Effects of the mussel *Mytilus edulis* L. on the invertebrate fauna of sediments

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Abstract

Two field experiments were carried out to investigate the effects of mussels (*Mytilus edulis*) on fauna and on sediment characteristics. In the first experiment mussels were removed from within an established mussel bed to create bare patches and in the second experiment mussels were transplanted to an adjacent bare sandflat. In the mussel removal experiment, mobile epibenthic crustaceans (predominately *Gammarus* spp. and *Jaera albifrons*) were markedly reduced in bare patches whereas infaunal species were much less affected. In the mussel transplant experiment, mobile epibenthic crustaceans (e.g. *Gammarus* spp. and *Jaera albifrons*) colonised mussel transplant plots, but were absent at all times from the adjacent sandflat sediments. The polychaetes *Eteone longa* and *Pygospio elegans* were both significantly reduced in mussel transplant plots, whilst *Capitella* spp. increased in numbers. Mussels clearly had marked effects on both the fauna and sediments probably through a combination of biodeposition and filtration by the mussels and the provision of a structurally complex habitat. © 1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

Mytilid mussels are one of the most characteristic features of rocky intertidal and estuarine flats world-wide (Suchanek, 1985). Competitive interactions between mussels and other large organisms for primary space and the roles of predation and physical disturbances in the mediation of such interactions have been well documented for rocky
shore systems (e.g. Dayton, 1971; Suchanek, 1978; Paine and Levin, 1981; Sousa, 1984; McCook and Chapman, 1991; Menge et al., 1994). On rocky shores, disturbances create open areas within mussel beds which are then available for colonisation by species with inferior competitive ability (Hewatt, 1935). Mussels themselves create a secondary space or habitat within which a highly diverse assemblage can develop (Tsuchiya and Nishihira, 1985; Tsuchiya and Nishihira, 1986; Tsuchiya and Bellan-Santini, 1989; Suchanek, 1992; Lintas and Seed, 1994) but the interactions between mussels and their associated secondary-space fauna are not well understood even for rocky shores (Suchanek, 1985, 1992; Lohse, 1993).

Perhaps because of the dramatic nature of the interactions between mussels and other organisms on rocky shores, comparatively little attention has been paid to the dynamics of mussel beds and their fauna in intertidal sediments. In Northern Europe, this biotope can cover extensive areas of estuarine flats (up to hundreds of hectares) and has traditionally provided an exploitable resource for fish bait and for human consumption (Fenton, 1978). A few studies have shown that the fauna within these mussel beds can differ markedly from that in adjacent non-mussel areas (Radziejewska, 1986; Commito, 1987; Dittmann, 1990; Jaramillo et al., 1992b; Reise et al., 1994) and several underlying mechanisms have been proposed which could apply to both rocky and sediment mussel beds. Firstly, the structural complexity of the mussel matrix creates microhabitats which provide organisms with shelter and a refuge from predation (e.g. Seed, 1976; Suchanek, 1985, 1992). Secondly, mussels biodeposit large amounts of faeces and pseudofaeces as well as enhancing deposition of fine particulate matter as a result of changes in the near bed hydrodynamic régime (Dahlbäck and Gunnarsson, 1981; Kaspar et al., 1985; Kautsky and Evans, 1987; Jaramillo et al., 1992a; Hatcher et al., 1994), which may have a significant impact (such as smothering and anoxia) on faunal composition and abundance as well as providing a secondary sediment habitat (Mattsson and Lindén, 1983; Radziejewska, 1986; Tsuchiya and Nishihira, 1986; Suchanek, 1992). Thirdly, dense beds of mussels can filter out large quantities of fine particulate matter (e.g. Officer et al., 1982; Doering and Oviatt, 1986), including larvae (Cowden et al., 1984; Morgan, 1992; see also Mileikovsky, 1974). Patch size, density and size of mussels can have large influence on the composition of associated fauna within beds (Tsuchiya and Nishihira, 1985, 1986).

