+		
Glycera spp.	P	+		
Macoma balthica	B	+		
Malacoceros fuliginosus	P	+		
Mytilus edulis	B	+		
Nemertea spp.	N*	+		
Oligochaeta spp.	O	+		
Pholoe assimilis	P	+		
Pinnotheres pisum	M	+		
Scololepis squamata	P	+		
Sthenelais boa	P	+		
Melita palmata	M	+	+	
Pholoe baltica	P	+	+	
Pseudomystides limbata	P	+	+	
Ampharetidae spp.	P		+	
Nephtys (juvenile) spp.	P		+	
Nereimyra punctata	P		+	
Ampharete acutifrons	P	+	+	+
Capitellides spp.	P	+	+	+
Capitomastus spp.	P	+	+	+
Cirratulidae spp.	P	+	+	+
Corophium volutator	M	+	+	+
Eteone picta	P	+	+	+
Nephtys hombergi	P	+	+	+
Nereis diversicolor	P	+	+	+
Notomastus latericeus	P	+	+	+
Phyllodoce maculata	P	+	+	+
Scoloplos armiger	P	+	+	+
Tubificoides benedeni	O	+	+	+
Abra spp.	B	+		+
Modiolula phaseolina	B	+		+
Myriochele oculata	P	+		+
Mysella bidentata	B	+		+
Pygospio elegans	P	+		+
Maldanidae spp.	P		+	+
Cardiidae spp.	B			+
Corophium multisetosum	M			+
Crangon spp.	M			+
Hydrobia spp.	G			+
Malmgrenia arenicolae	P			+
Nephtys kersivalensis	P			+
Nucella spp.	G			+
Pirakia punctifera	P			+
Podarkeopsis helgolandica	P			+
Polydora antennata	P			+
Polydora caulleryi	P			+
Turbellaria spp.	T			+

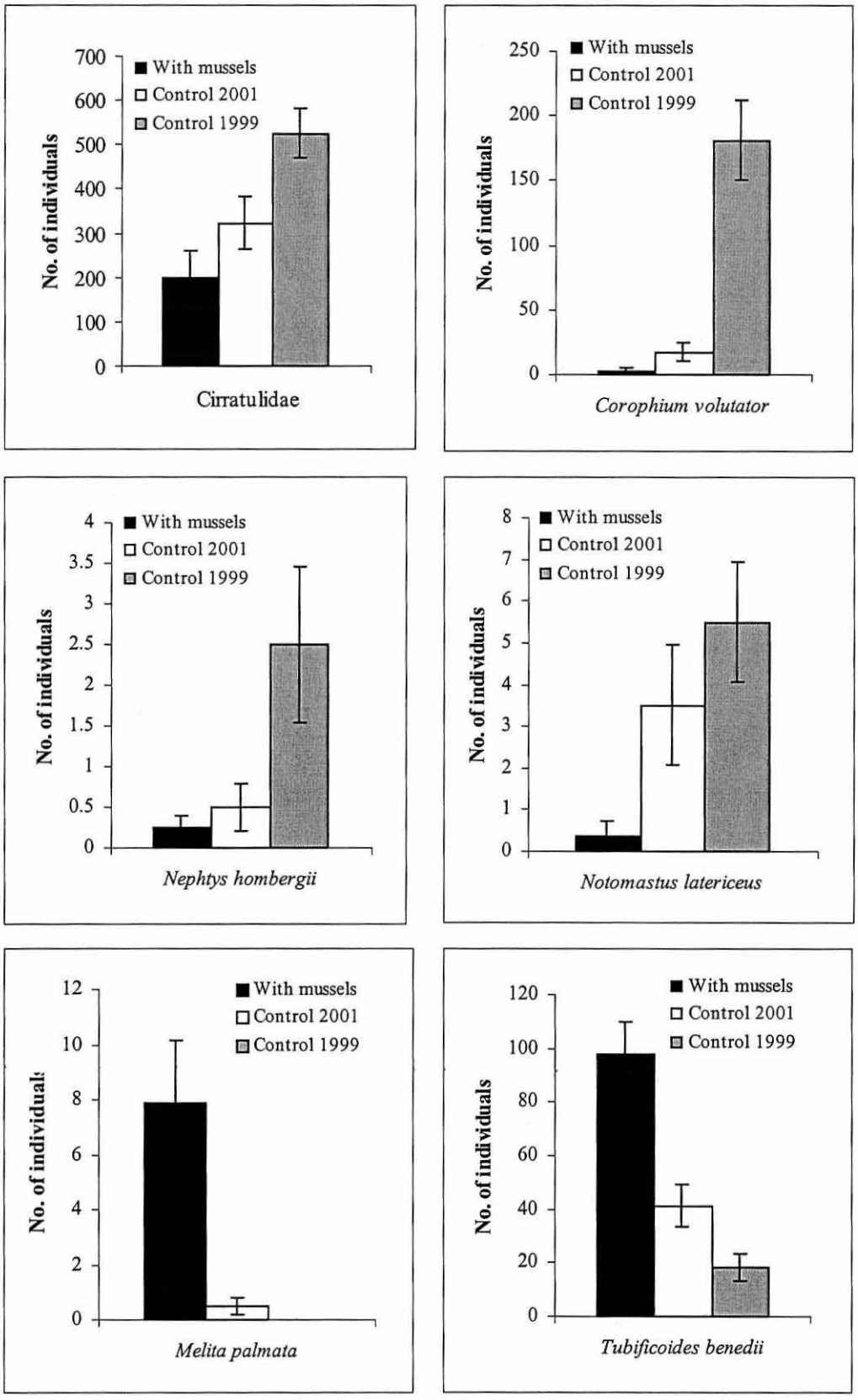

Fig. 6.6. Mean number of individuals (± SE) of species contributing to the major differences between infaunal communities of control (1999 - before mussels laid and 2001 - 18 months after mussels laid) and plots with mussels. Means and SE are shown for clarity rather than median values.

Table 6.2. Mann-Whitney Tests of individual species contributing to the major community difference between control (1999 - before mussels laid and 2001 – 18 months after mussels laid) and plots with mussels. * indicates significant difference $p<0.05$.

Species	Plots with mussels V	W	p
Cirratulidae spp.	1999 Control	143.0	0.0206*
	2001 Control	151.0	0.1190
Corophium volutator	1999 Control	136.0	0.0029*
	2001 Control	141.0	0.0123*
Nephtys hombergi	1999 Control	146.0	0.0422*
	2001 Control	159.0	0.4219
Notomastus latericeus	1999 Control	138.5	0.0061*
	2001 Control	146.5	0.0472*
Melita palmata	1999 Control	None present 1999	-
	2001 Control	191.0	0.0335*
Tubificoides benedeni	1999 Control	200.0	0.0159*
	2001 Control	194.0	0.0029*

b. Infaunal communities of 1999 control and 2001 control.

The infaunal communities of the controls taken in 1999 and 2001 were significantly different (ANOSIM $R=0.917$ $p<0.05$) (Fig. 6.2). This is reflected in both numbers of individuals and number of species which were both significantly lower in the 2001 controls (Mann-Whitney $W=10.0$ $p<0.05$ in both cases).

Of a total of 29 species found in the control plots in 1999, seventeen species were not found in the 2001 control plots and these species contribute to over 40% (SIMPER) of the dissimilarity between the two controls. A further 20% of the dissimilarity can be attributed to those species that occurred in both plots (Fig. 6.6). However, of these species only *Corophium volutator* shows a significant differences in numbers (Mann-Whitney $W=10.0$ $p<0.05$) and *Melita palmata* was only present in the 2001 control. There was no significant difference in the organic content of the two controls (Mann-Whitney $W=24.0$ $p=0.1124$).

2. Infaunal community associated with the mussel bed

a. Original seeding treatment

There was no significant difference in the infaunal communities between the plots of the Latin square when grouped according to the four original seeding densities laid in April 2000 (Fig. 6.2, ANOSIM R=0.133 p=0.061). There were no significant differences in the number of individuals or the number of species at each of the initial seeding densities (Kruskal-Wallis H=1.35 df=3 p=0.718, H=6.77 df=3 p=0.08 respectively). Similarly, there was no significant difference in the organic content of the sediment at the four different mussel treatments (Kruskal-Wallis H=0.11, df=3 p=0.991).

b. Mussel density at time of sampling

A RELATE test indicated that there was a highly significant correlation between the environmental and biological data (ρ=0.513 p=0.003). A BIOENV analysis demonstrated that the best correlation of the relationship between the infaunal community sampled and environmental data was achieved with mussel shell area and mussel volume (BIOENV ρ=0.643, ρ=0.642 respectively). The significance of the RELATE test gives confidence to the correlation calculated in the BIOENV reducing the chance that the BIOENV value was the result of a spurious correlation.

The gradient between the infaunal community and mussel shell area is supported by the relationships between both abundance of individuals and number of species present in the samples plotted against mussel area (Table 6.3). The number of individuals per plot [Ln (n+1)] showed a significant negative linear relationship with mussel area (Fig. 6.7). The number of species also showed a significant negative linear relationship with Ln (mussel area) (Fig. 6.8). Analysis of individual species [Ln (n+1)] showed significant negative relationships with mussel area for three taxa (Table 6.3), Cirratulidae, *Corophium volutator* and *Melita palmata* (Fig. 6.9).

