Changes in species richness with stocking density of marine bivalves

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Summary

1. Monocultures of mussels might alter the infaunal benthic community of adjacent and interstitial sediments through provision of a complex habitat, input of organically rich material and larval removal through filter feeding. At a site of commercial seabed mussel cultivation, we aimed to determine the effect of mussels on the infaunal community of an intertidal mudflat at different spatial scales and under different stocking strategies.

2. Mussels were laid at four different densities (2, 3, 5 and 7·5 kg m^{-2}) on 400-m^2 plots in a 4×4 Latin square. Benthic samples were collected within and 10–100 m distant from the cultivation area *c*. 7 months prior to and 18 months after seeding the plots with blue mussels. Benthic community characteristics were related to initial seeding density and to the actual surface area of mussels associated with each set of samples collected within replicate plots.

3. The presence of mussels significantly changed the occurrence of some species of the infaunal community within the cultivated area. The infaunal communities supported fewer individuals and species than control treatments at all but the lowest mussel cover.

4. Species richness and the abundance of individuals per unit area also declined with increased area of mussel cover. The abundance of cirratulids and amphipods declined strongly with increasing mussel surface area.

5. Although the species composition and abundance of individual invertebrate species were altered by the presence of mussels, the distribution of individuals among species remained relatively unchanged.

6. *Synthesis and applications*. Overall, mussel beds changed the infaunal community, but the effects were localized (0–10 m) and not detectable at larger scales (10–100 m). Changes in benthic community composition could be reduced (but not eliminated) by lowering the stocking density of mussels to either 2 or 3 kg m^{-2}. Given the small edge effects associated with cultivated mussel beds, the use of larger mussel beds would be preferable to many smaller mussel beds.

Key-words: community change, ecological impact, large-scale experiment, mussel cultivation, *Mytilus edulis*

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Introduction

Intensive monoculture of marine biota occurs globally and its contribution to marine-derived sources of protein has increased steadily over the last three decades (FAO 2003). However, marine aquaculture is associated with negative ecological and socio-economic impacts (Kaiser *et al*. 1998; Naylor *et al*. 2000). Given the social and economic importance of the coastal zone (Costanza *et al*. 1997), there is a pressing need to quantify the ecological consequences of different management approaches to mariculture. To date, the impact of intensive cultivation systems on biodiversity has focused primarily on terrestrial systems, often using appropriately designed

experimental manipulations. Such agriculture systems are associated with reductions in species richness and, in some cases, fewer associated plant, arthropod and vertebrate assemblages (Chamberlain *et al*. 2000; Symstad, Siemann & Haarstad 2000; Marshall *et al*. 2003). The ecological effects associated with the cultivation of fish or bivalves suspended from rafts have tended to be studied at the scale of the cultivation unit or multiples thereof, and have focused on issues relating primarily to the carrying capacity of specific marine systems. In contrast, the seabed cultivation of bivalve molluscs is more analogous to the monoculture of terrestrial crops in that the cultivated species replaces, to varying extents, the original biota and habitat. However, unlike terrestrial systems, monocultures of bivalves, such as mussels, oysters and clams, are rarely supplemented with artificial fertilizers or chemicals for pest control. Nevertheless, monocultures of bivalves often occur within or close to areas of nature conservation importance and have the potential to change the composition of local invertebrate assemblages and their dependent predators.

Mussels (Bivalvia: Mytilidae) are distributed globally and are a conspicuous feature of intertidal habitats on both hard and soft substrata (Seed 1976). They form a key component of many marine communities and are often 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, that supports a highly diverse associated community (Tsuchiya & Nishihira 1985, 1986; Ragnarsson & Raffaelli 1999) that differs from that of the surrounding sediments (Commito 1987; Dittman 1990; Guenther 1996; Ragnarsson & 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 & Suchanek 1992). Biologically, the mussels provide an input of sediment and organic matter in the form of faeces and pseudofaeces (Tsuchiya 1980; Kautsky & Evans 1987) and remove fine particulate matter and some larvae of benthic invertebrates through filter-feeding activities (Cowden, Young & Chia 1984; 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 cultivation. Mussels are cultivated throughout much of the world, including Europe, Asia and North America, with total mussel landings of more than 1·3 million tonnes in 2001 using a variety of methods such as long-line, raft and on-bottom culture (Kaiser *et al*. 1998; FAO 2003). 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 with good conditions for mussel growth. The mussel cultivator will lay mussels at the density and tidal height that will realize the greatest financial return when they are harvested. At high mus-

sel densities multilayering is likely to occur, which will increase mussel bed complexity. However, the accumulation of large amounts of sediment from biodeposition can produce a chemically reducing environment that will affect the density or diversity of the associated animals (Tsuchiya & Nishihira 1985). At low mussel densities, patches of mussels interspersed with bare substratum may be produced as the mussels clump together, and patch size affects the species richness and number of individuals of associated species (Tsuchiya & Nishihira 1985).