The relative importance of these processes is expected to differ between exposed rocky shores and sheltered mudflats. For instance, accumulation of deep layers of organic material are not a feature of exposed rocky shore sites and the range of megafaunal predators from which mussel bed invertebrates are protected is usually much greater in sheltered estuarine habitats (Reise, 1985).

Comparisons of the fauna of mussel bed and non-mussel bed locations are potentially confounded by location effects. For instance, mussel beds and non-mussel bed areas may experience different local hydrographic conditions. Also, non-mussel bed areas often have their own dominant species, such as lugworms (*Arenicola marina* (L.)), sand masons (*Lanice conchilega* (Pallas)) and eel-grass (*Zostera marina* L.), all of which have potentially structuring effects, so that the different fauna of these areas may not be solely due to the absence of mussels. With field experiments, where densities of mussels can be manipulated, the risk of confounding effects is reduced. Here we describe two field
experiments on the intertidal flats of the Ythan estuary, Aberdeenshire, Scotland, designed to specifically examine the proposition that it is the presence of mussels themselves which is responsible for observed differences in community structure and composition in mussel beds and non-mussel bed areas.

2. Materials and methods

In the first experiment mussels were removed in order to create open patches (1 m²) within an existing mussel bed, whilst in the second experiment, the effects of transplanting mussels onto mussel-free areas were investigated.

2.1. Mussel removal experiment

This experiment was carried out within an extensive mussel bed (5000 m²) at Red Inches, Ythan estuary, Aberdeenshire (1° 59’ W, 57° 2’ N). A general description of the estuary and its ecology can be found in Baird and Milne (1981), Gorman and Raffaelli (1993) and Gorman (1998). A 1 m × 25 m area was marked out parallel to the tide edge, 7 m downshore from the upper boundary of the mussel bed. This study area was chosen because it appeared representative of the mussel bed as a whole; the cover of mussels was homogeneous and their sizes similar (personal observation). Within this area 10 1 m² plots were alternately allocated as either treatment (mussel removal, n = 5) or control (n = 5), i.e. plots were dispersed in a systematic design (Hurlbert, 1984). An alternating pattern of control and treatment plots was preferred to one where plots were allocated treatments at random, because of the high chance of spatial segregation of treatments with only five replicates (Hurlbert, 1984). Adjacent plots were separated by 1.5 m.

On 13 April 1994, sheets of mussels were carefully removed by hand from treatment plots (hereinafter termed ‘cleared plots’). During removal, care was taken to minimise disturbance of the underlying substratum. Samples for fauna and sediments were collected immediately prior to removal of the mussels and subsequently on 27 April and on 27 May, 14 and 44 days after initiation of the experiment. One core of 7.5 cm diameter was taken at random within each of the two plot types to a depth of = 10 cm. To avoid edge effects, the area within 30 cm of the perimeter of each plot was not sampled. Samples were sieved through a 500 μm mesh and the animals retained were identified to the lowest taxonomic level possible.

Two cores were taken at random within each plot for estimation of sediment organic matter and silt content using a 2.5 cm diameter corer to a depth of 4 cm on days 0, 14 and 44. Four additional cores (pooled prior to analysis) were taken at random from each plot for sediment particle size analysis after 14 and 44 days. Cores for sediment analysis from control plots did not include mussels. The organic matter was estimated as loss of weight on ignition at 600°C, after treatment with hydrochloric acid to remove shell material (Holme and McIntyre, 1984). Silt content was estimated as the amount of sediment passing through a 63 μm mesh by wet sieving, and particle size analysis by dry sieving (Holme and McIntyre, 1984).

At each sampling occasion, species densities (log X + 1), silt content and organic
matter were compared between cleared and control plots using \textit{t}-tests. To reduce the risk of Type 1 error as a result of executing several \textit{t}-tests and the temporal non-independence of samples taken from the same plots through time, statistical tests were attributed at the 2.5\% level. It should be noted that no statistical comparisons of species abundances over time were carried out.