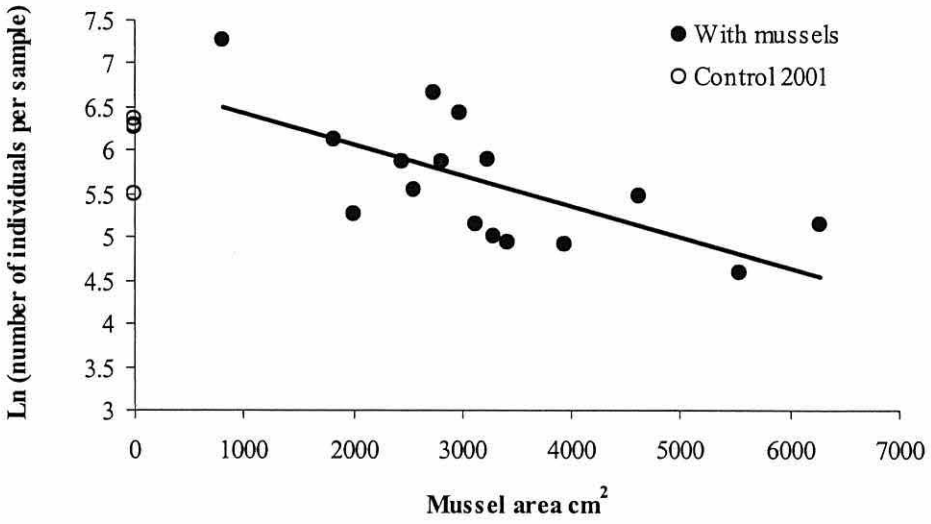

Fig. 6.7. Relationship between area of mussels and number of individuals. Controls are shown for comparison. Regression line $y = 6.77 - 0.000365x$ $r^2 = 0.404$.

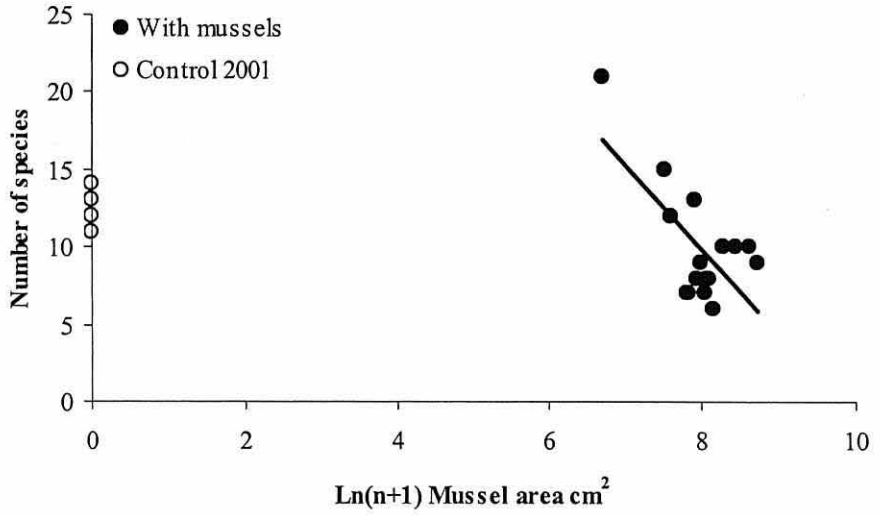

Fig. 6.8. Relationship between area of mussels and number of species in sample. Controls are shown for comparison. Regression line $y = 53.3 - 5.48x$ $r^2 = 0.425$

Table 6.3. Regression Analysis of infaunal community data with area of mussels per sample. Numbers of individuals are Ln(n+1). Number of species is regressed against Ln(mussel area).

Mussel area V	Correlation coefficient r	df	p	Slope (± SE)	Intercept (± SE)	Coefficient of determination r^2
Number of individuals per sample	0.64	13	0.005	-0.000365 ± 0.000106	6.77 ± 0.370	0.404
Number of species per sample	0.65	13	0.004	-5.48 ± 1.56	53.3 ± 12.5	0.425
Cirratulidae spp. per sample	0.74	13	0.001	-0.000858 ± 0.000196	7.22 ± 0.684	0.548
Corophium volutator per sample	0.60	13	0.009	-0.000473 ± 0.000155	1.99 ± 0.541	0.357
Melita palmata per sample	0.67	13	0.002	-0.000547 ± 0.000148	3.59 ± 0.515	0.459

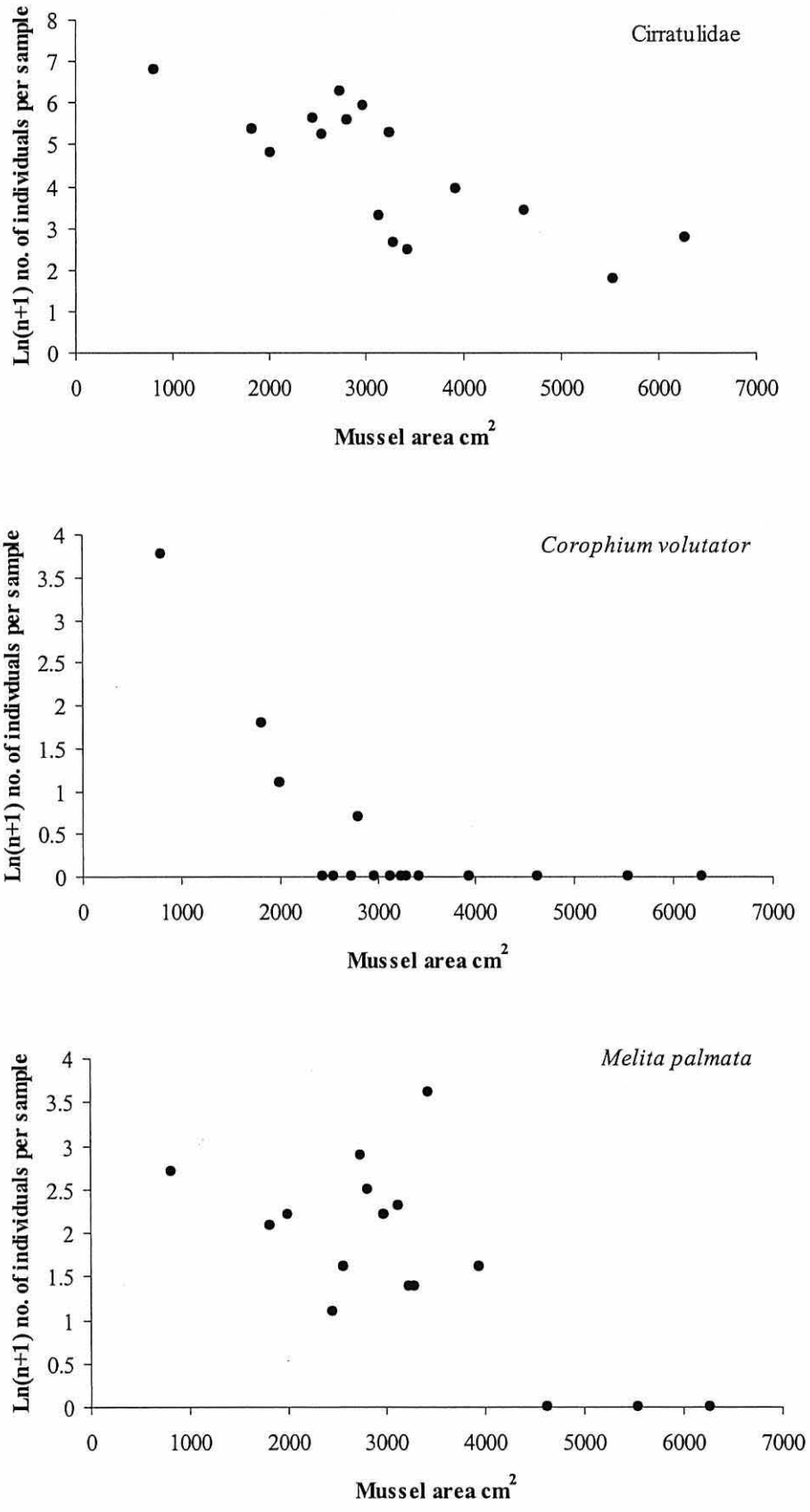

Fig. 6.9. Relationship between area of mussels and number of species in sample.

DISCUSSION

As in other previous studies (e.g. Dittman 1990; Guenther 1996; Commito 1987; Ragnarsson and Raffaelli 1999) it is clear that mussels affect the benthic faunal community of the sediment onto which they are laid in terms of both the numbers of individuals and species present (Fig. 6.3 and 6.4, Table 6.1). In this experiment the presence of mussels had a large impact on the abundance of epibenthic crustaceans, in particular *Carcinus maenas* and *Melita palmata*. Presumably, this can be attributed to the refuge that the mussel matrix provides from water movement, desiccation and predation (see also Dittman 1990; Ragnarsson and Raffaelli 1999). Commito and Boncavage (1989) suggested that the presence of mussels also caused an increase in oligochaete abundance. This concurs with the findings of the present study in which the abundance of *Tubificoides benedeni* is significantly greater in the mussel plots compared with areas with no mussels (Fig. 6.6). Other workers have found that the presence of mussels on soft sediments has been associated with a shift in the community from one dominated by polychaetes to one dominated by oligochaetes (Commito 1987; Commito and Boncavage 1989; Dittman 1990). Although such a trend is not as apparent in the present study, there is a suggestion that samples with higher numbers of mussels are associated with a reduced abundance of cirratulids (Fig. 6.9) while there is no concomitant change in the abundance of oligochaetes. Thus the latter become more dominant in terms of their overall contribution to the composition of the fauna. The high abundance of *T. benedeni* in mussel beds has been attributed to its tolerance of organically rich deoxygenated sediment (Commito and Boncavage 1989). Its reproductive strategy also overcomes the problem of ingestion by mussel filtration due to the production of non-larval benthic offspring from cocoons (Hunter and Arthur 1978).