In past studies, the effects of mussel density on invertebrate assemblages and other environmental parameters have been related to the mussel density encountered at the time of sampling (Commito 1987; Dittman 1990). 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-dependent effects). As a result, the infaunal assemblages encountered at the time of sampling may reflect not only the mussel density at that time but also the initial mussel stocking density. The latter may have a long-term influence through the biodeposition that has occurred prior to invertebrate sampling.

The need to determine the effects of various activities within the coastal zone has arisen due to growing environmental awareness and legislation. It is of particular importance to the mussel industry because the areas 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). Areas designated as Special Areas of Conservation (SAC) must undergo an appropriate assessment. Therefore, with the growth of the UK mussel industry it is important to establish the impact of expanding the areas of subtidal and intertidal mudflat on which mussels are laid.

The present study was carried out at a site of commercial mussel cultivation in the Menai Strait, north Wales, UK, which is a proposed SAC. The study formed part of an extensive mussel growth experiment that aimed to determine: (i) any differences in the infaunal community structure between areas of bare mud and areas on which mussels were grown; (ii) any impact of the experimental mussel bed on the infaunal community structure of areas of bare mud both within and surrounding the mussel bed, to determine the spatial extent of the potential impact; (iii) the relationship between species richness and mussel stocking density; (iv) whether the infaunal community encountered on the mussel bed at the time of sampling is related to the original density at which mussels were laid or more closely to the mussel presence at the time of final sampling.

Methods

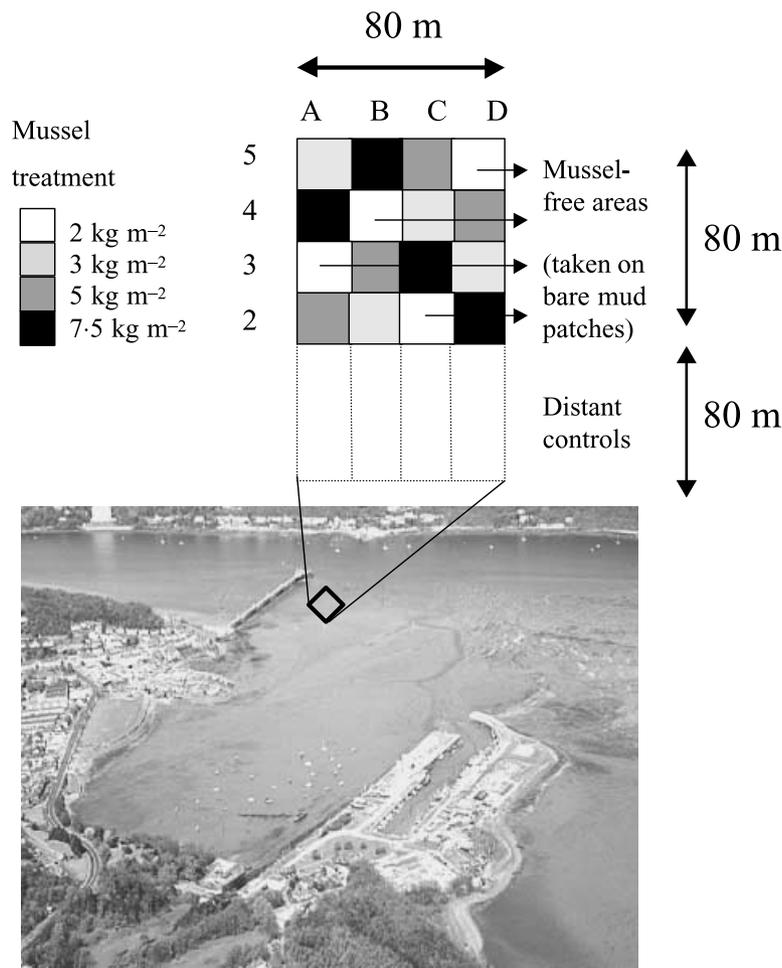The study was located on an intertidal mudflat adjacent to Bangor Pier on the Menai Strait, north Wales

Fig. 1. Experimental design and location adjacent to Bangor Pier in the Menai Strait, north Wales.

(53°14′N, 04°07′W), 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 *Mytilus edulis* (L.) growth experiment established in October 1999 consisting of a 4 × 4 Latin square of 16 individual plots (20 × 20 m). Initially, in October 1999, the infaunal community was sampled by taking five cylindrical cores (15 cm diameter × 15 cm deep) at random from four of the plots within (A3, B4, C2, D5), and from the four plots outside, the Latin square (Fig. 1). The samples taken within the Latin square were termed the 1999 'mussel-free area', and the samples taken outside were termed the 1999 'distant' controls. The distant controls were used to control for the wider-scale ecological variation that might occur outwith the experimental area, from 20 to 80 m distant from the experimental site. A sediment sample was taken in each plot using a

cylindrical core (5 cm diameter × 5 cm deep) and stored frozen until analysed.

