Helgol Mar Res (2012) 66:1–9
DOI 10.1007/s10152-010-0241-0

ORIGINAL ARTICLE

Comparative study of predatory responses in blue mussels (*Mytilus edulis* L.) produced in suspended long line cultures or collected from natural bottom mussel beds

Helle Torp Christensen · Per Dolmer · Jens Kjerulf Petersen · Ditte Tørring

Received: 10 June 2010 / Revised: 13 December 2010 / Accepted: 27 December 2010 / Published online: 18 January 2011

Abstract Blue mussels (*Mytilus edulis* L.) are a valuable resource for commercial shellfish production and may also have uses as a tool in habitat improvement, because mussel beds can increase habitat diversity and complexity. A prerequisite for both commercial mussel production and habitat improvement is the availability of seed mussels collected with minimum impact on the benthic ecosystem. To examine whether mussels collected in suspended cultures can be used for bottom culture production and as tool in habitat improvement, the differences in predatory defence responses between suspended and bottom mussels exposed to the predatory shore crab (*Carcinus maenas* L.) were tested in laboratory experiments and in the field. Predatory defence responses (byssal attachment and aggregation) and morphological traits were tested in laboratory, while growth and mortality were examined in field experiments. Suspended mussels had an active response in relation to the predator by developing a significantly firmer attachment to the substrate and a closer aggregated structure. Bottom mussels had a passive strategy by having a thicker shell and larger relative size of the adductor muscle. In a field experiment mussels originated from suspended cultures had a higher length increment and lower mortality when compared to bottom mussels. It is concluded that suspended mussels potentially are an alternative resource to bottom culture and can be used in habitat improvement of mussel beds, but that the use of suspended mussels has to be tested further in large-scale field experiments.

Keywords Predatory response · *Carcinus maenas* · *Mytilus edulis* · Habitat improvement · Bottom culture · Long line culture

Communicated by H.-D. Franke.

H. T. Christensen (✉) · P. Dolmer
Technical University of Denmark,
National Institute of Aquatic Resources,
Charlottenlund Castle, Jaegersborg allé 1,
2920 Charlottenlund, Denmark
e-mail: htc@aqua.dtu.dk

J. K. Petersen · D. Tørring
Danish Shellfish Centre, Oeroddevej 80,
7900 Nykoebing M., Denmark

Introduction

Blue mussels form biogenic reefs, thereby providing a complex structure to coastal habitats. In addition, blue mussels are a valuable resource for commercial shellfish production including fishery and culturing activities (Smaal 2002). The species also has perspectives as a tool in habitat improvement of costal habitats as the mussel beds increase habitat diversity and complexity (McDermott et al. 2008). Habitat improvement using bivalves is mainly known in relation to restoration of oyster reefs (e.g. Coen and Luckenbach 2000; Peterson et al. 2003; Coen et al. 2007), and the focus for many of the habitat improvement projects involving bivalves has typically been reduction in public health risk through improved water quality and to improve the harvest of bivalves for consumption (e.g. Leonard 1993). Only little work can be found in literature documenting the use of blue mussels as an improvement tool, though the species has proven to be suitable for the purpose (Szatybelko and Dubrawski 1999; McDermott et al. 2008). McDermott et al. (2008) reported that restoration of blue mussel beds can increase living marine resource utilisation and species diversity within a degraded habitat. Biogenic reefs are included in the EU Habitat Directive, and

consequently, mussel beds may be prioritised for protection in protected areas to fulfil Habitat Directive objectives.

The availability of seed mussels is fundamental for the success of both habitat improvement and culturing activities. The mussels for bottom culture are traditionally collected by dredging seeds on natural mussel beds and relaying the seed to an area with high primary productivity. In several European countries, the exploitation of natural populations of blue mussels is restricted or locally banned due to declining populations and changes in management strategies. Alternative resources of seed have to be found if a constant European market supply is to be maintained, and the use of mussels in habitat improvement should have a large-scale potential. Alternative sources of mussel seed have included the development of methods for collection of seed from suspended cultures (Kamermans et al. 2002, 2009). This method eliminates the risks of spreading unintended organisms, since transfer of seeds from one area to another potentially involves the risk of spreading of harmful algae (Hégaret et al. 2008) or other harmful organisms.

Predation is the single most important source of mortality in mussels (Gosling 1992). However, mussels from suspended cultures are grown on ropes in the water column with minimum exposure to invertebrate predators (Gosling 2003). In contrast, bottom mussels are exposed to predators such as shore crabs and starfish. It is, therefore, reasonable to assume that mussels originating from bottom beds with predators are more robust to predation than mussels from suspended cultures. A study of blue mussels from the Baltic Sea and the North Sea found that blue mussels from the predator-free Baltic Sea still exhibited inducible predator defence but the response was weaker than that exhibited by blue mussels from the North Sea (Reimer and Harms-Ringdahl 2001). In order to evaluate the growth and survival potential of mussels collected on suspended cultures, knowledge of their predatory response is central.