While some species increased in numbers in the presence of mussels other species showed a decrease. *Pygospio elegans* was less abundant in the mussel bed infaunal community than that of the surrounding sediment and this has also been demonstrated in the Wadden Sea (The Netherlands) and the Ythan Estuary (Scotland) (Guenther 1994; Ragnarsson and Raffaelli 1999). A decline in the number of *Pygospio elegans* has been attributed to unstable sediments (Wilson 1981; Flach 1996), which arise in a mussel bed due to the high deposition rates of faeces and pseudofaeces and the movement of the mussels themselves which may cause tube destruction (Kautsky and Evans 1987). *Corophium* spp., a burrow dwelling invertebrate also shows a decline in numbers in the mussel bed and this again can be attributed to the unstable sediment regime (Jensen and Kirstensen 1990; Flach 1993; 1995). In addition mussel beds

may prove a less suitable habitat for such tube dwelling organisms simply due to lack of space in which to construct their burrows as well as the movements and growth of adjacent mussels that impinge upon burrows. The other species that showed a decline in numbers in the mussel bed (Fig. 6.6) reflected both the physical environments of the mussel bed and the associated infaunal community. The capitellid *Notomastus laceritus* prefers cleaner muddy sand and is a more selective feeder than the other more opportunistic capitellid species and this is reflected by its higher abundance in both of the control treatments compared to the mussel treatment (Fauchald and Jumars 1979). The declining numbers of the carnivorous predator *Nephtys hombergii* may reflect the reduced total abundance of individuals (and hence prey) in the mussel bed compared to that of the surrounding sediments.

The 1999 control plots represent an area in relatively close proximity to the mussel beds (200-500m) compared to the 2001 controls which were immediately adjacent to the mussel bed (distance to mussels = 10 – 15 m). Examination of the results of the experiment with reference to this spatial gradient suggests that the effects of mussels on benthic infaunal communities of soft sediments reduce with increasing distance from the mussel bed. Although temporal changes may account for some of the differences between the 1999 and 2001 control plots the magnitude of difference in species composition suggests that this is not the main factor. It is therefore likely that the clear patterns observed in the data with increasing distance from the bed are indicative of a dilution of the influence of the mussel bed on the benthic community. These gradients are demonstrated in both the individual species data, and the community data where a shift in the species composition of the communities was observed (Table 6.1), together with gradients in the mean abundance and mean species number in each treatment. Dittman (1990) demonstrated a reduced abundance of individuals within a mussel bed compared to the surrounding sediment, which concurs with the present study where decreasing numbers of individuals with increasing proximity to the mussel bed are observed (Fig. 6.3), (although the opposite trend was observed by Commito (1987)). However, numbers of species were not significantly different between the mussel bed and surrounding area in Dittman's study (1990) and this again corroborates with this study regarding the numbers of species found in the mussel bed compared to that of the 2001 control. It is important to remember that although it appears from Table 6.1 that more species occurred overall in the mussel plots, the sampling effort is four times greater than for control plots. The mean number of species in the 1999 control was therefore significantly higher than in the other treatments. The control areas did not differ in terms of their

physical environment with respect to the organic content of the sediment, hence sediment conditions do not appear to be the cause of the observed community differences. It may be that the larvae of certain species of the infaunal community found in the vicinity of the mussel bed are more susceptible to removal through bivalve filtration. Woodin (1976) suggested that suspension-feeding bivalves could have a negative effect on the recruitment of infaunal species due to predation by filter feeding, although this hypothesis was refined by Commito and Boncovage (1989) to preclude organisms which do not have a pelagic development stage (e.g. *Tubificoides benedeni*). A study conducted at a much smaller spatial scale (1 m^2 experimental plots) did not detect a significant effect of bivalve density on larval settlement and juvenile recruitment (Hunt *et al.* 1987). Nonetheless, at the large scale used in this study filtration by the mussel bed is likely to have an effect not only on the benthic infaunal community within the bed (Cowden *et al.* 1984; Morgan 1992) but also the area in close proximity to it (Wahl 2001).

The infaunal community composition in terms of numbers of species, numbers of individuals and actual species present differed between the 1999 control, the 2001 control and the plots with mussels. However, the community structure as revealed by dominance plots indicates that the distribution of the number of individuals among species is similar for all treatments (Fig. 6.5). The community associated with all three treatments was dominated by a single species that accounted for over 50% of the abundance of individuals and less than 10 species accounted for over 95% of the community.

The effects of a mussel bed on its associated benthic community was variable within the bed as demonstrated by significant relationships between the benthic community parameters and the area covered by mussels in individual replicates. These relationships reflected the area of mussels at the time of sampling rather than the history of the mussel bed in terms of the initial stocking treatment. This suggests that the composition of the associated benthic community is closely linked to mussel density as it changes through time. No relationship could be found between the benthic communities and the original seeding treatment, and no lasting effect on the organic content of the sediment due to mussel treatment was detected. At the time of sampling, the lowest area of mussel cover was associated with the highest number of species compared with the 2001 controls and higher mussel densities (Fig. 6.8). These areas of low mussel cover are capable of supporting a greater number of species, as habitats suitable for both the mudflat fauna and mussel bed fauna are provided by the

extra microhabitats provided within isolated clumps of mussels. However, as the area of substratum covered by mussels increased a negative relationship occurred for both the abundance of individuals and the number of species (Figs. 6.7 and 6.8). This suggests that the negative factors of a highly anoxic environment, competition for food and space, and the filtration of pelagic larvae that occurred in areas of high mussel coverage outweighs the more positive benefits of increased habitat complexity and refugia provided within the mussel bed matrix. Similar responses of invertebrate species to increasing bivalve density have been reported elsewhere. For example, Spencer *et al.*. (1996) reported a linear decrease in the number of cirratulids with increasing bivalve density in plots of cultivated Manila clams (*Tapes philippinarum*).

Mussel beds alter the infaunal benthic community of the adjacent and interstitial sediments through provision of a complex habitat, input of organically rich material and larval removal through filter feeding. This study has demonstrated that this results not only in a change in the composition of species of the infaunal community, but also the number of individuals and number of species. At all but the lowest areas of mussel cover, the infaunal communities of plots with mussels were less abundant, in terms of both individuals and numbers of species, than the control areas. Within the mussel bed itself negative trends of species numbers and abundance of individuals with increased mussel shell area were also demonstrated. Furthermore, the data suggested that the effects of mussel beds on the infaunal communities of surrounding sediments were reduced with increasing distance from the mussel bed. However, although the species composition and abundance of individual invertebrate species may be altered by the presence of mussels, the distribution of individuals among species remained relatively unchanged.

Expanding the extent of present seabed mussel cultivation will have an effect on the invertebrate assemblage of the surrounding sediments. However, the results of this study indicate that this is a localised effect that decreases with increasing distance from the mussel bed, and that the community structure remains relatively unchanged. The significance of the change in infaunal community must therefore be judged on the importance of the reduced invertebrate abundance and number of species.

Chapter 7

Potential applications of mussel modelling

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ABSTRACT

Mussels are extensively cultivated worldwide and are of growing economic importance. However, constraints on the exploitation of wild mussel resources have necessitated the need for tools to improve the management of mussel cultivation towards increased production. Ecological models are increasingly being used as a management tool, and therefore the existing approaches to modelling mussels have been reviewed with respect to their possible application to the improvement of shellfish management strategies. Dynamic energy budget (DEB) models are suggested to have the greatest potential in this area, and the mussel DEB models that have been developed to date are discussed in terms of their physiological complexity, accuracy of prediction of individual mussel growth and ability to predict mussel population production. Individual mussel production has been predicted; however, the focus of many of the models has been on the growth and reproduction of a single mussel and therefore population effects generally have not been included. Other models at the population level have included only limited population effects, and this has reduced the capacity of many of the models to accurately predict mussel production at the population level. Interactions at the population level (self-thinning and predation) are discussed and the models that describe the consequences of these processes are examined. In future DEB models will need to include the ability to parameterise population level processes if we are to have greater confidence in their application to shellfish management.

INTRODUCTION

Mussels (Bivalvia:Mytilidae) are distributed globally and are a conspicuous feature of many intertidal habitats on both hard and soft substrata (Seed 1976). Mussels are often the dominant organism in terms of their biomass and form a key component of many marine communities (Herman 1993; Seed 1976). Mussel beds support their own diverse communities as the mussel matrix, composed of layers of mussels with accumulated sediment and debris, provides numerous microhabitats and an organically enriched environment (Ragnarsson and Raffaelli 1999). The diversity of the associated invertebrate communities increases with the size and age of the mussel beds, as the latter is proportionally linked to the structural complexity and thickness of the bed (Tsuchiya and Nishihira 1985,1986).