2.2. Mussel transplant experiment

This experiment was also conducted at the Red Inches site, on an intertidal flat (henceforth termed ‘sandy site’) of fine sand located 250 m from the edge of the mussel bed already described and at the same shore level. The fauna at the site is typical of fine sand (Raffaelli et al., 1991a; Fernandes, 1992; Ragnarsson, 1996) and differs markedly from that in the mussel bed (Raffaelli et al., 1990). On 16 May 1994, sheets of mussels were collected from within the mussel bed described above. Because mussels are attached to each other by byssal threads, sheets ranging in size from 0.1 m\(^2\) to 0.2 m\(^2\) could be removed intact. Sheets were brought to the laboratory (10 min travel time) and thoroughly washed in a steady stream of seawater for several minutes followed by vigorous agitation in seawater in order to remove all associated invertebrates. For each sheet, this procedure was repeated three times.

Subsequently, 10 sheets were chosen at random and within each sheet a sample of 44 cm\(^2\) was analysed for any remaining associated fauna. No invertebrates were recorded and we are certain that this process removed associated fauna except for barnacles \textit{(Semibalanus balanoides L.)} attached to mussel shells. The mussel sheets were kept overnight in clean aerated seawater prior to transplantation.

On 17 May, five 4 m \(\times\) 4 m\(^2\) areas (blocks) were marked out at 3 m intervals parallel to the tide edge along the lower shore at the sandy site at the same level as that from which the mussels were collected. Within each of these areas, one treatment plot (mussel transplant) and one control plot, each 0.6 m\(^2\), were randomly located 2 m apart. In each mussel transplant plot the cleaned mussels were placed on the sediment surface at a density similar to that in the original mussel bed. These were initially anchored with a rigid coarse wire mesh to prevent potential displacement of mussels by water movement but after 4 days the mussels had firmly attached to the substratum and the mesh was removed. Tests for possible experimental artefacts due to the mesh indicated no effects (Ragnarsson, 1996).

One sample from each of the mussel and control plots was collected within each block immediately prior to adding the mussels (day 0) and then subsequently on 31 May and on 29 June, days 14 and 43, respectively. Samples were taken with a corer of internal diameter 7.5 cm to a depth of \(\approx\) 10 cm, the material sieved through a 500 μm mesh and the organisms retained were identified and enumerated. Samples for silt content analysis were collected on days 0, 14, 26 and 43. Samples for granulometric analysis were obtained on days 14 and 43. No samples for estimation of organic matter in sediments were collected. The analytical methods for sediments and the statistical procedures used are as described for the mussel removal experiment.
3. Results

3.1. Mussel removal experiment

In total, 27 taxa were recorded during the course of this experiment. Prior to the initiation of the experiment, none of the taxa differed significantly in density between plots from which mussels were to be removed and in undisturbed (control) plots, although the mean abundance of most taxa tended to be lower in plots from which mussels were to be removed.

Following mussel clearance, there was a significant decline in the total number of individuals (day 14, \( P = 0.004 \)) and the number of taxa (day 14, \( P = 0.002 \); day 44, \( P = 0.006 \)) in the cleared plots (Fig. 1). *Gammarus* spp. (*Gammarus salinus* Spooner and *Chaetogammarus stoerensis* (Reid)) and the isopod *Jaera albifrons* Leach were almost completely absent in plots following mussel removal (Fig. 1), but remained significantly more abundant in the undisturbed mussel bed (*Gammarus* spp. day 14, \( P = 0.004 \); *J. albifrons* day 44, \( P = 0.002 \)).

Chironomid larvae, mites (Acarina) and the shore crab *Carcinus maenas* (L.) were absent from all cleared plots on days 14 and 44, but occurred in low (although variable) numbers in control plots. Because of their absence from cleared plots, no formal statistical analysis was possible. Of the infaunal species, only the oligochaete *Tubifex costatus* (Claparede) (Fig. 1) was significantly less abundant in cleared plots (day 14, \( P = 0.014 \)).

