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Predator-induced clumping behaviour in mussels (*Mytilus edulis* Linnaeus)

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Abstract

This study examined the aggregation behaviour of blue mussels, *Mytilus edulis*, under threat of predation by European lobster, *Homarus gammarus* Linnaeus. Risk of predation was simulated using water in which a hungry lobster had been for 24 h, and mussels were initially set in experimental containers either near (0.5 body length apart) or far (1.5 body length apart) from each other. We found that mussels exposed to lobster effluent formed more clumps, more rapidly than mussels in control conditions. The initial distance separating the mussels had no effect on their aggregation tendencies. Overall, a greater proportion of mussels were aggregated in the lobster treatment at the end of the 22-h experiment. This was not simply the result of increased locomotion. Although mussels in lobster effluent did exhibit greater crawling speed in the first hour of the experiment, mussels initially set far apart also showed enhanced locomotion in both lobster and control treatments. Yet, of the mussels initially far from each other, those in lobster effluent formed clumps on average 5 h sooner than mussels in control water. This suggests that chemotaxis may be involved. Although mussels do aggregate under risk of predation in the laboratory, it is not yet known whether predation plays a significant role in the formation of natural mussel beds.

Keywords: Group living; *Homarus gammarus*; Predator–prey interactions; Protective behaviour

1. Introduction

Predators can impose important selection pressures on their prey. As a result, prey species have evolved an impressive array of morphological and behavioural defenses against predators. In molluscs, morphological deterrents range from shell thickening and sculpturing (Vermeij, 1976; Bertness and Cunningham, 1981; Boulding, 1984; Johannes-

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son, 1986; Appleton and Palmer, 1988; Harper and Skelton, 1993) to a wide variety of chemical defenses (e.g., McClintock et al., 1994; Day et al., 1995). Behavioural defences among mobile gastropods include many avoidance, escape and sometimes aggressive behaviours which are well developed and often predator-specific, (e.g., Pratt, 1974; Phillips, 1975; Geller, 1982; Alexander and Covich, 1991; Marko and Palmer, 1991; Dix and Hamilton, 1993; Legault and Himmelman, 1993). In the generally less mobile bivalves, anti-predatory behavioural tactics are more limited and include burying deeper (Blundon and Kennedy, 1982; Haddon et al., 1987; Lin, 1991), secreting more and thicker attachment threads (Côté, 1995; Reimer and Tedengren, 1997), and living in groups (Bertness and Grosholz, 1985; Okamura, 1986; Haddon et al., 1987; Lin, 1991; Reimer and Tedengren, 1997).

Living in close proximity to conspecifics can reduce the rate of predation on individuals. It has been shown, for example, that blue mussels (*Mytilus edulis*) in the centre of a bed suffer lower predation than mussels at the edge of the bed (Okamura, 1986). Similarly, mortality due to predation and to winter ice scour is reduced in dense beds of ribbed mussels (*Geukensia demissa*) (Bertness and Grosholz, 1985). These benefits are, however, accompanied by significant costs. Okamura (1986) found that mussels at the centre of beds, where predation rates were lower, grew more slowly and had a lower reproductive output. Reduced growth and reproduction at high densities has also been demonstrated in other species of sessile marine invertebrates (bivalves: Harger, 1972; Bertness and Grosholz, 1985; Kamermans et al., 1992; Svane and Ompi, 1993; barnacles: Wethey, 1983; bryozoans: Buss, 1981; Gappa, 1989; ascidians: Yund and McCartney, 1994). The net benefits of group living in bivalves are thus not clear. The gregariousness of sessile bivalves may also be ecologically enforced through limitation of suitable habitat, in which case group-living individuals may entail a net cost.

The most convincing evidence that predation, rather than space limitation, causes clumped prey distribution is provided by experimental studies which show active group formation in response to variation in risk of predation. Studies of clumping behaviour of sessile bivalves, such as mussels, have been understandably rare (but see Reimer and Tedengren, 1997), since it is often assumed that bivalves display little post-settlement movement. Yet, there is evidence that mussels, even as adults, do move (*Mytilus californianus*: Paine and Levin, 1981; *Mytilus edulis*: Harger, 1968; McGrorty and Goss-Custard, 1995; *Mytilus viridis*: Tan, 1975; *Hormomya mutabilis*: Senawong, 1970; *Limnoperna fortunei*: Urya et al., 1996). They may therefore be suitable candidates to investigate experimentally the adaptive basis of group living in relatively sessile bivalves.