Blue mussels use a variety of defence responses to reduce predation risk (Beadman et al. 2003). The mussel can induce both shell thickening (Reimer and Tedengren 1996; Leonard et al. 1999) and shell lip thickening (Smith and Jennings 2000) in response to predatory exposure. Furthermore, development of strong attachment of byssal threads to the substrate, or even to the predator, can occur when there is a high predation rate (Côté 1995; Dolmer 1998; Leonard et al. 1999; Farrell and Crowe 2007). Living in aggregations does also reduce predation (Bertness and Grosholz 1985; Okamura 1986; Reimer and Tedengren 1997) since it prolongs predator search time (Frandsen and Dolmer 2002). The shore crab is one of the most important predators of blue mussels (Davies et al. 1980) and may thus have a large influence of the success of mussels relayed on the sea bed.

In order to test whether mussels produced on suspended cultures can be used for on-growing on the sea bed, laboratory and field experiments were used to explore differences in predatory defence responses between suspended and bottom mussels. Byssal attachment strength, aggregation behaviour and differences in morphological traits were tested in laboratory, while growth and mortality were examined in field experiments.

Materials and methods

Laboratory experiments

Mussels used in the experiments were collected in the central part of Limfjorden, Denmark (N56 40 E8 45). Mussels used in the experiments were produced on suspended line systems (suspended mussels) and mussels collected from natural mussel beds (bottom mussels). Bottom mussels were marked to make it possible to distinguish them from suspended blue mussels. Shore crabs were collected in cage traps and held unfed in running seawater in the laboratory for 4 days to standardise level of hunger. Information on collection and sizes of mussels and shore crabs is given in Table 1.

Attachment strength, aggregation behaviour and predation of bottom and suspended mussels were tested using shore crabs placed inside cages with mussels. The cages were 48 cm in diameter and submerged. In each cage, a PVC plate divided into 36 squares of 5 × 5 cm was placed at the bottom of the cage, with one mussel placed in each square. Six cages contained 36 bottom blue mussels (separate bottom cages), six cages contained 36 suspended blue mussels (separate suspended cages) and six cages contained a mix of 18 bottom blue mussels and 18 suspended blue mussels (mixed cages). In three cages of each treatment, shore crabs were introduced after 48 h (exposed), and in the other three cages, no shore crabs were introduced (controls). After another 48 h, the crabs were removed, their sex was determined and carapace width was measured and the experimental parameters of the mussels measured (Table 1). Running sea water (salinity 30–32) supplied the cages with fresh sea water during the experiment. The experiment was conducted once in August 2007 and repeated again in September 2007. Identical protocols were used in both laboratory experiments. After the first experiment in August, the size of adductor muscle and shell density for the two types of mussels were determined.

Aggregation behaviour

After each experiment, the PVC plate with mussels attached was removed from the cage and the distribution of mussels photographed. Numbers of bottom mussels and suspended mussels on each plate were counted.

Table 1 Overview of number of days blue mussels were caught before experiment, mean length of mussels used and mean carapace width of shore crabs used in the experiments

Experiment	Origin of blue mussels (*M. edulis*) (bottom/suspended)	Number of days bottom/suspended blue mussels (*M. edulis*) were collected before experiment	Mean length (±SD) of bottom/suspended blue mussels (*M. edulis*) (mm)	Number of days shore crab (*C. maenas*) were collected before experiment	Mean carapace width (±SD) for shore crab (*C. maenas*) (mm) $N = 18$
August	Kaas Bredning/ Sallingsund	17/10	37.9 ± 1.8/34.9 ± 2.2	5	65.2 ± 3.4
September	Commercial fishery/ Sallingsund	2/20	37.0 ± 1.9/40.2 ± 2.4	5	62.6 ± 2.6

Distribution of mussels was quantified by recording the number of mussels in each of the 36 squares. Squares where umbo was located were recorded as a placement square. Coefficient of variance (CV) of density of mussels was used as measure for aggregation.

Attachment

Mussel attachment was measured with a spring scale attached to individual mussels with a clamp. Attachment was given as the maximum weight (g), and the byssal threads were held before the mussels detached. Attachment was quantified for 10 randomly chosen mussels from each cage. In cages with a mixture of bottom and suspended mussels, 10 of each mussel type were measured.

Predation

Predation rate (M_{pre}) was estimated as the number of eaten mussels per day and calculated as:

$$M_{\text{pre}} = \ln\left(\frac{N_{t0}}{N_{t1}}\right) \times t^{-1}$$

where N_{t0} is the number of mussels at start of the experiment, N_{t1} is the number of mussels at the end of the experiment and t is the duration of the experiment in days (Frandsen and Dolmer 2002). All factors were assumed to be independent of density, and rates were estimated to be constant throughout the experiments.

Adductor muscle

To investigate differences in the shell closure strength of bottom mussels and suspended mussels, the posterior adductor muscle diameter was quantified from mussels used in the August experiment. The posterior adductor muscle was exposed by cutting the muscle along the plane of the shell edge and measuring the diameter (mm) under a dissection microscope. To obtain the relative size of the posterior adductor muscle, mean muscle diameter (m) was related to the length (l) of the shell (Hancock 1965):

$$\text{Relative adductor muscle size} = \left(\frac{m}{l}\right)$$

Shell index

A subsample of 10 mussels was used to quantify shell density before the experiment. An index of shell density was calculated from shell ash weight and surfaces area. Ash weight (AW_{shell}) was determined via furnace ignition (4 h at 550°C) followed by weighing. The surface of the mussel shell can be described as a cylinder with an elliptical cross section (Reimer and Tedengren 1996). Surface area was calculated via:

$$A = l \times \sqrt{h^2 + w^2} \times \pi/2$$

where l was shell length, h was shell height and w was shell width given in mm. Index of shell density was given as:

$$\text{Shell density} = \frac{\text{AW}_{\text{shell}}}{A}$$

Statistical analysis

Data on attachment strength were tested in a three-way ANOVA as a function of mussel type, the presence of shore crab and experiment run. In *a posteriori* test, the factor Time was excluded from the analysis due to a non-significant effect and attachment was tested in a reduced ANOVA model with only mussel type and the presence of shore crabs. The tests were conducted on the mean attachment strength of bottom or suspended mussels in each cage, as the measurements in each cage may not be independent. Prior to the analysis, data were tested for normality distribution and variance homogeneity. Pairwise multiple comparison Tukey tests were used to establish significant differences between separate groups of data.

Coefficient of variation of aggregation behaviour (CV) was measured together with information on predation, mussel and time for 24 cases. The possible linear relationship was investigated using the linear model E(CV) = Mussel + Predation + Time + Predation:Time. The results of the model are given in Table 2. The table shows that the interaction effect is non-significant on a 95% confidence

level. Hence, this effect is then removed from the model and the reduced model E(CV) = Mussel + Predation + Time was analysed (Table 3). Results indicated that the effect of predation was just non-significant and the model was reduced to the final model $E(\mathrm{CV}) = \mathrm{mussel} + \mathrm{time}$. A Q–Q plot indicates that observations may be considered to be normally distributed.

The predation of mussel types in separate and mixed cages was tested by the use of one-way ANOVA.

Data on adductor muscle and shell density did not meet the assumptions of normal distribution and variance homogeneity. Data were divided into the different treatments and tested separately using non-parametric Student *t*-tests and Mann–Whitney rank sum tests.

Field experiment

A field experiment was conducted in Sallingsund (5–6 m of water depth) in the central part of Limfjorden (N56 42 E8 48) from August to November (105 days) 2007. In August, bottom and suspended mussels were relayed in 10 open frames of 2 × 2 m. In each frame, 25 kg of bottom or suspended mussels were relayed (6.25 kg m^{-2}).

Growth, density, mortality, biomass and condition index

Before the mussels were placed in the frames, length was measured from 60 randomly chosen mussels in each frame. Mean length (±SE) of mussels was 40.6 ± 0.6 mm for bottom mussels and 43.0 ± 0.8 mm for suspended mussels.

After the experiment, all mussels in three smaller subsample frames (0.25 m^2) within each of the 10 frames were collected. Mussels were counted, weighed and length measured, and shell length increment (mm) was estimated.

Since mortality due to predation and mortality due to other factors could not be distinguished in the field experiment, the rate of total mortality (M_{total}) was used as a measure of predation. M_{total} was calculated as:

$$M_{\mathrm{total}} = \ln\left(\frac{N_{t0}}{N_{t1}}\right) \times t^{-1}$$

where N_{t0} is the number of mussels at the start of the experiment, N_{t1} is the number of mussels at the end of the experiment and t is the duration of the experiment in days. All factors were assumed to be independent of density, and rates were estimated to be constant throughout the experiments.

As a measure of intraspecific competition, the condition index (CI) for mussels was estimated as:

$$\mathrm{CI} = \left(\frac{\mathrm{Biomass}_{\mathrm{end}}}{\mathrm{Length}_{\mathrm{end}^3}}\right) \times 1,000$$

where $\mathrm{Biomass}_{\mathrm{end}}$ is the wet weight (g) of mussels at the end of the experiment and $\mathrm{Length}_{\mathrm{end}}$ is the shell length (mm) of the mussels at the end of the experiment.

Statistical analysis

Differences in density and growth measured as shell length increment for bottom and suspended mussels were tested with Student t-test. A one-way ANOVA was used to test for differences in mortality between the two mussel types.

Table 2 Results of linear model on aggregation behaviour in bottom and suspended mussels given as coefficient of variance (CV)

Coefficients	Estimate	SE	*t*-value	*P*
Intercept	1.821	0.164	11.08	9.8e−10
Mussel	0.362	0.147	2.46	0.036
Predation	0.164	0.208	0.79	0.4405
Time	−0.635	0.208	−3.05	0.0065
Predation time	0.214	0.294	0.73	0.4763

The interaction effect is non-significant on a 95% confidence level. Hence, the effect was removed from the model

Table 3 Results of linear model on aggregation behaviour in bottom and suspended mussels given as coefficient of variance (CV)

Coefficients	Estimate	SE	*t*-value	*P*
Intercept	1.768	0.145	12.17	1.06e−10
Mussel	0.362	0.145	2.49	0.0217
Predation	0.217	0.145	1.86	0.0772
Time	−0.528	0.145	−3.63	0.0017

Predation was non-significant on a 95% confidence level. Hence, the effect was removed from the model

Results

Laboratory experiments

Aggregation behaviour

The experiments showed that suspended blue mussels form significantly more aggregated bed structure in cages than bottom mussels (Linear model $P = 0.03$) (Fig. 1; Table 4). The presence of predators did not affect aggregation ($P = 0.08$; Table 3).