Cleared plots experienced erosion resulting in excavation of the surface to a depth of about 2–5 cm. Fine particulate matter present was lost, leaving behind larger and heavier particles (mainly shell fragments) which accounts for the larger median particle size \( \phi 1.62 \) (310 \( \mu m \)) and \( \phi 1.36 \) (385 \( \mu m \)) in cleared plots compared to \( \phi 1.74 \) (286 \( \mu m \)) and \( \phi 1.65 \) (305 \( \mu m \)) in control plots on day 14 and 44, respectively. No significant differences were found between cleared and control plots in silt content and organic matter on any of the sampling dates (Fig. 2).

3.2. Mussel transplant experiment

A total of 25 taxa were recorded during the course of this experiment. Prior to addition of mussels, no significant differences were found in the density of the numerically dominant taxa in the areas designated for mussel transplant or controls (Fig. 3). After addition of mussels to the sandy site, *Gammarus* spp., *Jaera albifrons*, *Carcinus maenas*, chironomid larvae and mites were recorded from the mussel plots on days 14 and 43 (Fig. 3, Table 1), but were absent from control plots thereby precluding any formal statistical analysis. No individuals of the polychaete *Eteone longa* (Fabricius) were found in mussel transplants on days 14 and 43, but this species occurred in controls (Fig. 3). The total number of individuals was significantly lower in mussel transplant plots on day 14 (\( P = 0.005 \)), but not on day 43 (Fig. 3).

Colonisation by *Capitella* spp. in mussel transplant plots was rapid, with numbers significantly greater compared to control plots on day 43 (\( P = 0.007 \)). Densities of the
tube-building polychaete *Pygospio elegans* Claparède were significantly lower in mussel plots on both sampling days ($P = 0.002$ on day 14 and $P = 0.002$ on day 43). The large number of *P. elegans* in control sandy plots on day 14 was due to heavy larval settlement, and the subsequent decline due to high larval mortality. In a nearby area of the Ythan, data collected over a 3-year period consistently showed this ‘boom and bust’ pattern of abundance for *P. elegans* (Ragnarsson, 1996). The snail *Hydrobia ulvae* (Pennant) was significantly less abundant in mussel transplant plots ($P = 0.0002$) on day 14.

Sediment particle size was smaller in mussel transplant plots during the course of the
Fig. 2. Mussel removal experiment. Mean percentage of silt and organic matter (±95% confidence limits, n = 5) in the pre-defined cleared plots (solid bar) and in control plots (open bar) prior to mussel clearance at day 0 (left of the dashed line), and in cleared plots (solid bars) and control plots (open bars) 14 and 44 days after clearance of mussels.

experiment. In control plots the median particle diameter was around φ1.75 (286 μm) for both sampling days whilst in mussel transplant plots it was φ1.84 (282 μm) and φ2.07 (235 μm) on day 14 and 43, respectively. There was no significant difference in the silt content between plot types on day 0, but silt content was significantly greater (P < 0.01) in mussel plots on all subsequent sampling days (Fig. 4; P = 0.0025 on day 14, P = 0.0019 on day 26 and P = 0.0029 on day 43).

4. Discussion

The removal and transplant experiments indicate that the presence of mussels has an impact on several taxa, particularly epibenthic crustaceans. Comparison of the mussel bed and the sandflat fauna at Red Inches reveals little overlap in the dominant species in the two kinds of habitat and there are several species which only occurred in one of the habitats (Table 1). Thus, eight species were recorded from the transplanted mussel sheets but never from the control plots. None of these taxa occurred in the sheets of cleaned mussels prior to setting up the experiment and we are confident that these individuals were immigrants facilitated by the presence of the mussel matrix. Gammarus salinus, Jaera albifrons and juvenile stages of Carcinus maenas have been reported to actively enter the water column (e.g. Carvalho, 1989; Armonies, 1994; Thiel and Dernedde, 1994) and are frequently encountered in plankton samples from the Ythan (personal observation). High mobility on the scale of tens of metres has been demonstrated for other gammarid amphipods (Gunnill, 1982; Virnstein and Curran, 1986) and it is likely that these taxa originated from other beds, the nearest of which is located on the opposite bank about 150 m distant. All three of these crustaceans probably require the secondary space afforded by the mussel matrix as a refuge from water movement, desiccation and predation (e.g. Suchanek, 1992; Lintas and Seed, 1994).