In this paper, we offer experimental evidence for active clumping of blue mussels in response to threat of predation by European lobsters (*Homarus gammarus*). Lobsters co-occur with blue mussels in the wild (Hayward and Ryland, 1990) and, although little is known of the natural diet of *H. pagurus*, its congener *H. americanus* does feed, and may specialise, on *M. edulis* (Elner and Campbell, 1987; Moody and Steneck, 1993). European lobsters also take blue mussels readily in the laboratory (personal observations). Although crabs, starfish and boring bivalves may be the more common predators of mussels, we chose lobsters in part to investigate the sensitivity of mussels' responses

to uncommon predators. We simulated risk of predation by exposing mussels to lobster-conditioned water. This technique has been shown to cause anti-predatory responses in a variety of molluscs, including mussels (Geller, 1982; Appleton and Palmer, 1988; Marko and Palmer, 1991; Dix and Hamilton, 1993; Côté, 1995; Reimer and Tedengren, 1997). We then monitored mussel movement and clumping behaviour to test whether clumping was enhanced under risk of predation.

2. Materials and methods

2.1. Mussel collection

Two days before the start of the experiment, mussels were collected from a natural mussel bed in the middle of the intertidal zone near Stiffkey Marsh on the North Norfolk coast, UK. Unlike the typical extensive and dense beds found on rocky substrata, the Stiffkey mussel bed consists mainly of small clumps of mussels (range: 5–30 mussels; I.M.C., unpublished data) embedded in a mixture of gravel and sand. Mussels ranging in length from 16–33 mm were removed carefully from their clumps by cutting their byssus threads with scissors, brought into the laboratory, and placed in a 350-l glass aquarium with 5 cm of coarse gravel on the bottom and filled with recirculating natural seawater. The seawater was kept at constant ambient temperature (12°C) and salinity (32.0‰) throughout the experiment. Mussels filter-fed on suspended particles available in the seawater. This was supplemented by frozen phytoplankton (Dutch Select Food Co.) 24 h before the experiment. The light regime in the experimental room was 16 L:8 D.

2.2. Lobster effluent preparation

To prepare the lobster and control effluents, two 110-l glass stock tanks (60 cm × 45 cm × 45 cm) were removed from the closed circulation system, emptied and washed thoroughly with hot water. The bottom of each tank was then covered with 5 cm of clean, coarse gravel (5–10 mm diameter). Forty-eight hours before the start of the experiment, both tanks were filled with unused seawater pumped directly from a large storage tank containing natural seawater collected from Lowestoft (UK) (salinity: 32‰). This water had not yet circulated through the closed system and could therefore not have acquired the odour or taste of the various animals held in the aquarium. Each tank was provided with its own air supply.

One European lobster *Homarus gammarus* (carapace length: 96.3 mm) was placed in one of the stock tanks to create the predator effluent. No predator was added to the second stock tank which served as a control effluent.

2.3. Experimental design

Mussel length was measured to the nearest mm with callipers. Mussels were then divided into 60 groups of seven equal-sized (±2 mm) individuals to minimise any

size-related variation in locomotion within group. Mean mussel size per group ranged from 16 to 33 mm. Mussels in each group were individually numbered using white correction fluid. The 60 groups were then assigned to one of four experimental treatments, such that the overall mean length of mussels in all treatments was similar ($F_{3,56} = 0.081,\ p = 0.97$). The four experimental treatments were as follows: (1) mussels separated by 0.5 shell length in lobster effluent, (2) mussels separated by 0.5 shell length in control seawater, (3) mussels separated by 1.5 shell length in lobster effluent, (4) mussels separated by 1.5 shell length in control seawater.

Thirty glass (Pyrex) crystallising dishes varying from 9 to 19 cm in diameter were filled to a depth of 3 cm with water from the predator effluent tank (treatments 1 and 3), while a similar number were filled to a depth of 3 cm with water from the control tank (treatments 2 and 4). Each dish received a group of mussels placed equidistant from each other in a hexagonal pattern with one mussel in the centre of the hexagon. In half of the mussel groups placed in each effluent (i.e., 15 groups in each case), mussels were positioned 0.5 shell length from each other (hereafter referred to as the near treatment). In the remaining half of the groups, mussels were separated by 1.5 shell length (i.e., the far treatment). Inter-mussel distance thus varied between groups, depending on mean mussel length. To minimise variation in the distance between mussels and the walls of the container, we adjusted dish diameter in relation to mussel length, smaller mussels being housed in smaller dishes. All treatments were carried out concurrently, and each individual mussel was subjected to a single treatment.