The dynamics of the mussel bed will be related to spat supply and recruitment. Supply limitation, as is demonstrated in other species with similar life histories (e.g. barnacles; Roughgarden *et al.* 1988), could therefore be significant for mussel bed structure. Predators can also be important structuring agents of mussel beds. Many of the classical studies that demonstrate zonation patterns of intertidal mussels have focussed on the effects of mussel/predator interactions (e.g. with starfish [Seed 1969; Paine 1976] and lobster [Elner and Campbell 1987; Robles 1987] interactions). Where they occur, the abundance and high biomass of mussels means that they provide an abundant food resource for a wide variety of marine invertebrate and avian predators (Seed 1993). The main invertebrate predators of mussels in Northern Europe include gastropods, starfish and decapod crustaceans (Seed 1993), while vertebrate predators include birds such as oystercatchers (*Haematopus* spp.) (Meire and Ervynck 1986; Cayford and Goss-Custard 1990) and eider ducks (*Somateria mollisima*) (Dunthorn 1971, Guillemette *et al.* 1992), fish (Dare 1976) and even seals, walruses and turtles (Seed 1993). Furthermore the mussels themselves can serve as self-structuring agents through self-thinning. This is thinning imposed by a population on itself at high density with an observed negative relationship between individuals per area and average individual mass (Westoby 1984).

As with other reef-forming bivalve molluscs, such as oysters, mussels play an important role in exchange of material between benthic and pelagic systems (Asmus and Asmus 1993). The filter-feeding activities of bivalve beds can process large bodies of water in a short time span. For example the volume equivalent to South San Francisco Bay is filtered at least once a day by the abundance of filter feeders (Cloerne 1982), and in one area of the Potomac River, Marlyand, the volume of water

could be pumped through the population of Asiatic clam (*Corbicula fluminea*) in 3 to 4 days (Cohen *et al.* 1984). Consequently, filter feeding by mussels is a major mechanism for the removal of suspended material such as phytoplankton, detritus and inorganic seston from the water column to the benthos. In addition some species have been shown to actively absorb organic compounds dissolved in coastal waters (Manahan *et al.* 1982). In turn, mussels output faeces and pseudofaeces that enrich the surrounding sediments, where the nutrients are remineralised by microbial activity (Dame 1993). Mussel metabolites (e.g. ammonium and orthophosphate) are also released into the water column and provide an accelerated link of nutrients to primary producers. Thus mussels form an integral part of the ecosystem in which they occur. They provide unique habitats that are generally higher in diversity that surrounding sediments, exert a major influence on overlying primary producers, are important in the biogeochemical cycling of minerals, nutrients and energy within the system and are a major food resource for many other species.

In addition to the significant ecosystem services that they provide, mussels are also the focus of important artisanal and commercial fisheries. The wide distribution of mussels has resulted in their cultivation throughout much of the world including Europe, Asia, and North America using a variety of methods such as longline, raft and on-bottom culture (Hickman 1992). The extensive cultivation of mussels has become an activity of growing economic importance (Smaal 1991), with world-wide mussel landings increasing by 25% between 1994 and 1998. Despite the relatively buoyant nature of mussel fisheries, mussel stocks are only able to sustain limited levels of exploitation. In situations where mussels are relaid for on-growing from wild stock this resource/stock is subject to natural fluctuations in recruitment and hence will be susceptible to over-exploitation. Furthermore, suitable sites for relaying may themselves be a limited resource.

These constraints on the exploitation of wild mussel resources have prompted the necessity for tools to improve the management of mussel cultivation. In order to improve the use of the limited mussel resources available, one management objective may be to improve yield (the ratio of kg/m^2 of marketable mussels to kg/m^2 seed mussels laid). To achieve this aim, it is necessary to understand the complex suite of biological and physical factors that ultimately affect mussel growth and survival. From a commercial perspective, this information needs to be integrated such that it can be used to predict the outcome of various management regimes on the growth performance and yield of cultivated mussels. One way that such predictions might be

achieved is through the development of ecological models that link interactions between the key factors that impinge upon growth and survival.

The definition of a model is a simplified (often mathematical) description of a system, created in order to assist in understanding, calculations and predictions. Models are particularly useful in the identification of areas that require further research but are also useful for practical management of complex systems. Each model is developed from a particular perspective and with a particular set of objectives in mind. These objectives to a large extent will define the limitations of that model. Historically mussels have been extensively researched and this knowledge base has no doubt influenced the extensive range of modelling approaches used to study their ecology (Gosling 1992). With the increasing interest in more applied aspects of mussel ecology, it is useful to review the existing approaches to modelling mussels and to see how these might be applied to improving their management. Models that will be useful in a management context will permit production (growth and reproduction) to be forecast as a function of food supply and other environmental factors. Dynamic Energy Budget (DEB) models are a plausible approach. However, complicated interactions at the population level (mortality - self-thinning and predation) requires that models of individual production (e.g. DEB models) are integrated with models that describe the consequences of these processes on the production of mussels at the population level. To better describe the levels of model complexity, Fig. 7.1 illustrates a hierarchy of modelling. Fig. 7.1 demonstrates how with a need to represent important processes at higher levels in the hierarchy (e.g. population level), the potential complexity of the modelling task increases. As a consequence there is a need to consider the appropriate level of detail required of the physiological DEB model, while meeting the objectives of a useful and ecologically relevant management tool. Thus, with the increasing complexity of the models simpler model components may be required.

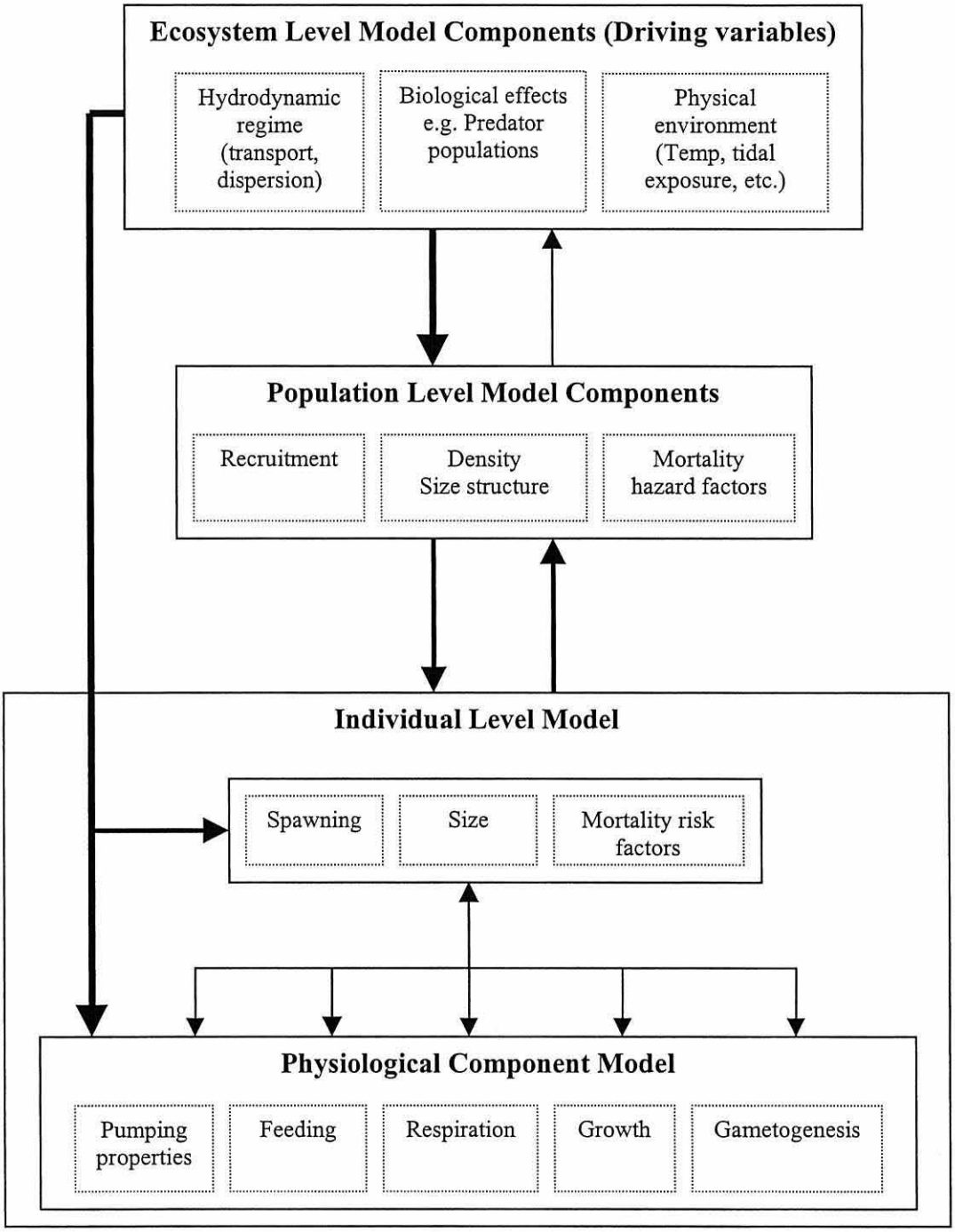

Fig. 7.1. Hierarchy of Mussel Modelling, showing components at each level and interactions between levels. The strength of interactions is indicated by the thickness of the arrows.