Attachment

For both bottom and suspended mussels, the attachment strength was significantly stronger when predators were present compared to when no predators were present

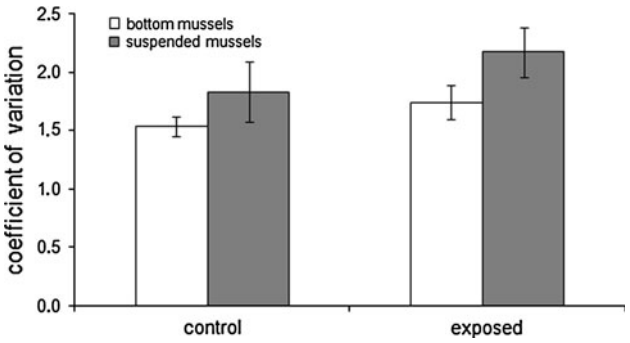

Fig. 1 Aggregation of mussels (*M. edulis*) measured as coefficient of variance (±SE) of density of bottom and suspended mussels, when exposed and not exposed to shore crab (*C. maenas*) ($n = 6$ replicates per treatment)

Table 4 Results of linear model on aggregation given as coefficient of variance (CV) with the parameters type of mussel (mussel) and experimental run (time)

Coefficients	Estimate	SE	*t*-value	*P*
Intercept	1.9032	0.1330	14.313	2.65e−12
Mussel	0.3616	0.1535	2.355	0.0283
Time	−0.5278	0.1535	−3.438	0.00247

(Fig. 2; Table 5). When exposed to predators, suspended mussels (624 ± 34 g) had a significantly stronger byssal attachment (±SE) than both bottom mussels separately (365 ± 24 g) (Tukey test $P = 0.002$) and bottom mussels from cages mixed with suspended mussels (407 ± 25 g) (Tukey test $P = 0.012$).

Predation

Mortality due to predation varied between 0.07 and 0.25 for bottom mussels, 0.07 and 0.41 for suspended mussels, 0.09 and 0.29 for bottom mussels in mixed cages and 0.16 and 0.41 for suspended mussels in mixed cages. Due to large variation in mortality rates within treatments, no differences were observed in predation of suspended

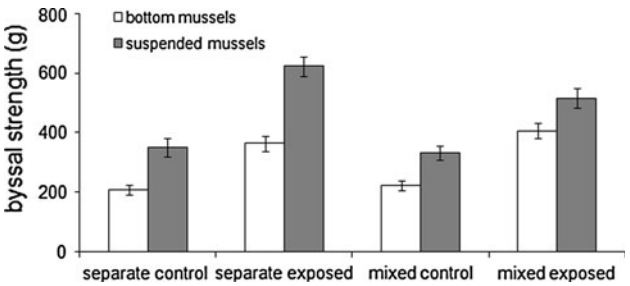

Fig. 2 Difference in strength of byssal treads (g) (±SE) for bottom and suspended mussels (*M. edulis*), in separate and mixed cages exposed and not exposed to shore crab (*C. maenas*) ($n = 6$ replicates per treatment)

Table 5 Results of two-way ANOVA on byssal attachment strength of bottom and suspended mussels

Comparison	*df*	SS	MS	*F*	*P*
Mussel	3	320475.227	106825.092	7.937	<0.001
Predation	1	463512.948	463512.948	34.436	<0.001
Mussel × predation	3	24008.114	8002.705	0.595	0.622
Residual	40	538398.737	13459.968		
Total	47	1346395.076	28646.704		

mussels or bottom mussels, either when mussels were kept separately or when mixed (One-way ANOVA $P = 0.134$) (Fig. 3; Table 6). Mortality rates in control cages varied between 0 and 0.01 for bottom mussels, 0 and 0.09 for suspended mussels, 0 and 0.06 for bottom mussels in mixed cages and 0 and 0.03 for suspended mussels in mixed cages. There were no significant differences in mortality between suspended mussels or bottom mussels, either when mussels were kept separately or when mixed (Kruskal–Wallis test $P = 0.636$) (Fig. 3; Table 6).

Adductor muscle

Comparison of adductor muscle size (±SD) between bottom and suspended mussels showed that bottom mussels (4.6 ± 0.1) had a significantly larger relative size of adductor muscle than suspended mussels (4.2 ± 0.1) (Mann–Whitney rank sum test $P < 0{,}001$). There were no

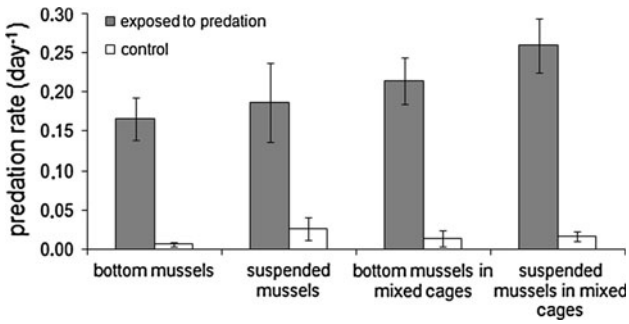

Fig. 3 Predation rate (±SE) in laboratory experiment on bottom and suspended mussels (*M. edulis*) in separate and mixed mussel cages, respectively. Predation rates are estimated as total mortality in each cage. Due to large variation in predation rates within the treatments, statistical test showed no significant differences between treatments

Table 6 Results of one-way ANOVA on differences in mortality due to predation on bottom and suspended mussels

Comparison	*df*	SS	MS	*F*	*P*
Mussel	3	0.0291	0.00971	1.214	0.330
Residual	20	0.160	0.00799		
Total	23	0.189			

significant differences between treatments exposed or not exposed to predators for either bottom mussels (exposed 4.7 ± 0.7, not exposed 4.5 ± 0.5; Student *t*-test $P = 0.173$) or suspended mussels (exposed 4.2 ± 0.3, not exposed 4.3 ± 0.5; Mann–Whitney rank sum test $P = 0.084$).