In April 2000 each of the plots in the Latin square was seeded with mussels at one of four different stocking treatments (7·5, 5, 3 and 2 kg m^{-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. It was unfeasible to lay mussels by walking the plots as this would have caused more disturbance than the mussel cultivation due to the soft nature of the sediment. 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 walking around the experimental site at low tide 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 from those areas within the experimental area that were covered with mussels. In the lower density plots, the mussels had clumped together in large patches, thereby leaving areas within each plot that were not covered with mussels. As a result it was

possible to take an extra set of samples from patches of mussel-free mud from within the lowest mussel treatment plots. From direct observation the mussel clumps were found to form within 2–3 weeks after the mussels were initially seeded, providing areas of bare mud of relatively the same size within the low density treatment plots. The samples taken in these areas of bare mud were termed the 2001 mussel-free areas, and controlled for the presence of the mussels within the immediate area of the experimental plots. Five cores were taken randomly within the four distant control plots, termed the 2001 distant controls, and were used as a temporal control. Additionally they provided a control for the effect of the presence of mussels at a greater spatial scale. A sediment sample was taken in each plot within the experimental area, after first removing any mussels covering the substratum.

The infaunal samples were washed over a 0·5-mm mesh and the residue preserved in 4% formalin. Animals were identified to the lowest possible taxonomic level. The total number of individuals and the total number of species for each sample were counted excluding mussels.

Mussels in each sample were counted separately and their length was measured, using Vernier callipers, as the distance between the umbone and the edge of the posterior margin of the shell. 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 h and then incinerating a known weight of dry sediment at 550 °C for 6 h. The percentage organic content was determined from the loss of weight on ignition (Holme & McIntyre 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 three ways, as described below.

Data were grouped initially according to the presence or absence of mussels, creating three groups: (i) with mussels; (ii) mussel-free areas (2001); (iii) distant controls (2001). The PRIMER ecological statistical software package (Clarke & Warwick 1994) was used for multivariate analyses. Cluster analyses on the community data were performed using the Bray–Curtis index of similarity on fourth root-transformed data, followed by multidimensional scaling (MDS). The overall percentage contribution of each species to the average dissimilarity between two groups was ascertained using SIMPER. 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 pairwise 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 pairwise tests. Non-parametric tests were used, as the data were not normally distributed (Anderson–Darling test). Data presented in either tables or figures show means rather than medians to aid visual interpretation.

The 1999 mussel-free area and 1999 distant control plots were compared to determine if there was spatial homogeneity across the site prior to the seeding of mussels. Comparisons were made of the 1999 and 2001 distant control plots and 1999 and 2001 mussel-free area plots to ascertain the temporal variation between 1999 and 2001. The 2001 mussel-free area and distant controls were compared to test if the potential impact of the experimental mussel bed on the infaunal community operated at different spatial scales. The data were subjected to the multivariate community analyses outlined above. The abundance of individual taxa and sediment characteristics were treated as above.

In order to analyse specifically the effects of mussel density upon the associated infaunal community within the mussel bed, the control data were excluded from the analysis. The data were grouped according to the four original seeding treatments. Cluster analyses again involved the use of the Bray–Curtis index of similarity on fourth root-transformed data followed by MDS. Significant differences between treatments were determined using an a priori ANOSIM test. Kruskal–Wallis tests were used to test for significant differences in the median number of individuals, the median number of species between treatments, and differences in the median organic content of the sediment samples at each treatment.

The mussel density at the time of sampling was not grouped *post hoc*. The data were analysed according to the 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 (number, area, volume, dry weight) and sediment organic content, and the benthic community were investigated using BIOENV and the RELATE test (Clarke & Warwick 1994). BIOENV compares the similarity matrix generated using community data with a similarity matrix generated using environmental parameters for the same sites or replicate treatments. The mussel parameters were considered to be 'environmental' parameters as mussels were not included in the community data set. BIOENV is used to match biotic to environmental patterns in data. The procedure considers increasing levels of complexity, i.e. single variables then combinations of two variables, etc. The variable or combination of variables that best explains the patterns observed in the biological data set is identified. The significance of the correlation between the biological and environmental data was tested using the RELATE permutation test. This tests the hypothesis
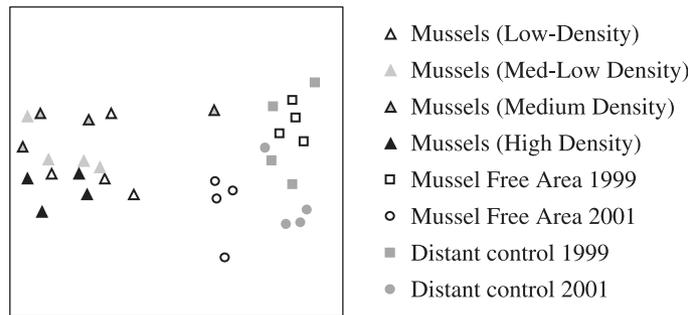
Fig. 2. Two-dimensional MDS ordination of community data found in the controls, mussel-free areas and plots with mussels 2001 (stress = 0·1).
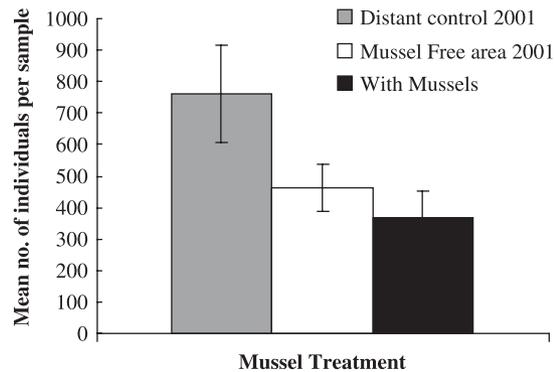