Collectively the physiological components determine the size and reproductive capacity of a mussel. The individual mussels in turn interact at the population level influencing both the size structure and recruitment to the population. The mussel population will have a limited effect on the ecosystem through providing a food source for predator populations and altering the local topography. The ecosystem provides the largest influence from population level to component level as the driving force providing food and the environmental conditions in which the mussel population is situated.

For discussion purposes this review has been divided into two main sections that address DEB models, and a broader group that encompasses other models. However, the review is focussed towards dynamic energy budget modelling as this is the area with the greatest potential for synthesising our understanding of processes governing the energetic and population dynamics of mussels.

Dynamic Energy Budget Models

There are a number of DEB models specifically designed to represent mussel growth (Table 7.1). Each of these seeks to represent mussel growth as the balance between components of feeding, respiration and reproductive output. Within each model this is achieved with differing levels of complexity of mussel physiology and by the inclusion of various physical and biological factors (Table 7.2). The differences between each of the models occur as a direct result of the approach taken during the development of the model and are to some extent dependent on the specific aim(s) of the model.

The most sophisticated model, in terms of physiological complexity, is that of Scholten and Smaal (1998). This model was developed to simulate the growth and reproduction of a subtidal mussel incorporating all the available ecophysiological knowledge. Specifics in the model are detailed from filtration through to ingestion, absorption (incorporating the optimal feeding model of Willows 1992), respiration and excretion. Energy flow is represented by carbon and nitrogen fluxes between the five main compartments in the model: blood, body tissue, storage products, the organic component of the shell, reproductive tissues and activity (gametes and spawning). Growth and reproduction are ascertained from the rates and efficiency of the physiological processes that vary with seasonal variation in temperature, food quality and quantity, and metabolic demands. The incorporation of all the available knowledge on the ecophysiology of mussels resulted in a highly complex and over parameterised model, which is difficult to calibrate (Scholten and Smaal 1998). The complexity has also made the model unidentifiable i.e. there are redundant or ambiguous hypotheses within the model (Scholten and Smaal 1998), and this must be addressed before further meaningful development of the model can occur. However, Scholten and Smaal (1998) state that at present there is insufficient knowledge of mussel ecophysiology to rectify the situation. Nonetheless, the model predicted growth well for the site for which it had been calibrated and moderately well for another site with a high seston level. However, it was not successful in predicting growth at an alternative site that had a low seston and food input. This may be as a

result of the adaptation of the mussels to their environment of low total particulate matter (TPM). To overcome this problem would require either a separate calibration of the model with adapted mussels for use in low TPM environments, or further complexity added into the model to account for mussel functions altered by the adaptation to low TPM.

The Scholten and Smaal (1998) model has since been developed to examine the ecophysiological response of mussels to differing inorganic nutrient loads. In this investigation the model was simplified. The number of compartments in the model was reduced from five to four with the removal of the blood compartments. The complexity of the reproductive mechanism was reduced, with no gamete reabsorption mechanism and no link between respiration and spawning, as had been used in the earlier version of the model. The number of input parameters was also reduced from 38 to 30. The resulting model adequately predicted growth in the various inorganic nutrient regimes, although the uncertainty bands (minimum and maximum values of the simulations) remained rather wide. The model also appears to inadequately represent the extent to which mussels can adjust to poor food conditions, even though a specific mechanism had been included within the model to allow for adaptation to these conditions.

The models of Scholten and Smaal (1998, 1999) have been designed to be comprehensive, but the approach of including all available mussel ecophysiological information has resulted in models that are complex. The authors of these papers recognise the problem identified by Beck (1987) of a comprehensive model that makes correct predictions but with little precision, compared to a simple model that makes incorrect predictions with great precision.

Table 7.1. Dynamic Energy Budget Models of Mussels.

Reference	Aim	Conclusions	Limitations
Scholten and Smaal 1998	To produce an ecophysiological model of the mussel (EMMY), for use as a management tool and to identify knowledge gaps.	Complex ecophysiological model developed. No acceptable growth could be predicted for the system under certain conditions. Gaps in knowledge identified.	Model developed is complex and unidentifiable.
Scholten and Smaal 1999	Assess the effects of different nutrient loads on the growth and reproduction of mussels using the model EMMY.	The EMMY model was simplified and good results were obtained to predict mussel growth and reproduction under different nutrient loads.	Uncertainty bands within the predictions of the model are large. The model underestimates the adaptability of mussels to poor food conditions.
Ross and Nisbet 1990	Develop models to represent growth and reproduction of a mussel population	Mainly successful in predicting growth and reproduction in test populations. Suggested differences in populations largely explained by differences in food and seston dynamics.	Simplistic view of feeding used – assumed constant assimilation efficiency and no selection. Assumption that spawning trigger is related to core weight.
Van Haren and Kooijman 1993	Successfully apply DEB model, which had previously been used on a variety of other species, on the blue mussel.	Varying growth rates in the field described by changes in food density, quality and temperature.	Large assumptions of mussel physiology. Complete retention of POM assumed with no loss of organics to pseudofaeces.
Grant and Bacher 1998	To test the use of a simple statistical model over a more mechanistic model to simulate growth of a mussel.	Statistical model has limited applicability to turbid environments. Mechanistic model reasonably predicts mussel growth.	Mechanistic model is still fairly simplistic regarding bioenergetics. Shell growth is not included and absorption efficiency coefficients are not given seasonal variability.
Grant *et al.* 1993	Determine the carrying capacity of a longline commercial mussel farm.	Physical – biological model produced with specifics of a field study.	Less detailed account of mussel energy budget. No specification of selection or pseudofaeces production. No reproduction.
Dowd 1997	Predict the growth of cultured bivalves through a box model approach.	General features of mussel growth able to be predicted at test sites by model.	Highly sensitive to small changes in physiological parameters of mussel energy budget. Less detailed account of mussel energy budget. Spawning effect averaged.
Campbell and Newell 1998	To seed bottom culture lease sites in Maine to their carrying capacity.	Demonstrated importance of food quality and quantity in mussel growth. Optimum carry capacity identified using MUSMOD©	Not all details of mussel physiology included. Spawning not fully included (not calibrated or validated). Non-transferability.

Table 7.2. Selected variables included in Dynamic Energy Budget Mussel Models.

Feature Identified	Model								
	Schol-ten & Smaal 1998	Schol-ten & Smaal 1999	Ross & Nisbet 1990	Van Haren & Kooij-man 1993	Grant & Bacher 1998a	Grant & Bacher 1998b	Grant *et al.* 1993	Dowd 1999	Camp-bell & Newell 1998
Physical Characteristic									
Temperature	✓	✓		✓			✓	✓	✓
Water Depth									✓
Water Flow							✓	✓	✓
Water particles									
TPM	✓	✓	✓	✓		✓	✓	✓	✓
POM	✓				✓				
POC	✓	✓		✓	✓	✓			
PON	✓	✓							
Phytoplank-ton/Chla	✓	✓	✓	✓		✓	✓	✓	✓
Physiological Components									
Selection efficiency	✓	✓		✓		✓		✓	
Ingestion rate	✓	✓	✓	✓	✓	✓	✓	✓	
Absorption efficiency	✓	✓	✓	✓	✓	✓	✓	✓	✓
Pseudofaeces production	✓	✓	✓	✓		✓			✓
Respiration	✓	✓	✓	✓	✓	✓	✓	✓	✓
Basal and active respiration	✓	✓			✓	✓		✓	✓
Energy Partitioning									
Core	✓	✓	✓	✓	✓	✓	✓	✓	✓
Storage	✓	✓	✓						
Shell	✓	✓							✓
Reproduction	✓	✓	✓	✓					
Other									
Predation								✓	✓
Mortality							✓	✓	✓
Mussel density							✓	✓	✓

a = Statistical model
b = Mechnaistic model

TPM = total particulate matter; POM = particulate organic matter; POC = particulate organic carbon; PON = particulate organic nitrogen.

The benefits of simpler models have been investigated by Ross and Nisbet (1990), Van Haren and Kooijman (1993) and Grant and Bacher (1998). Ross and Nisbet (1990) developed two models of an intertidal mussel, one a slightly modified version of a model developed by Kooijman (1986) and the other a new model. The two models differed in the partitioning of energy between growth, reproduction and maintenance. In the modified Kooijman model the energy assimilated by the mussel initially goes through a storage compartment and is then split between reproduction, overheads of growth and reproduction and growth, with maintenance as a direct expense of growth. The new model differs in that maintenance is taken out of the assimilated energy first, with extra energy provided from storage when the assimilated energy is insufficient. The remaining energy, termed production, is then divided between growth, overheads and storage. The reproductive allocation is taken from storage, but only when storage is above a predetermined level. However, the analysis showed that neither modelling approach was better in terms of its predictive capabilities. Both models predicted growth acceptably well at three test sites, even with the simplifications to mussel ecophysiology of constant assimilation efficiency and no selection of food particles. Neither model was able to predict observed total reproduction for the site where they had been calibrated, and did not predict the observed timing and number of spawning in another of the test populations. The spawning trigger was related to body tissue weight, and this was accepted as a weak point in the models. Ross and Nisbet's (1990) main conclusion was that food and seston dynamics are the key factor in growth and reproduction. They identified the interaction between feeding and food/seston concentration as an area of the models that requires further refinement. This is of particular importance since it is also the specific area in the models in which many of their physiological simplifications are apparent.