Shell density

Comparisons of relative shell density (mg mm^{-2} ± SD) between bottom mussels and suspended blue mussels show that bottom mussels (1.04 ± 0.22) had a significantly higher shell density than suspended mussels (0.84 ± 0.08) (Mann–Whitney rank sum test $P < 0.001$). There were no significant differences between treatments exposed or not exposed to predators for either bottom mussels (exposed 1.04 ± 0.25, not exposed 1.04 ± 0.21; Mann–Whitney rank sum test $P = 0.818$) or suspended mussels (exposed 0.87 ± 0.06, not exposed 0.81 ± 0.10; Student *t*-test $P = 0.209$).

Field experiment

Growth

Difference in mean lengths of bottom mussels and suspended mussels was significant both before (Student *t*-test $P = 0.016$) and after (Student *t*-test $P < 0.001$) the experiment (Fig. 4). Shell length increment (±SE) during the experiment was significantly higher for suspended mussels (5.2 ± 0.4 mm) compared to bottom mussels (3.5 ± 0.5 mm) (Student *t*-test $P = 0.026$).

Density, mortality and biomass

Mean density of mussels was reduced during the experiment. Initial mean density of suspended blue mussels was 803 mussels m^{-2}, which decreased to 259 mussels m^{-2} at the end of the experiment. In contrast, mean density for bottom blue mussels was 978 mussels m^{-2} at the start of the experiment and 147 mussels m^{-2} at the end of the experiment. Estimates of mortality rates (day^{-1}) showed that suspended mussels (0.01 ± 0.0) had a significantly lower mortality than bottom mussels (0.02 ± 0.0) (One-way ANOVA $P = 0.006$; Table 7). Despite the significant differences in mussel shell length before the experiment, there was no significant effect of initial shell length on mortality (One-way ANOVA $P = 0.151$).

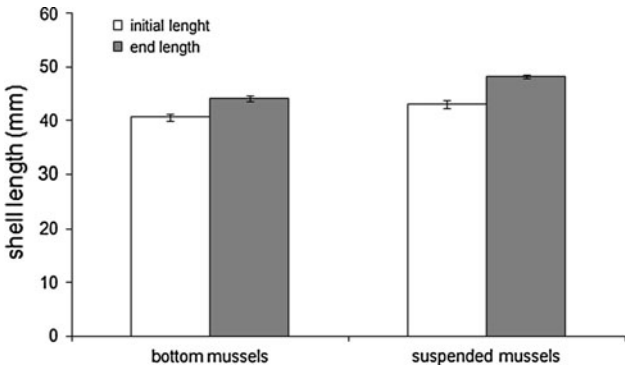

Fig. 4 Initial and end shell length (mm) (±SE) of mussels collected from natural mussel beds and suspended cultures

Table 7 Results of a one-way ANOVA on differences in mortality due to predation of bottom and suspended mussels

Comparison	*df*	SS	MS	*F*	*P*
Mussel	1	1.501	1.501	14.116	0.006
Residual	8	0.851	0.106		
Total	9	2.352			

At the start of the experiment, the biomass of both bottom and suspended mussels in the frames was 6.25 kg m^{-2}. When the experiment ended, the biomass (±SE) of suspended mussels was 2.8 ± 0.3 kg m^{-2} and the biomass of bottom mussels was 1.2 ± 0.2 kg m^{-2}, a reduction of 55 and 81% of the total relayed biomass, respectively. The biomass of suspended mussels was significantly higher than the biomass of bottom mussels after the experiment (Student *t*-test $P = <0.001$).

Condition index

After the experiment, there was no significant difference in condition index between bottom (0.10 ± 0.01) and suspended mussels (0.10 ± 0.00) (Student *t*-test $P = 0.249$).

Discussion

The present study found that mussels produced on suspended long lines and mussels collected from natural mussel beds responded differently in relation to predatory defence, growth and mortality. In the laboratory experiment, suspended mussels had a more active predator response in relation to aggregation behaviour and attachment compared to bottom mussels. Bottom mussels have been adapted to predators over time and showed a more passive predator response by their significantly thicker shell density and adductor muscle diameter. The field experiment showed that shell growth was significantly higher for suspended mussels compared to bottom mussels. Furthermore, mortality of bottom mussels was higher than the mortality of suspended mussels, and in total, biomass of suspended mussels was larger when contrasted to bottom mussels.