The decrease in numbers of Pygospio elegans, the absence of Eteone longa and
Fig. 3. Mussel transplant experiment. Mean number of individuals and taxa per core (±95% confidence limits, \( n = 5 \)) in the pre-defined mussel transplant plots (solid bar) and control plots (open bar) prior to addition of mussels at day 0 (left of the dashed line), and in mussel transplant (solid bars) and control plots (open bars) 14 and 43 days after addition of mussels. Note that *Gammarus* spp. comprises *Gammarus salinus* and *Chaetogammarus stoerensis*. Oligochaetes refer to all species of oligochaetes other than *Tubificoides benedeni*.
Table 1
Species either recorded within the mussel transplant plots and/or the musselbed, or within the sandflat only

<table>
<thead>
<tr>
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<th>Mussel bed</th>
<th>Mussel transplant plots</th>
<th>Sandflat</th>
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<tr>
<td><em>Gammarus salinus</em> Spooner</td>
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<td><em>Chaetogammarus stoerensis</em> (Reid)</td>
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<td><em>Melita palmata</em> (Montagu)</td>
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<td><em>Jaera albifrons</em> Leach</td>
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<td><em>Carcinus maenas</em> (L.)</td>
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<td><em>Acarina</em></td>
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<td><em>Pholis gunnellus</em> (L.)</td>
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<td><em>Chironomidae</em> (larvae)</td>
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<td><em>Nereis virens</em> (Sars)</td>
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<td><em>Littorina littorea</em> (L.)</td>
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<td><em>Mediomastus fragilis</em> Rasmussen</td>
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<td><em>Micralymma marinum</em> (Ström)</td>
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<td><em>Cerastoderma edule</em> (L.)</td>
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<td><em>Eteone longa</em> (Fabricius)</td>
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<td><em>Scoloplos armiger</em> (Müller)</td>
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<td><em>Corophium volutator</em> (Pallas)</td>
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<td><em>Oedicerotidae</em></td>
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<td><em>Lanice conchilega</em> (Pallas)</td>
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<td><em>Arenicola marina</em> (L.)</td>
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Increase in abundance of *Capitella* spp. under transplanted mussels is probably due to the enhanced deposition of fine particulate matter from the water column as a result of reduced flow of water through the mussel matrix as well as from mussel faeces and pseudofaeces (e.g. Kautsky and Evans, 1987). The sudden increase in silt content in mussel transplants suggests an increase in organic matter and deoxygenation of sediments. *Capitella* spp. are known to increase in patches recently enriched with organic matter (Young and Young, 1978; Tenore and Chesney, 1985; Raffaelli et al.,

Fig. 4. Mussel transplant experiment. Mean percentage of silt (±95% confidence limits, n = 5) in the pre-defined mussel transplant plots (solid bar) and control plots (open bar) at day 0 (left of the dashed line), and in mussel transplant (solid bars) and control plots (open bars) 14, 26 and 43 days after addition of mussels.
such as in sediments exposed to intense biodeposition under hanging mussel lines (Mattsson and Lindén, 1983). *P. elegans* is known to decline in areas where sediments are unstable, either through sediment deposition (Wilson, 1981; personal observation), erosion (Zühlke and Reise, 1994) or re-deposition of very fine particulate matter (Rhoads and Young, 1971; Brenchley, 1981). The larval stages are probably most vulnerable in this respect (Rhoads and Young, 1970). The decline of *E. longa* in mussel transplant plots may well be due to the decrease in *P. elegans*, its main prey (Reise, 1985).