The significance of the relationship between seston/food concentrations and mussel feeding highlights why physiological simplifications are an important factor when examining the potential of a mussel model to predict growth accurately. Van Haren and Kooijman (1993) devised a model to represent the growth and reproduction of a subtidal mussel by modifying a model that had previously been applied to other species. In their model the relationships between seston/food concentration and feeding are simplified by assuming complete retention of particulate organic matter (POM) and no loss of organic material as pseudofaeces. This assumption has the potential to overestimate the level of organic matter that is assimilated by the mussel and hence over predict growth.

Other models that demonstrate simplifications in physiological functions are those of Grant and Bacher (1998). They developed two models, a statistical and a mechanistic bioenergetic model, to compare just how complex models need to be to accurately predict mussel growth rate. In the statistical model ingestion was related to a single food source component (POM), which was converted to particulate organic carbon (POC). Absorption rate was then calculated using a constant absorption efficiency. The statistical model was unsuccessful at predicting growth at sites with high water turbidity, and was very sensitive to the absorption efficiency. The mechanistic model, while simpler than that of Scholten and Smaal (1998), was more complex than, and performed better than the statistical model. Two food components were used, phytoplankton and detrital POC. Clearance, particle rejection and ingestion were then related to turbidity and the availability of these food types. However, the model was sensitive to mussel absorption efficiency, which had two fixed percentage values based on the two food sources. This model would benefit from variable absorption efficiencies related to the quality and quantity of available food. This model was specifically developed with an emphasis on feeding, and for this reason does not include reproduction. Growth is therefore only predicted for juvenile mussels, which means that the application of the model on mussel growth to marketable size is limited since the mussels will have gonads by this stage.

The models discussed to this point have aimed to accurately represent growth, and in some cases reproduction, of a single mussel. Population level effects need to be included if we are to model the production of a mussel population. This can be achieved by modelling the carrying capacity of a system (but for management purposes requires mussel growth rate in the model to be maintained at a level that compares with cultivated mussels). Carrying capacity modelling has been undertaken for both longline commercial cultivation of mussels (Grant *et al.* 1993; Dowd 1997) and for a bottom culture site (Campbell and Newell 1998). These models are of intermediate physiological complexity (Scholten and Smaal 1999), though they also include transport of food within the system. The investigations of Grant *et al.* (1993) and Dowd (1997) refer to the same study, but have examined it from different perspectives. They used a box model approach to represent the system, with interactions between seston, zooplankton, phytoplankton and mussels. The carrying capacity of the system is defined as the number of bivalves that can be sustained at a specific growth rate. This is determined by predicting the growth rate of a single mussel and then increasing mussel numbers in the system until the specified growth rate is no longer maintained. However, individual mussel growth was found to be

very sensitive to specific physiological parameters, such as seston ingestion rate and assimilation efficiency. This model is therefore constrained by a limited inclusion of mussel physiology. The model does not fully incorporate reproduction, but averages out the effect of weight gain and loss. Dowd (1997) does include density effects of mussel numbers through competition for food, by reducing the concentration of phytoplankton in the water column, an effect that has been demonstrated by Fréchette and Bourget (1985a, b). Others have suggested that direct physical interference between mussels, another example of a population level interaction, can exert a direct effect on individual mussel's growth performance and survival probability (Okamura 1986; Fréchette *et al.* 1992). This has not been incorporated within the model of Dowd (1997) although predator induced mortality is included through an overall mortality factor, which varies with time, calculated on a site-specific basis. The model was able to predict the general features of mussel growth in the test areas. However, the adaptation of mussels to their environment is an area that was identified as needing improvement to refine the model.

Another model that has been developed to consider carrying capacity is that of Campbell and Newell (1998). This model was developed to be as simple as possible regarding both mussel physiology and physical parameters, with the aim of predicting mussel production using food quality and quantity, water flow and depth. The model of Campbell and Newell (1998) was successful in so much as mussel yields were improved by following the seeding density and timing recommendations of the model. Nonetheless, its predictions were not accurate at one of the validation sites and this was attributed to reproduction not having been included in the original model. The model was modified to include spawning but it was neither calibrated nor validated. At present the model, MUSMOD©, cannot accurately predict mussel growth over the entire range of physical conditions where mussels are cultured.

The DEB models discussed previously have been shown to predict mussel growth with moderate success and in many cases have been successful in answering the questions that they have been designed to address. Areas in which further research would be advantageous have also been identified. The importance of the relationship between the seston/food concentration and the rate at which carbon or energy is assimilated has been highlighted in many model developments. Much laboratory research has been conducted into this area (e.g. Hawkins and Bayne 1985; Bayne *et al.* 1987, 1988; Newell and Gallagher 1992; Hawkins *et al.* 1996, 1998). However, to use this physiological information to manage fisheries, or predict mussel growth *in*

vivo, we need to know more about the characteristics of the available food supply. Another area which has been highlighted by both Scholten and Smaal (1998, 1999) and Dowd (1997) is the adaptability of mussels to their ambient environmental conditions, which makes modelling the system more challenging. However, many of the models focus solely upon the growth of a single mussel and so in the cultivation of mussels there are still large areas in which these models do not predict. The mussel models developed to date do not generally include population effects e.g. relationships between growth, predation and other sources of mortality which are known to be significant (Goss-Custard and Willows 1996). The lack of population level components within many modelling approaches has precluded the incorporation of feedback mechanisms between the organisms and the environment (Fig. 7.2). The external conditions are mainly given as conditions that the organism reacts to but does not determine or effect, and this is particularly crucial when field situations and model results are to be compared. Therefore, there is much scope for development of models that better predict mussel production.

Models have been developed that are concerned with population effects, such as predation, particularly regarding birds, and self-thinning. While some of these models are dynamic others are static, but both provide a greater understanding of the interactions that operate within a system. Therefore, if these models could be coupled to, or the processes assimilated within a dynamic model, such a model may allow us to more accurately forecast mussel production. Models that could be used in this capacity are considered in the next section.

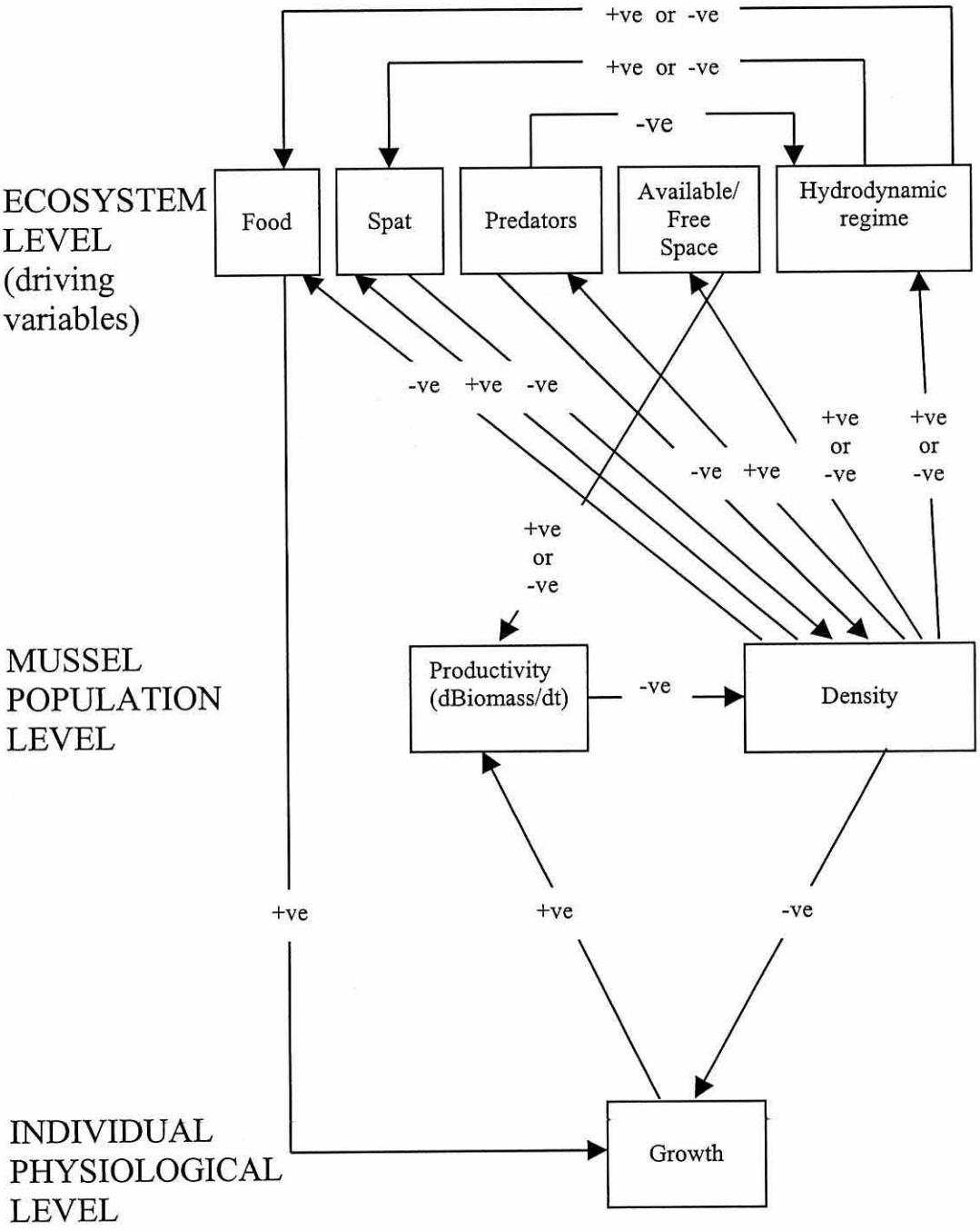

Fig. 7.2. Feedback mechanisms and interactions operating within different levels of mussel modelling. Arrows indicate an increase (+ve) or decrease (-ve).