Fig. 3. Mean abundance of infaunal animals in the 2001 distant controls, mussel-free areas and plots with mussels (± SE). Means and SE are shown for clarity rather than median values.
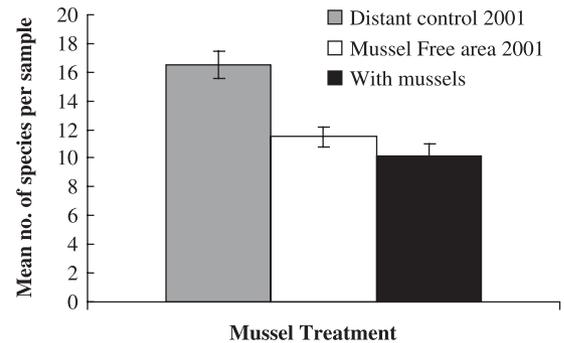

Fig. 4. Mean number of species of infaunal animals in the 2001 distant controls, mussel-free areas and plots with mussels (± SE). Means and SE are shown for clarity rather than median values.

that there is no relationship between the biological information and a specific abiotic/environmental pattern, i.e. that ρ_w is zero. This is examined by a randomization test in which ρ_w is recomputed for all permutations of the samples in one of the two underlying similarity matrices. If the observed value of ρ_w exceeds that found in 95% of the simulations, then the null hypothesis can be rejected at the 5% level. Regression analysis was used to determine whether significant relationships occurred between mussel area and total number of species, total abundance of individuals (all taxa pooled) and the abundance of individual species. The data was tested for normality using the Anderson–Darling test.

Results

There was a significant difference between the infaunal communities of both of the treatments without mussels (the mussel-free area 2001 and distant control 2001) and the areas of mudflat on which mussels were present. (ANOSIM; $R = 0.830$, $P < 0.001$; $R = 0.934$, $P < 0.001$, respectively; Fig. 2). These differences were partly explained for the distant controls by a greater number of animals per replicate and a higher number of species per replicate compared with the plots with mussels (Mann–Whitney; $W = 144.0$, d.f. = 14, $P < 0.05$; $W = 141.0$, d.f. = 14, $P < 0.05$, respectively; Fig. 3). The median abundance and number of species in the plots

with mussels were not significantly different from the 2001 mussel-free area (Mann–Whitney; $W = 153.0$, d.f. = 14, $P = 0.171$; $W = 152.0$, d.f. = 14, $P = 0.157$, respectively) (Fig. 4). However, the identity of some of the species recorded was different between the two treatments (Table 1). There was no clear difference in community structure between the treatments in terms of dominance by rank species abundance.

An analysis of the individual species that contributed to the major difference between the 2001 treatments with no mussels (mussel-free area and distant control) and plots with mussels illustrated the differences in the infaunal communities. For example, *Pseudopolydora antennata* and *Pygospio elegans* (only one individual was present in the lowest density mussel sample) were only present in the control plots. Conversely, *Carcinus maenas* and *Scolelepis squamata* were only found within the plots with mussels (mean ± SE, 8·56 ± 1·22 and 0·94 ± 0·87, respectively). Other taxa showed either increased (Cirratulidae, *Corophium* spp., *Nephtys hombergii*, *Notomastus latericeus*) or decreased (*Melita palmata*, *Tubificoides benedeni*) numbers of individuals in both 2001 control plots compared with the plots with mussels (Fig. 5 and Table 2).

Organic content of the sediment was significantly higher in the plots with mussels than in either of the 2001 treatments with no mussels (Mann–Whitney; $W = 200$ d.f. = 14 $P < 0.05$ in both cases).

Table 1. Taxa recorded within the mussels plots, in the 2001 mussel-free area, and 2001 distant controls (sampling effort, respectively, $n = 16$, $n = 4$, $n = 4$)