The position of individual mussels in each dish was recorded 1, 3, 7, 16 and 22 h after the start of the experiment. At every reading each dish was covered with a glass plate upon which a transparent acetate sheet was taped firmly into place. Reference points were drawn onto the acetates, and these could be aligned with similar reference points made on the bottom of each dish, allowing for a very precise positioning of the acetates. The point of insertion of byssus threads between the valves was chosen to represent mussel position, and this was represented on the acetates as a single point for each mussel at every reading. Clump formation was recorded on the acetates. Clumps were defined as two or more mussels attached to each other with byssus threads. The identity of individuals forming a clump was also noted.

After 22 h, when the glass plates were removed, all the mussels and clumps were examined. Any mussel that had either not moved or moved without secreting any byssus threads was marked; these were ignored in the analysis. The straight-line distances moved by each mussel were measured on the acetates using a ruler.

2.4. Analysis

Two-way analyses of variance (ANOVAs) were used to detect the influence of the two factors: (a) the effect of lobster effluent (presence of predator waterborne chemicals) and (b) the effect of the original distance separating individual mussels. For each time period, the distance travelled by mussels, number of clumps formed and number of mussel per clump were averaged for each dish. Each container thus contributed a single datum to any analysis. Proportions were angularly transformed prior to analysis.

3. Results

Nearly all of the mussels (603/640 or 94%) showed some movement during the experiment. The 37 mussels that did not were excluded from the analysis. Nineteen immobile mussels were found in lobster effluent and 18 in control water.

The total distance moved by individual mussels over the 22-h period varied from 11 to 97 mm. Despite the limited mussel size range, there was a significant negative relationship between mussel length and average total distance moved per mussel in each dish ($r^2 = 0.24$, $F_{1,58} = 18.00$, $p < 0.001$). In addition, the distance travelled per hour decreased significantly over the duration of the experiment ($r = -0.99$, $p = 0.0005$, $n = 5$). Mussels were therefore most active during the first hour of the experiment. Mussels also tended to travel towards each other: in 36 of the 60 dishes, the average nearest-neighbour distance between mussels was smaller at the end than at the start of the experiment (binomial test, $Z = 1.87$, $0.05 < p < 0.10$).

A total of 66 clumps were observed at the end of the experiment, and the number of mussels per clump ranged from two to five (overall mean = 2.5±0.77 S.D.). Significantly more clumps formed in water containing lobster effluent than in control water (Fig. 1; two-way ANOVA, $F_{1,56} = 12.84$, $p = 0.0007$), but the number of mussels per clump did not differ in lobster and control water (two-way ANOVA, $F_{1,56} = 1.60$, $p = 0.21$). Overall, a significantly greater proportion of mussels were found clumped in lobster effluent at the end of the experiment (Fig. 2; two-way ANOVA, $F_{1,56} = 10.46$, $p = 0.002$).

The initial distance separating mussels had no effect on either the number of clumps

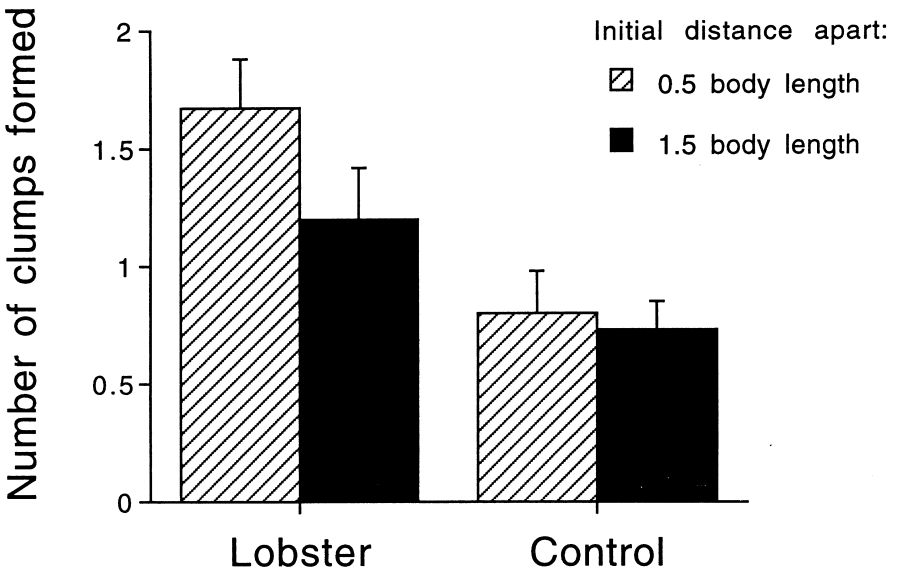

Fig. 1. The number of clumps formed after 22 h by mussels held in lobster effluent and in control water. Means are shown + 1 S.E. $n = 15$ for each of the four groups.