The ecosystem provides the driving variables in the system. The hydrodynamic regime influences supplies of food (and hence growth) and spat. Spat settlement is a component in the amount of available/free space. Space limitation can be a significant aspect of self-thinning, and hence may influence population productivity. Density is at the centre of many of the feedback mechanisms as the physical presence of the mussels can affect the hydrodynamic regime, reduce or increase the amount of available/free space and influence spat settlement. The size and number of the mussels will affect the numbers and type of predators, and determine the level of food depletion in the water column.

Models relevant to the management of mussel production

There is another suite of models that are of particular relevance in the prediction of mussel population production. Fundamentally, these models all address mussel stock dependent factors and can be separated into three main groups that deal with self-thinning food/particle depletion, and predation.

Self-thinning is potentially a key component in predicting population productivity, especially under conditions of cultivation. Self-thinning describes the negative relationship that is observed between individual mean size and mean population density in a cohort of growing organisms (Westoby 1984). Self-thinning has been most extensively studied by plant ecologists and has been a subject of interest for the past three decades (Yoda *et al.* 1963; White 1980; Westoby 1984; Weller 1987), where the limiting factor has been identified as space.

The concept has been adapted to sedentary animals by Hughes and Griffiths (1988), who describe a geometry of packing leading to observed self-thinning. Food-regulated self-thinning has also been suggested (Begon *et al.* 1986; Elliott 1993) but generally has focussed on mobile animals. However, Fréchette and Lefaivre (1990) have suggested that in benthic suspension feeders both food and space may regulate self-thinning. The cause of self-thinning in mussels is therefore a question that remains unanswered as is it may be regulated by food or space limitation (the latter resulting in physical interference).

Nonetheless, models that predict the effect of self-thinning on a population have been devised. Fréchette *et al.* (1992) developed a hypothesis to explain the change in absolute growth of a mussel resulting from competition for surface space between neighbouring mussels. The change in absolute growth of the mussels is presumed to be brought about through a size dependant effect of pressure on the mussel shell, resulting in reduced valve gape and hence filtration rate. Guinez and Castilla (1999) proposed a three-dimensional self-thinning model for multi-layered intertidal mussels. This model suggests that density dependence could be more frequent than has previously been indicated by two-dimensional models, and is of particular importance to bottom cultivation where layering is more likely to occur. Nonetheless, their model is space-driven and does not consider that competition for food resources may influence self-thinning by reducing growth rate.

Self-thinning as a result of food limitation has not been modelled; though, the flow of water over a mussel bed and the corresponding depletion in phytoplankton caused by the filtration of the water has been addressed. Fréchette *et al.* (1989) developed a two-dimensional model of horizontal advection and vertical diffusion to represent phytoplankton movement within the boundary layer to examine the effect of mussels on phytoplankton distribution. The model has since been modified (Butman *et al.* 1994) to represent near-bed conditions more accurately. The model allows prediction of phytoplankton depletion where the filtration rate of the population of organisms is known and where the flow is steady and uniform. Unfortunately this is not a condition regularly found in the field; many mussel beds are found in turbulent conditions. Turbulent conditions can result in the resuspension of sea-bed material (Navarro and Inglesias 1993) and this can provide additional organic material, in the form of organic rich detritus and benthic micoalgae, and promote growth where phytoplankton is limiting (Fréchette and Grant 1991). The resuspension of sea-bed material can also promote the growth of phytoplankton and this is an effect that may be particularly important to bivalve communities on a larger spatial scale, such as whole estuaries, embayments etc. Nonetheless the model of Butman *et al.* (1994) does provide a line of investigation along which to continue further study.

Apart from mortality that is intrinsic to the mussel population, external sources of mortality must also be addressed i.e. predation. The most important predators of mussel cultivation are starfish, crabs and shore birds (Seed 1969). The impact of these predators can be very seasonal, for example crabs are generally more active in the spring and summer, and in the winter the impact of birds is greater when large flocks temporarily over-winter in coastal areas (Seed and Suchanek 1992).

Predation has been modelled most extensively regarding the effects of birds on mussels. Hilgerloh and Siemoneit (1999) developed a dynamic model of bird predation on mussel beds in the tidal flats of Lower Saxony, Germany. While the quantitative effect was small, it did establish than mussels larger than the mean of the population were more often predated upon. This suggests that where populations suffer significant bird predation the apparent growth of a mussel cohort will be reduced, resulting in a smaller mean mussel size than in a population without predation. Other studies have focused upon single species, for example oystercatchers (*Haematopus ostralegus*). Oystercatcher feeding can be used to calculate the carrying capacity of mussel beds, and formed the basis of a model developed by Goss-Custard *et al.* (1995), using an empirical game theory distribution

model of oystercatchers feeding on mussels. This involves a description of how a population of oystercatchers, in which individual birds vary in their competitive ability and foraging efficiency, become spatially distributed over the spatially variable mussel food supply. Manipulation of the model output can produce estimates of the mussel biomass removed from the beds, giving an indication of the effect of oystercatcher predation on intertidal mussel beds.

There is a paucity of specific models relating to invertebrate predation on mussels, although a considerable amount of research has been conducted into this area. Feeding mechanisms by both crabs (e.g. Ameyaw-Akumfi and Hughes 1987, Elner 1978, Jubb *et al.* 1983, Seed 1969) and starfish (Norberg and Tedengren 1995, O'Neill 1983) are well documented. Size selection is also demonstrated with smaller mussels suffering disproportionately high losses from crabs (Seed 1976) and starfish feeding on mussels equal to or larger than the mean size of the mussel population (Dolmer 1998).

There is a distinct relationship between the size of mussel taken and type of predator, with crabs responsible for mortality of the smaller mussels in the population and birds and starfish predating on the larger mussels. Therefore, a way of including predation mortality within a mussel population model may be to apply a size specific mortality function dependent on the composition of the predator community. The reduction in mussel population density as a result of predation mortality may also have effects on other density dependent functions operating within the mussel bed e.g. self-thinning and thus may require further interactions within the model.

Conclusions

The approach of using DEB models has enabled predictions to be made regarding individual mussel growth and production. This method of modelling is of particular value since it has the capacity to represent changes in the mussel populations resulting from variations in the factors operating on the mussel population. Differing levels of complexity of mussel ecophysiology have been used and problems have been encountered in both complex (due to over-parameterization) and simple models (lack of accuracy). Since many of the models were developed to represent the growth and reproduction of a single mussel, population effects have generally been ignored and this reduces their ability to accurately predict population production. However, some of the models have included varying degrees of population effects and models that specifically address these effects have been identified. To enable DEB models to

be used in shellfishery management with greater confidence will require models that are not over-paramiterised, yet include population level processes. A sensible future approach would be to develop models based on an integration of physiological knowledge of individual processes with a well designed field experiment with the objective of simultaneously estimating predation, density and food limitation effects on growth and mortality. Thus, this may allow more of the necessary factors in mussel production to be simultaneously parameterised and incorporated into a model that includes the most important individual and population level processes.

Chapter 8

General Discussion

MUSSEL GROWTH AND MORTALITY

In the present study, both the density and shore height at which mussels are cultivated affected mussel growth and mortality. This study has provided clear evidence of reduced growth rates, in terms of mussel shell length and flesh weight, with increasing shore height and initial stocking density (Chapter 3). Reduced growth at higher shore elevations is primarily a result of reduced immersion times and time available for feeding (Baird 1966), and the increasingly stressful environment associated with wide variations and extremes of salinity, temperature and desiccation (Bayne *et al.* 1976). At high mussel densities food depletion (Bertness and Grosholz 1985; Frechette and Bourget 1985a; 1985b), and physical interference by conspecifics (Okamura 1986; Fréchette *et al.* 1992) can lead to the observed reductions in mussel growth. Mussel growth also displayed a distinct seasonal pattern with higher growth over the summer months compared to the relatively food depleted winter months. For the experimental sites, statistical models were developed of seasonal mussel growth as a function of initial stocking density and shore height and predicted mussel growth with a high level of precision. The advantage of using such statistical models is that it allows mussel production, using several different management scenarios, to be predicted enabling informed judgements to be made in the commercial cultivation of mussels on the seabed. A better understanding of the relationship between stocking density and shore height should result in a more sustainable approach to mussel cultivation.