| Taxa	Class	Mussel plots	2001 mussel-free area	2001 distant control
Abra spp. Lamarck, 1818	Pe	+		
Anemone spp.	A	+		
Amphicteis gunneri (M Sars, 1835)	P	+		
Amphipholis squamata (Chiaje, 1829)	Op	+		
Carcinus maenas (Linnaeus, 1758)	M	+		
Gammarus locusta (Linnaeus, 1758)	M	+		
Macoma balthica (Linnaeus, 1758)	Pe	+		
Malacoceros fuliginosus (Claparède, 1868)	P	+		
Modiolula phaseolina (Philippi, 1844)	Pe	+		
Mysella bidentata (Montagu, 1803)	Pe	+		
Mytilus edulis (Linnaeus, 1758)	Pe	+		
Nemertea	N*	+		
Oligochaeta	O	+		
Pholoe assimilis Oersted, 1845	P	+		
Pinnotheres pisum (Linnaeus, 1767)	M	+		
Scolelepis squamata (Abildgaard, 1806)	P	+		
Sthenelais boa (Johnston, 1839)	P	+		
Pseudomystides limbata (Saint-Joseph, 1888)	P	+	+	
Melita palmata (Montagu, 1804)	M	+	+	+
Ampharete acutifrons Grube, 1860	P	+	+	+
Capitellides spp. Mesnil, 1897	P	+	+	+
Capitomastus spp. Eisig, 1887	P	+	+	+
Cirratulidae spp.	P	+	+	+
Corophium spp. Latreille, 1806	M	+	+	+
Mysta picta (Quatrefages, 1866)	P	+	+	+
Nephtys hombergii Savigny, 1818	P	+	+	+
Hediste diversicolor (O F Müller, 1776)	P	+	+	+
Notomastus latericeus M Sars, 1851	P	+	+	+
Anaitides maculata (Linnaeus, 1767)	P	+	+	+
Pholoe inornata Johnston, 1839	P	+	+	+
Scoloplos armiger (O F Müller, 1776)	P	+	+	+
Tubificoides benedenii (Udekem, 1855)	O	+	+	+
Glycera spp. Savigny, 1818	P	+		+
Galathowenia oculata Zaks, 1922	P	+		+
Pygospio elegans Claparède, 1863	P	+		+
Maldanidae	P		+	
Nephtys (juvenile) spp. Cuvier, 1817	P		+	
Nereimyra punctata (O F Müller, 1788)	P		+	+
Ampharetidae	P		+	+
Gastrosaccus sanctus (van Beneden, 1861)	M			+
Lanice conchilega (Pallas, 1766)	P			+
Nephtys assimilis Oersted, 1843	P			+
Nephtys kersivalensis McIntosh, 1908	P			+
Nucella spp. Röding, 1798	G			+
Owenia fusiformis Chiaje, 1842	P			+
Pseudopolydora antennata (Claparède, 1870)	P			+
Sphaerodoropis balticum (Reimers, 1933)	P			+
Spiophanes bombyx (Claparède, 1870)	P			+
Sthenelais limicola (Ehlers, 1864)	P			+

Class: A, Anthozoa; G, Gastropoda; M, Malacostraca; O, Oligochaeta; Op, Ophiuroidea; P, Polychaeta; Pe, Pelecypoda.
*N, phylum Nemertea.

There was no significant difference between the infaunal communities of the treatments with no mussels in 1999 prior to seeding with mussels (ANOSIM; $R = 0.031$, $P = 0.42$; Fig. 2). In addition, there was no significant difference in the total number of individuals and number of species in the mussel-free area and distant control areas in 1999 (Mann–Whitney; $W = 14.0$, d.f. = 6, $P = 0.312$; $W = 21.0$, d.f. = 6, $P = 0.471$, respectively). There was no significant difference in the organic content of the treatments with no mussels in 1999 (Mann–Whitney; $W = 19.0$, d.f. = 6, $P = 0.885$).

The infaunal communities of the mussel-free areas taken in 1999 and 2001 were significantly different (ANOSIM; $R = 0.854$, $P < 0.05$; Fig. 2). This was reflected in both the numbers of individuals and number of species, which were significantly lower in the 2001 samples (Mann–Whitney; $W = 26.0$, d.f. = 5, $P < 0.05$ in both cases). Of a total of 29 species found in the plots in
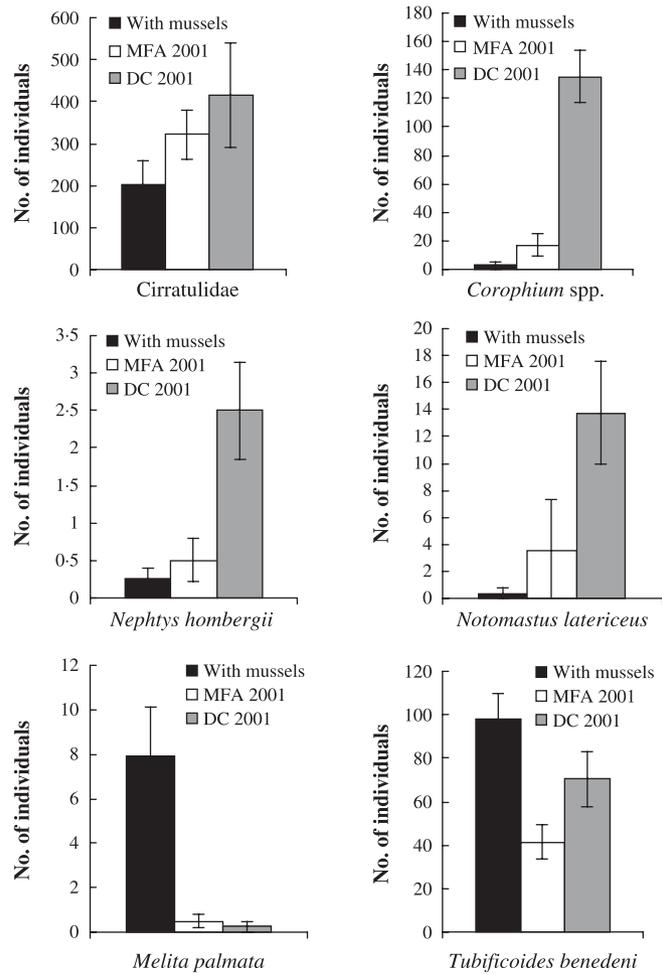
Fig. 5. Mean number of individuals (± SE) of taxa contributing to the major differences between infaunal communities of the 2001 mussel-free areas (MFA), distant controls (DC) and plots with mussels. Means and SE are shown for clarity rather than median values.