Formation of mussel beds by byssal attachment and aggregation may include a trade-off between advantages in relation to reduction in predation and a cost of increased intraspecific competition for food depending on where in the bed structure the mussel is attached (Okamura 1986). In the centre of a mussel bed, individuals reduce the risk of predation but intraspecific competition for food is likely to be greatest (Bertness and Grosholz 1985). In a field experiment, Frandsen and Dolmer (2002) observed that mussels had an increased survival in complex substrates, but a lower growth rate due to a reduced transport of food particles and intraspecific competition. Intraspecific competition does not occur to the same extend on the edge of a mussel bed, where mussels are more exposed to predators (Okamura 1986; Auster 1988). However, in our study, there was no significant difference in condition index between bottom and suspended mussels, indicating that there was no intraspecific competition between mussels during the experimental period.

Aggregation behaviour

Comparison of bottom and suspended mussels showed that suspended mussels formed significantly denser bed structure than bottom mussels. Living in aggregations can reduce the rate of predation on individuals (Bertness and Grosholz 1985; Okamura 1986; Côté and Jelnikar 1999). Okamura (1986) found that blue mussels in the centre of a mussel bed suffer lower predation than mussels on the edge of the bed. The tendency for blue mussels to clump is enhanced under the risk of predation (Côté and Jelnikar 1999). The same pattern is known from for example zebra mussel (*Dreissena polymorpha*). In the presence of predators, attachment strength and the tendency to form aggregations increased among small- and medium-sized zebra mussels (Kobak and Kakereko 2009).

Attachment

Both bottom and suspended blue mussels increased byssal attachment when exposed to predators. This response to predators was also reported by Leonard et al. (1999), where both mussels from field populations and from cultures had significant higher attachment strength in a habitat with a high density of predators compared to a habitat with a low predator density. In the present experiment, suspended mussels showed significantly stronger attachment and established a more dense bed structure than bottom mussels. Attachment strength was significantly higher for suspended mussels than for both bottom mussels either in separated or in mixed populations. The opposite was found in Kirk et al. (2007), where bottom mussels from intertidal beds in general exhibited stronger byssal attachment than suspended mussels. The experiments by Kirk et al. (2007) were conducted on mussels collected from intertidal habitats and long line mussel farms. Mussels from the intertidal may be exposed to wave surge and therefore may form more byssal threads for attachment than the bottom mussels used in the present experiment.

Byssal treads are not produced continuously but respond to e.g. wave activity (Witman and Suchanek 1984; Young 1985) and predation (Côté 1995; Dolmer 1998; Leonard et al. 1999). Côté (1995) observed that byssal treads become shorter and stronger on mussels exposed to predators. The greater byssal attachment strength of suspended blue mussels in the present study may therefore indicate that suspended blue mussels have developed a strong byssal attachment because they are hanging from ropes exposed to waves in contrast to bottom mussels (Kirk et al. 2007) or suspended mussels that are compensating for a lack of a thick shell as a predatory defence.

Adductor muscle

Bottom mussels had a significantly larger adductor muscle relative to shell length compared to suspended mussels. Due to the relatively short time span of our experiment and the uncertainties of the measurements, it would not be possible to detect differences in relative adductor muscles size between mussels exposed and not exposed to predation. This was confirmed since there were no significant differences between either bottom or suspended mussels exposed and not exposed to predation. Differences are assumed to be a result of the origin of the two types of mussels. Field studies from Limfjorden have shown that blue mussels on smooth substrate develop a significantly larger adductor muscle than mussels on a more complex substrate due to higher predator exposure (Frandsen and Dolmer 2002). The relative size of the adductor muscle in our laboratory experiment is comparable to the adductor muscle size from field experiments where mussels were laid on a smooth substrate and exposed to predators (Frandsen and Dolmer 2002). Reimer and Harms-Ringdahl (2001) showed that mussels can adjust their predatory defences depending on the type of predator and their prey handling. Larger adductor muscles are developed when mussels are exposed to starfish (Reimer and Tedengren 1996). Contrary, thicker shells are developed when mussels are exposed to shore crabs (Reimer and Harms-Ringdahl 2001).

Shell density

Lack of or reduced predator exposure of suspended mussel cultures may result in a reduced development of inducible

shell density, compared to bottom mussels exposed to predators (Kirk et al. 2007). This result was also evident in the present study. The mean shell density (±SE) for bottom mussels in our experiment was 1.03 ± 0.28 mg mm^{-2} which is comparable to the values given by Reimer and Tedengren (1996), where blue mussels exposed to predators on a wave-exposed rocky shore had a shell thickness of 99 mg cm^{-2}. Suspended mussels in our experiment also exhibited thinner shell relative to length, which is comparable to results from controls in the study by Reimer and Tedengren (1996) and Kirk et al. (2007). Development of thicker shells was observed in mussels exposed to predation by crabs or cues from crab predators (Leonard et al. 1999; Reimer and Harms-Ringdahl 2001). The thinner shells in suspended mussels are also a result of faster growth rates when the mussels are suspended in the water column (Garen et al. 2004).

Suspended mussels are reported to have lower shell thickness and weaker byssal attachment due to differences in environmental conditions and predation regimes (Kirk et al. 2007). Because of the relatively short time span of our experiment, it would not have been possible to detect any change in shell density as a result of predator exposure. This was also confirmed by the non-significant difference between bottom and suspended mussels exposed and not exposed to predation. The significant difference between suspended and bottom mussel is therefore assumed to be due to the differences in origin as shown in Kirk et al. (2007).