Food and space limitation at high population densities ultimately can cause increased mortality and this was demonstrated by the negative regression relationship of Ln(mussel density) over time that indicated more mussels were lost at the highest densities (Chapter 4). As the mean size of the mussel cohort at the experimental site increased the linear relationship between mean mussel weight and density also became increasingly negative. This implied that at the higher densities the mussels were becoming more restricted in their growth and hence displayed density dependence (Chapter 5). The relationship between the mean weight and density of mussels changed more rapidly over the summer than the winter and the differences in the change of the relationship appeared to be related to seasonal growth rates and the effects of predation. While mortality rates changed between the summer and winter on the main experimental site, in the caged experiment where predators were excluded, a seasonal change was not detected in the mortality rate (Chapter 4). Additionally, the mortality rates at the caged mussel site were much lower than on the main site, which suggested that the higher mortality rates on the main site resulted

from high crab predation pressure. However, crab predation accounted for only a relatively small proportion of the total mortality on the main site. Other factors such as density dependent effects, as a result of the high growth rates that occurred over the summer, may have lead to the high mortality rate on the main site, although it is not clear why this did not occur to a similar extent at the caged mussel site. The sides of the cages may have provided an additional surface to which mussels attached and hence were less vulnerable to the effects of layering that occurs with on-bed cultivation at the main experimental site.

Mussel mortality due to predation was strongly seasonal. The effects of crab predation on the main site reflected the findings of other studies (Hunter and Naylor 1993; Aagaard et al. 1995) with low levels of predation in the winter that increased over the spring and peaked in summer (Chapter 3). In comparison, oystercatcher numbers were greatest over the winter months (R Caldow pers. comm.). Mussel mortality due to predation differed according to shell characteristics (Chapter 2). Shell compressive strength rather than overall thickness influenced crab dietary preference. Higher shell compressive strength limits the number of crab predators that have sufficient strength to crush a mussel (Boulding 1984; Elner 1978) and increases handling time thereby reducing the net rate of energy intake and likelihood of consumption (Robles et al. 1990; Boulding 1984). In comparison shell thickness rather than compressive strength was the most important shell characteristic that affected predatory choices made by oystercatchers, which concurs with other studies (Durrell and Goss-Custard 1984; Sutherland and Ens 1987 and Cayford and Goss-Custard 1990). As in the case of crabs, increased shell thickness and associated handling time increases the chance that a particular mussel will be abandoned without being opened and will decrease the number of mussels a bird is able to consume over a given time (Meire and Ervynck 1986).

The research herein indicates that there is considerable potential for the improved management of cultivated mussels with respect to the factors that control mussel growth and mortality. There is the potential to both improve the mussel yield and provide a more sustainable approach to mussel cultivation by reducing the amount of seed mussels that are required to yield similar returns at harvest as presently achieved.

PROPOSED MANAGEMENT STRATEGY

Based on the present study, wild harvested seed mussels should be re-laid on the cultivation plots in the Menai Strait at a density of between 3 and 5 kgm^{-2}. Above this initial seeding density the mussels will incur both increased mortality rates (Chapter 4) and reduced growth rates (Chapter 3). Below this seeding density the cultivation area will not be utilised to its fullest capacity. If there is limited space on the cultivation plots due to the presence of older mussel year classes the smaller seed mussels should preferentially be laid on the intertidal areas rather than the subtidal areas. This will reduce the predation pressure from the main predators of the seed mussels (*Carcinus maenas*, and potentially starfish), while also allowing the mussels to develop thicker shells of higher compressive strength that will provide future protection from avian and crab predators (Chapter 2). Oystercatchers show relatively little interest in these smaller mussels even though they are exposed on the intertidal areas for longer periods of time. When the mussels are larger they can then be transferred further down shore and subtidally for faster growth and to reduce predation from oystercatchers, by this point the increased mussel size and predator resistant attributes of the mussel shell will also reduce losses from crab predation.

When the main cultivation areas are covered with on-growing mussels, excess seed should be 'banked' on higher areas of the shore, which are not normally used for cultivation. In years when fewer seed mussels are available these mussels can then be transferred further down the shore and subtidally where they could on-grow at a faster rate to marketable size. Thus the unpredictable supply of seed mussels for on-growing could be evened out from one year to the next. Additionally these mussels will grow a thicker shell of higher compressive strength that could confer increased predator resistance.

Once these areas have been laid with seed there will be no benefit in collecting more seed mussels since laying the mussels at any higher densities would result in increased mortality (Chapter 4). The provision of guidelines to indicate optimal seeding densities could therefore reduce the total amount of the natural mussel seed that is collected providing a more sustainable approach to mussel cultivation.

This study has provided not only a general management strategy for mussel cultivation, but has also developed statistical models of seasonal mussel growth and mortality. These models predict mussel growth in terms of shell length (Chapter 3) according to initial seeding density, shore height and season. The seasonal dry

weight model also enable flesh weight to be calculated which gives the mussel industry the possibility of anticipating exactly the quality of the mussel meat per unit shell length. Through the combination of these models together with the statistical mortality model (Chapter 3), the potential yield from various management scenarios could be calculated to determine the best possible cultivation strategy.

ENVIRONMENTAL IMPACTS OF MUSSEL CULTIVATION

Mussels affect the benthic faunal community of the adjacent and interstitial sediments onto which they are laid through provision of a complex habitat, input of organically rich material and the removal of benthic larvae through filter feeding (e.g. Dittman 1990, Guenther 1996, Committo 1987, Ragnarsson & Raffaelli 1999). This study has demonstrated that this results not only in a change in the composition of species of the infaunal community, but also the number of individuals and number of species. At all but the lowest areas of mussel cover, the infaunal communities of plots with mussels were less abundant, in terms of both individuals and numbers of species, than the control areas. Within the mussel bed itself negative trends of species numbers and abundance of individuals with increased mussel shell area were also demonstrated. However, although the species composition and abundance of individual invertebrate species may be altered by the presence of mussels, the distribution of individuals among species remained relatively unchanged.

Mussel cultivation clearly has an effect on the invertebrate assemblage of the both the surrounding and underlying sediments of the mussel bed. However, the results of this study indicate that this is a localised effect that decreases with increasing distance from the mussel bed, and that the community structure remains relatively unchanged. Therefore if the current area of mussel cultivation is to be expanded the significance of the change in infaunal community must be judged on the importance of the reduced invertebrate abundance and number of species.

The consequences of the change in the infaunal community, as a result of mussel cultivation, for birds that feed on the intertidal areas has been investigated in a complimentary project undertaken by the Centre for Ecology and Hydrology, Dorset. In this experimental study oystercatchers and redshank responded positively to the presence of mussels (Caldow *et al.* in prep). In model simulations of the geographic area it was also suggested that the loss of the cultivated mussel beds could have a detrimental effect on the over-wintering oystercatcher population, as the birds would be forced to feed elsewhere on less profitable food sources. Moreover, the change in

the invertebrate community caused by the introduction of a mussel bed had no detrimental effect on the bird community. No species were lost from the area, and not one of the five most common species that feed on the mudflats in the area declined in abundance (Caldow *et al.* in prep).

FUTURE RESEARCH

In order to improve the use of the limited mussel resources available the complex suite of biological and physical factors that ultimately affects mussel growth and survival need to be integrated such that the outcome of various management regimes can be predicted (Chapter 7). The research conducted in this study has provided the basis for further work to be carried out in order to develop a dynamic ecological model that would link the interactions between the key factors that impinge upon mussel growth and survival. Such a model would predict production (growth and reproduction) as a function of food supply and other environmental factors. In particular interactions at the population level (mortality - self-thinning and predation) should be integrated with models of individual production (e.g. Dynamic energy budget models). The mussel growth data together with the food availability (chlorophyll a and particulate organic carbon) data that was collected throughout this study could provide a good foundation to develop a dynamic energy budget model. In addition the total mortality and the quantified crab and oystercatcher predation pressure would allow interactions at the population level to be included.

While such a model would have the capacity to improve mussel production the lack of feedback at the ecosystem level would limit the use of the model. There is increasing concern regarding the effect of mussel cultivation at the ecosystem level and in particular on the carrying capacity of coastal waters to support bivalve mariculture (e.g. Smaal *et al.* 1998; Dame and Prins 1998). In order to develop the model to address this wider issue further fieldwork would be required to determine how the interactions of vertical mixing, plankton biomass, SPM properties and the filtration by mussels themselves could affect their food supply and growth. Additionally such a model would be of use in assessing the impact of mussel cultivation on local particle concentrations and hence the potential impact on other filter-feeding populations within the system.

Management Recommendations

- Seed mussel should initially be stocked at a density of between 3 and 5 kgm^{-2}.
- Excess seed should be 'banked' for use in subsequent years of low seed fall.
- To reduce losses from predation the:
  - smallest mussel should be laid intertidally (reducing crab and starfish predation).
  - largest mussels should be laid subtidally (avoiding oystercatcher predation).
- To achieve maximum growth rates mussels should be stocked at the lowest densities and the lowest shore levels.
- To achieve the maximum flesh weight for a mussel of given shell length harvest should take place in September.
- Recognising density-dependent effects mussel stocking density should be reduced with increasing mussel size, and in cultivation areas and seasons that have increased mussel growth rates.

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