Table 2. Mann–Whitney tests (d.f. = 18) of the individual taxa that contributed to the major community difference between either 2001 distant controls or 2001 mussel-free areas and plots with mussels

Taxa	Plots with mussels compared with	W	P
Cirratulidae	Distant control 2001	19·0	0·885
	Mussel-free area 2001	151·0	0·119
Corophium spp.	Distant control 2001	136·0	0·003
	Mussel-free area 2001	141·0	0·012
Nephtys hombergii	Distant control 2001	138·5	0·061
	Mussel-free area 2001	159·0	0·421
Notomastus latericeus	Distant control 2001	137·0	0·004
	Mussel-free area 2001	146·5	0·047
Melita palmata	Distant control 2001	192·5	0·021
	Mussel-free area 2001	191·0	0·033
Tubificoides benedenii	Distant control 2001	178·5	0·345
	Mussel-free area 2001	194·0	0·003

1999, 17 species were not found in these plots in 2001 and these species contributed to more than 40% (SIMPER) of the dissimilarity between the mussel-free area plots in 1999 and 2001. A further 20% of the dissimilarity could be attributed to those species that occurred in both 1999 and 2001 (Fig. 5). However, of these taxa only *Corophium* spp. had significant differences in numbers (Mann–Whitney; $W = 10·0$, d.f. $= 6$, $P < 0·05$) and *Melita palmata* was only present in 2001. There was no significant difference in the organic content of the mussel-free area plots in 1999 and 2001 (Mann–Whitney; $W = 24·0$, $P = 0·112$).

The distant controls did not change significantly between 1999 and 2001 in either the infaunal community

Table 3. Regression analysis of infaunal community data with area of mussels per sample [except number of species, which is regressed against ln(n + 1)mussel area]. Numbers of individuals are ln(n + 1)

| Mussel area (V)	Correlation coefficient (r)	d.f.	P	Slope ($\pm$ SE)	Intercept ($\pm$ 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 per sample	0·74	13	0·001	−0·000858 ± 0·000196	7·22 ± 0·684	0·548
Corophium spp. 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

(ANOSIM; R = 0·448, P = 0·06) (Fig. 2), the total number of individuals or the number of species (Mann–Whitney; W = 22·0, d.f. = 6, P = 0·312; W = 17·5, d.f. = 6, P = 1·00, respectively). There was no significant difference in the organic content of the distant control treatments in 1999 and 2001 (Mann–Whitney; W = 18·0, P = 0·885).

The infaunal communities of the mussel-free area and distant control treatments sampled in 2001 were significantly different (ANOSIM; R = 0·635, P = 0·03) but there was no significant difference in the total number of individuals between these treatments (Mann–Whitney; W = 13·0, d.f. = 6, P = 0·194). However, there was a significantly lower number of species found per replicate plot for the mussel-free area vs. the distant control treatment (Mann–Whitney; W = 10·0, d.f. = 6, P < 0·05). There was no significant difference in the organic content of the sediment in the mussel-free area and distant control in 2001 (Mann–Whitney; W = 24·0, P = 0·112).

The infaunal communities associated with plots within the Latin square, when grouped according to the four original seeding densities laid in April 2000, were not significantly different from each other (Fig. 2; ANOSIM; R = 0·133, P = 0·061). Similarly, there were no significant differences in the number of individuals or the number of species (Kruskal–Wallis; H = 1·35, d.f. = 11, P = 0·718; H = 6·77, d.f. = 12, P = 0·08, respectively), and there was no significant difference in the organic content of the sediment for the four different mussel density treatments (Kruskal–Wallis; H = 0·11, d.f. = 11, P = 0·991).

RELATE indicated that there was a highly significant correlation between the environmental and biological data (ρ = 0·513, P = 0·003). BIOENV demonstrated that the strongest correlation between infaunal community and environmental data was with mussel shell area and mussel volume (BIOENV; ρ = 0·643; ρ = 0·642, respectively).