Mortality

In the present field experiment, the mortality rates were at same level as previously estimated rates of mortality due to predation by shore crab on a smooth substrate in Limfjorden (Frandsen and Dolmer 2002). The increased aggregation by suspended mussels observed in current study increases the substrate complexity and may therefore explain the difference in predation or mortality. In the field experiment, the mortality rate of bottom mussels was higher than the rate for suspended mussels, whereas no differences in mortality were seen in the laboratory experiment. Measured predation rates may be influenced by different initial sizes of suspended and bottom mussels (Reimer and Tedengren 1996; Kirk et al. 2007). However, statistical test stated that there were no significant effects of shell length on predation. In the laboratory experiment, mussels were exposed to predation in an experimental set-up without a natural bed structure, as was the case in the field experiments. Therefore, predation rates from laboratory experiments can only be used to compare the two types of mussels and should not be used as an exact measure of mortality due to predation.

Active versus passive predator response

Analysis of byssal thread attachment and aggregation showed that suspended mussels develop a more predation-resistant bed structure than bottom mussels. In contrast, bottom mussels had a thicker shell density and a larger adductor muscle. The predation rate of suspended mussels in field experiments was significantly lower for suspended mussels compared to bottom mussels.

The field experiment differs from the laboratory experiment in not controlling the density and species composition of the naturally present predators. An unknown number, species and size composition and activity of shore crabs (*Carsinus maenas*) and starfish (*Asterias rubens*) predated on mussels. Defence responses against the different predatory species can differ since the presence of starfish often facilitates a larger adductor muscle, and shore crabs are known to increase mussel attachment (Côté 1995; Leonard et al. 1999). Attempts to estimate the density of these two predators failed, and therefore, it is not possible to distinguish the effect of the natural predators. In a controlled cage study by Kamermans et al. (2009), consumption of mussel seed by starfish was much lower than by crabs, which is why we assume that the main predation in the field experiment was from crabs.

Selection of prey by a predator can be influenced by the size and the morphology of the prey items (Kirk et al. 2007). Parameters as growth rate, byssal thread strength and shell thickness of mussels can affect both predation attempts and success (Norberg and Tedengren 1995; Reimer and Tedengren 1996). In a study by Reimer and Harms-Ringdahl (2001), where blue mussels from the North Sea and the Baltic Sea were compared in terms of predator inducible changes, it was concluded that inducible plasticity was still present in blue mussels from the Baltic Sea even though they were not naturally exposed to predatory crabs and starfish. Correspondingly, suspended mussels in our experiment still show predatory defence mechanisms despite their origin on predator-free suspended long lines.

Use of suspended blue mussels in relaying of mussels

Both laboratory and field experiments demonstrated that blue mussels produced on suspended systems represent a viable alternative to bottom mussels both in relation to bottom culturing activities and for relay in relation to habitat improvement. It should be noted that mussels used in present study were generally (about 20 mm) larger than the typical size of mussels used for culturing and habitat improvement activities. However, since the predatory responses we have reported in our experiments also have been reported in smaller mussels (20–45 mm Norberg and Tedengren 1995; 16–33 mm Côté and Jelnikar 1999; 15–30 mm Reimer and

Harms-Ringdahl 2001), we expect that our results are also valid for mussels in the size range typically used for relay and transplantation. Survival and growth in the field experiment was higher for suspended mussels due to a more adaptive predator defence response, which included higher byssal production and higher aggregation activity compared to bottom mussels. This conclusion is supported by Kamermans et al. (2009) who tested the applicability of mussels from seed collectors as a seed source in bottom culture production in relation to predation loss caused by crabs and starfish. The use of suspended mussels as seed for bottom cultures and habitat improvement requires a full-scale test comparing the two types of mussel over time.

Acknowledgments Thanks to statistician Peter Lewy, National Institute of Aquatic Resources, for valuable help with statistics, to Carsten Fomsgaard and Michael Gramcow, Danish Shellfish Centre and Benni Winding Hansen, Roskilde University, Denmark, for comments on an earlier version of the manuscript. Also thanks to the anonymous reviewers for valuable comments. The experiments described in this paper were part of a project on integration and optimising of production methods for blue mussel production. The project was financially supported by the EU fishery developing program and The Directorate for Fisheries, The Ministry of Food, Agriculture and Fisheries.

References

Auster PJ (1988) Response of mega faunal predators to synchronous settlement of sessile prey. J Shellfish Res 7:108–109

Beadman H, Caldow RWG, Kaiser MJ, Willows RI (2003) How to toughen up your mussels: using mussel shell morphological plasticity to reduce predation losses. Mar Biol 142:487–494

Bertness MD, Grosholz E (1985) Population dynamics of the ribbed mussel, *Geukensia demissa*: the costs and benefits of an aggregated distribution. Oecologia 67:192–204

Coen LD, Luckenbach MW (2000) Developing success criteria and goals for evaluating oyster reef restoration: ecology function or resource exploitation. Ecol Eng 15:323–343

Coen LD, Brumbaugh RD, Bushek D, Grizzle R, Luckenbach MW, Posey MH, Powers SP, Tolly SG (2007) Ecosystem services related to oyster restoration. Mar Ecol Prog Ser 341:303–307