Removal of mussels from an established mussel bed resulted in a loss of epibenthic crustaceans, confirming their requirement for secondary space, but there was no concomitant increase in those sandy shore species (e.g. *Pygospio elegans*) which declined in the mussel transplants. In this respect the outcomes of the two experiments are not symmetric, probably due to differences in the relative mobilities of the different taxa and the rates of change of sediment characteristics in the two experimental areas. Mussel bed epifaunal crustaceans are highly mobile and were able to rapidly colonise the mussel transplants, whilst the adult stages of many sandy shore species are infaunal and much less mobile (e.g. Wilson, 1981). Similarly, surface sediment characteristics were affected rapidly by the presence of the mussel transplants, presumably due to changes in near-bed hydrography and biodeposition by living mussels. Removal of mussels from established beds promoted erosion of fine sediments creating shallow pits which persisted for many months and did not revert to a sandy environment, probably due to a lack of sand in nearest surroundings. Erosion of the mussel bed sediments had no significant effects on the infauna, (except for *Tubifex costatus* on day 14), possibly because the normal response of most species to sediment erosion is simply to burrow deeper, as has been shown for *Tubificoides benedeni* (Udekem) (Zühlke and Reise, 1994).

Comparing the outcomes of the two experiments is not entirely straightforward since they were not carried out contemporaneously. However, we believe that this effect is likely to be minor given the large differences between the sandflat and the mussel bed communities on the Ythan estuary at any time of the year (Raffaelli et al., 1990, 1991a; Fernandes, 1992; Ragnarsson, 1996). Also, scale effects are possible since different plot sizes (1 m$^2$ versus 0.6 m$^2$) were employed in the two experiments, but these effects are only likely to be significant where the difference in plot size is much greater.

Clearly, sandflat and the mussel bed habitats differ in their overall assemblage structure but they also occupy different areas of the Ythan and their relative locations are rigidly fixed (at least over the last 35 years for which aerial photographic data are available). There remains the question as to why mussels are restricted to particular areas of the Ythan (or any other estuary). After 60 days, around half of the mussels from the mussel transplants were either lost or found dead, covered with bedload transported sand, which has been shown to be an important source of mortality (Kuenen, 1942). It seems unlikely that juvenile mussels are able to successfully recruit at this site because of the negative impact of a high bedload transport. Indeed, we have recorded large numbers of juvenile (2–4 mm) mussels from an adjacent sandflat (Raffaelli et al., 1991a) but these individuals never survived to establish mature beds (personal observation).

In summary, our experiments have shown that the mussel matrix facilitates the
recruitment of epibenthic crustaceans, whilst biodeposition seems to reduce the abundance of some infaunal taxa and increases the abundance of others. Similarly, removal of mussels lead to a loss of epibenthic species, but did not result in changes in infaunal species, at least at the spatial and temporal scales of the present study. At a larger scale, Kuenen (1942) and Theisen (1968) describe how storms can displace entire mussel beds and Obert and Michaelis (1991) reported reduced abundances of mussels and associated fauna following a period of ice cover. In field experiments there may also be scale effects. For instance, Commoto and Boncavage (1989) and Raffaelli et al. (1990) have investigated experimentally whether the removal of the mussel protective microhabitat has effects on the associated infauna, by recording invertebrate succession in artificially cleared patches of 0.01 m$^2$ and 1 m$^2$, respectively. In the study by Raffaelli et al. (1990) few significant differences were found (as was the case in the present study), whereas in the experiment by Commoto and Boncavage (1989) there were large shifts in the abundance of the oligochaete *Tubificoides benedeni*. Manipulation on even larger scales than carried out here would have been very difficult, but may be of great interest, especially if the longer-term dynamics of mussel transplants can be considered.

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**References**


Tsuchiya, M., Bellan-Santini, D., 1989. Vertical distribution of shallow rocky shore organisms and community structure of mussel beds (Mytilus galloprovincialis) along the coast of Marseille, France. Mésogée 49, 91–110.