The gradient between the infaunal community and mussel shell area was supported by the relationships between both abundance of individuals and number of species present in the samples plotted against mussel area (Table 3). The number of individuals per plot [ln(n + 1)] had a significant negative linear relationship with mussel area (Fig. 6). The number of species also had a significant negative linear relationship with ln(n + 1) mussel area (Fig. 7). Analysis of the mean
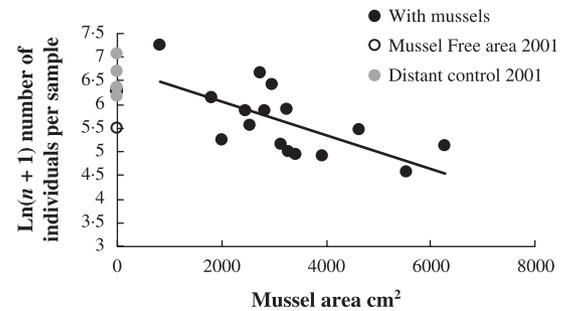
Fig. 6. Relationship between area of mussels and number of individuals. Values of 2001 distant controls and mussel-free areas are shown for comparison. Regression line y = 6·77 – 0·000365x, r^2 = 0·404.
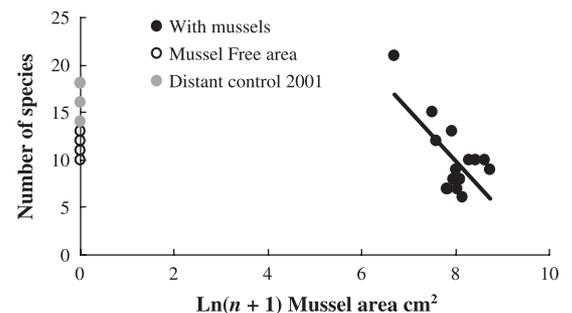
Fig. 7. Relationship between area of mussels and number of species in sample. Values of 2001 distant controls and mussel-free areas are shown for comparison. Regression line y = 53·3 – 5·48x, r^2 = 0·425.

abundance [ln(n + 1)] of individual species revealed significant negative relationships with mussel area for three taxa: Cirratulidae, *Corophium* spp. and *Melita palmata* (Table 3 and Fig. 8).

Discussion

As in other studies (Commito 1987; Dittman 1990; Guenther 1996; Ragnarsson & Raffaelli 1999), it is clear that mussel beds affect the composition, richness and abundance of the benthic fauna of the sediment onto which they are laid, in terms of both the numbers of individuals and species present (Figs 3 and 4 and Table 1). In this large-scale experiment the presence of mussels had a large impact on the abundance of epibenthic crustaceans, in particular *Carcinus maenas*
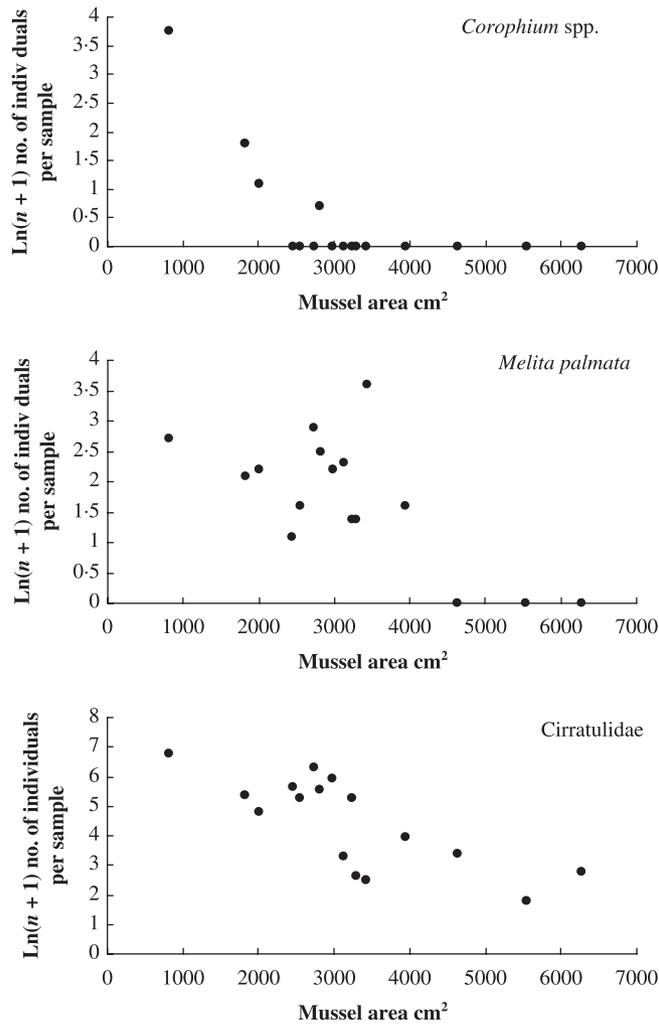
Fig. 8. Relationship between surface area of mussels and the associated number of selected taxa.

and *Melita palmata*. This can be attributed to the refuge provided by the mussel matrix from water movement, desiccation and predation (Dittman 1990; Ragnarsson & Raffaelli 1999). Commito & Boncavage (1989) suggested that the presence of mussels also caused an increase in oligochaete abundance. This concurs with our findings in which the abundance of *Tubificoides benedeni* was greater in the mussel plots compared with areas with no mussels (Fig. 5). 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 & Boncavage 1989; Dittman 1990). Although such a trend was not as apparent here, there was a suggestion that samples with more mussels were associated with a reduced abundance of cirratulids (Fig. 8) while there was no concomitant change in the abundance of oligochaetes. Thus the latter became more dominant in terms of their overall contribution to faunal composition. The high abundance of *Tubificoides benedeni* in mussel beds has been attributed to its tolerance of organically rich deoxygenated sediment (Commito & 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 & Arthur 1978).