Côté IM (1995) Effects of predatory crab effluent on byssus production in mussels. J Exp Mar Biol Ecol 188:233–241

Côté IM, Jelnikar E (1999) Predator-induced clumping behaviour in mussels (*Mytilus edulis* Linnaeus). J Exp Mar Biol Ecol 235:201–211

Davies G, Dare PJ, Edwards DB (1980) Fenced enclosures for the protection of seed mussels (*Mytilus edulis* L.) from predation by shore crabs (*Carcinus maenas* L.). In: Soemodihardjo S, Nontji A, Djamali A (eds) Fish Res Tech Rep Dir Fish Res (G.B.), (No. 56), MAFF, Lowestoft, pp 18

Dolmer P (1998) The interactions between bed structure of *Mytilus edulis* L. and the predator *Asterias rubens* L. J Exp Mar Biol Ecol 228:137–150

Farrell ED, Crowe TP (2007) The use of byssus threads by *Mytilus edulis* as an active defence against *Nucella lapillus*. J Mar Biol Assoc UK 87:559–564

Frandsen R, Dolmer P (2002) Effects of substrate type on growth and mortality of blue mussels (*Mytilus edulis*) exposed to the predator *Carcinus maenas*. Mar Biol 141:253–262

Garen P, Robert S, Bougrier S (2004) Comparison of growth of mussel, *Mytilus edulis*, on longline, pole and bottom culture sites in the Pertuis Breton, France. Aquaculture 232:511–524

Gosling E (ed) (1992) The mussel *Mytilus*: ecology, physiology, genetics and culture. Elsevier, Amsterdam, p 128

Gosling E (ed) (2003) Bivalve molluscs: biology, ecology and culture. Blackwell, Oxford, pp 296–302

Hancock DA (1965) Adductor muscle size in Danish and British mussels and its relation to starfish predation. Ophelia 2:253–267

Hégaret H, Shymway SE, Wikfors GH, Pate S, Burkholder JM (2008) Potential transport of harmful algae via relocation of bivalve molluscs. Mar Ecol Prog Ser 361:169–179

Kamermans P, Brummelhuis E, Smaal A (2002) Use of spat collectors to enhance supply of seed for bottom culture of blue mussels (*Mytilus edulis*) in the Netherlands. World Aquac 33:12–15

Kamermans P, Blankendaal M, Perdon J (2009) Predation of shore crabs (*Carcinus maenas* (L.)) and starfish (*Asterias rubens* L.) on blue mussels (*Mytilus edulis* L.) seed from wild source and spat collectors. Aquaculture 290:256–262

Kirk M, Esler D, Boyd WS (2007) Morphology and density of mussels on natural and aquaculture structure habitats: implications for sea duck predators. Mar Ecol Prog Ser 346:179–187

Kobak J, Kakereko T (2009) Attachment strength, aggregation and movement of the zebra mussel (Dreissena polymorpha, Bivalvia) in the presence of potential predators. Fund Appl Limnol 174:193–204

Leonard DL (1993) Turning the tide on water quality and declining shellfish resources. World Aquac 24:456–464

Leonard GH, Bertness MD, Yund PO (1999) Crab predation, waterborne cues, and inducible defences in the blue mussel, *Mytilus edulis*. Ecology 80:1–14

McDermott S, Burdick D, Grizzle R, Green J (2008) Restoring ecological functions and increasing community awareness of an urban tidal pond using blue mussels. Ecol Restor 26:254–262

Norberg J, Tedengren M (1995) Attack behaviour and predatory success of *Asterias rubens* L. related to differences in size and morphology of the mussel *Mytilus edulis* L. J Exp Mar Biol Ecol 186:207–220

Okamura B (1986) Group living and the effects of spatial position in aggregations of K. Oecologia 69:341–347

Peterson CH, Grabowski JH, Powers SP (2003) Estimated enhancement of fish production resulting from restoring oyster reef habitat: quantitative valuation. Mar Ecol Prog Ser 264:249–264

Reimer O, Harms-Ringdahl S (2001) Predator-inducible changes in blue mussels from the predator-free Baltic Sea. Mar Biol 139:959–965

Reimer O, Tedengren M (1996) Phenotypical improvements of morphological defences in the mussel *Mytilus edulis* induced by exposure to the predator *Asterias rubens*. Oikos 75:383–390

Reimer O, Tedengren M (1997) Predator-induced changes in byssal attachment, aggregation and migration in the blue mussel, *Mytilus edulis*. Mar Freshw Behav Physiol 30:251–266

Smaal AC (2002) European mussel cultivation along the Atlantic coast: production status, problems and perspectives. Hydrobiologia 484:89–98

Smith LD, Jennings JA (2000) Induced defensive responses by the bivalve *Mytilus edulis* to predators with different attack modes. Mar Biol 136:461–469

Szatybelko M, Dubrawski R (1999) The biotechnical possibility of removing pollution from significantly degraded marine environment. Bull Sea Fish Inst Gdynia 146:57–72

Witman JD, Suchanek TH (1984) Mussels in flow: drag and dislodgement by epizoans. Mar Ecol Prog Ser 16:259–268

Young GA (1985) Byssus-thread formations by the mussel *Mytilus edulis*: effects of environmental factors. Mar Ecol Prog Ser 24:261–271