While some species increased in numbers in the presence of mussels, other species decreased. *Pygospio elegans* was less abundant in the mussel bed infaunal community than in surrounding sediment and this has also been demonstrated in the Wadden Sea (the Netherlands) and the Ythan Estuary (Scotland) (Guenther 1996; Ragnarsson & 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 & Evans 1987). *Corophium* spp., a burrow-dwelling invertebrate, also declined in numbers in the mussel bed and this again can be attributed to the unstable sediment regime (Jensen & Kirstensen 1990). Mussel beds may prove a less suitable habitat for such organisms simply due to lack of space for burrow construction 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. 5) reflected both the physical environments of the mussel bed and the associated infaunal community. The capitellid *Notomastus latericeus* prefers cleaner muddy sand and is a more selective feeder than the other, more opportunistic, capitellid species, and this was reflected by its higher abundance in both of the control treatments compared with the mussel treatment (Fauchald & 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 with the surrounding sediments.

The distant control plots represented an area close to the mussel beds (20–80 m distant) compared with the mussel-free area plots that were among the mussel bed treatments. Examination of this spatial gradient suggests that the effects of mussels on benthic infaunal communities of soft sediments are reduced with increasing distance from the mussel bed, and there was no significant effect on the infaunal community of the distant controls. Although natural changes over time may account for some of the differences between the 1999 and 2001 treatment plots with no mussels, the magnitude of the difference in species composition suggests that this was not the main factor. This was supported by the lack of significant change in the community of the distant controls over time. Prior to the seeding of the mussel bed the spatial homogeneity of the site was confirmed by comparison of the 1999 plots with no mussels, hence the distant controls and mussel-free area plots were directly comparable. It is likely that the clear patterns with increasing distance from the mussel bed treatments indicated a steep dilution of the influence of the mussel bed on the benthic community. Thus it would appear that the influence of the mussel bed on benthic invertebrate communities is undetectable at a distance of between 20 m and 80 m from the mussel bed. This effect is demonstrated in both the median abundance and the median species number in each treatment. Dittman (1990) demonstrated a reduced abundance of individuals within a mussel bed compared with the surrounding sediment, which concurs with our study, with a reduced abundance number of individuals with increasing proximity to the mussel bed (Fig. 3) (cf. Commito 1987). However, the number of species was not significantly different between the mussel bed and surrounding area in Dittman's study (1990). This does not concur with our results, in which the numbers of species found in the mussel bed were lower than in the 2001 distant control treatment plots. Although it appears from Table 1 that more species occurred overall in the mussels plots, the sampling effort is four times greater that for the plots with no mussels.

The treatments with no mussels (mussel-free area and distant control) 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.

Multivariate analysis revealed that the mussel-free area and distant control areas were significantly different in 2001, largely attributed to a significantly lower median number of species in the mussel-free area compared with the distant control. 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, either through size selection by the mussels or due to some behavioural characteristics of different invertebrate larvae. 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 & Boncavage (1989) to preclude organisms that do not have a pelagic development stage (e.g. *Tubificoides benedeni*). A study conducted at a much smaller spatial scale (1-m² experimental plots) did not detect a significant effect of bivalve density on larval settlement and juvenile recruitment (Hunt, Ambrose & Peterson 1987). Nonetheless, at the large scale used in this study filtration by the mussel bed is likely to have an effect on the benthic infaunal community within the bed, either through larval removal or through competition for food (Cowden, Young & Chia 1984; Morgan 1992).

The effects of a mussel bed on its associated benthic community were 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. 7). 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 and 7). 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, outweigh 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, Kaiser & Edwards (1996) reported a linear decrease in the

number of cirratulids with increasing bivalve density in plots of cultivated Manila clams (*Tapes philippinarum* Adams & Reeve 1950).

CONCLUSIONS

Mussel beds can alter the infaunal benthic community of the adjacent and interstitial sediments. 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 had fewer individuals and fewer species. 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 localized to 0–10 m, and no significant effect occurred at a scale of 20–80 m. 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 affect the invertebrate assemblage of the sediments on which the mussels are laid. However, changes in benthic community composition could be reduced by proportional lowering of the stocking density of mussels within mussel beds or by restriction of the final surface area of coverage of the seabed. It would also appear that in intertidal areas, the effects of seabed cultivation of mussels are restricted to the immediate area of cultivation and that wider-scale effects are not apparent. Therefore, controlling the area available for cultivation would be an effective management measure to reduce impacts on benthic fauna.

Acknowledgements

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