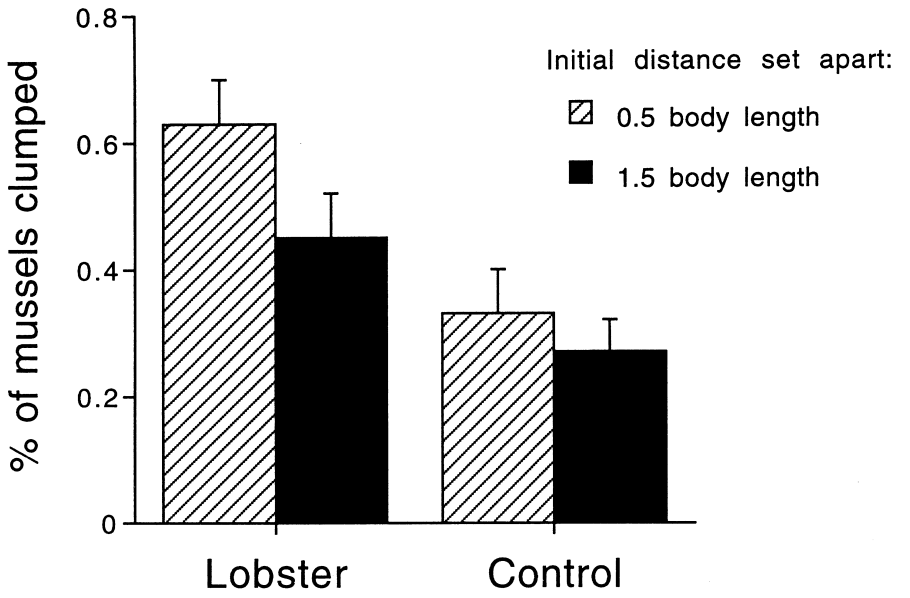

Fig. 2. The proportion of mussels found in clumps after 22 h for mussels held in lobster effluent and in control water. Untransformed means are shown + 1 S.E. $n = 15$ for each of the four groups.

produced (two-way ANOVA, $F_{1,56} = 2.06$, $p = 0.16$), the number of mussels per clump (two-way ANOVA, $F_{1,56} = 0.75$, $p = 0.39$), or on the proportion of mussels found in clumps (two-way ANOVA, $F_{1,56} = 2.27$, $p = 0.14$). Furthermore, there was no significant interaction between water type (lobster or control) and the initial distance separating mussels in explaining variation in number of clumps (two-way ANOVA, $F_{1,56} = 1.16$, $p = 0.29$), number of mussels per clump (two-way ANOVA, $F_{1,56} = 0.32$, $p = 0.58$), or proportion of mussels in clumps (two-way ANOVA, $F_{1,56} = 1.07$, $p = 0.31$).

The speed of first clump formation was significantly faster in lobster effluent than in control water (Fig. 3; two-way ANOVA, $F_{1,56} = 12.08$, $p = 0.0012$). Mussels also formed clumps more quickly when initially set closer together (two-way ANOVA, $F_{1,56} = 7.64$, $p = 0.008$). Most mussels in lobster effluent, particularly those set close together, formed clumps in the first 3 h of the experiment, while mussels in control water were found in groups after 5 h or more.

Finally, locomotory speed in the first hour of the experiment was significantly greater for mussels in lobster effluent (Fig. 4; two-way ANOVA, $F_{1,56} = 12.35$, $p = 0.0009$). Speed in the first hour was also greater for mussels that were initially set far apart (Fig. 4; two-way ANOVA, $F_{1,56} = 7.65$, $p = 0.008$). Post hoc tests revealed that these differences stemmed from the lower speed observed for control mussels in the near treatment (Fig. 4; control vs. lobster effluent in near treatment: $t = 5.07$, $p = 0.0001$, $n = 30$). There was no significant difference in speed among mussels held in control and lobster effluent in the far treatment (Fig. 4; $t = 0.65$, $p = 0.52$, $n = 30$), and there were

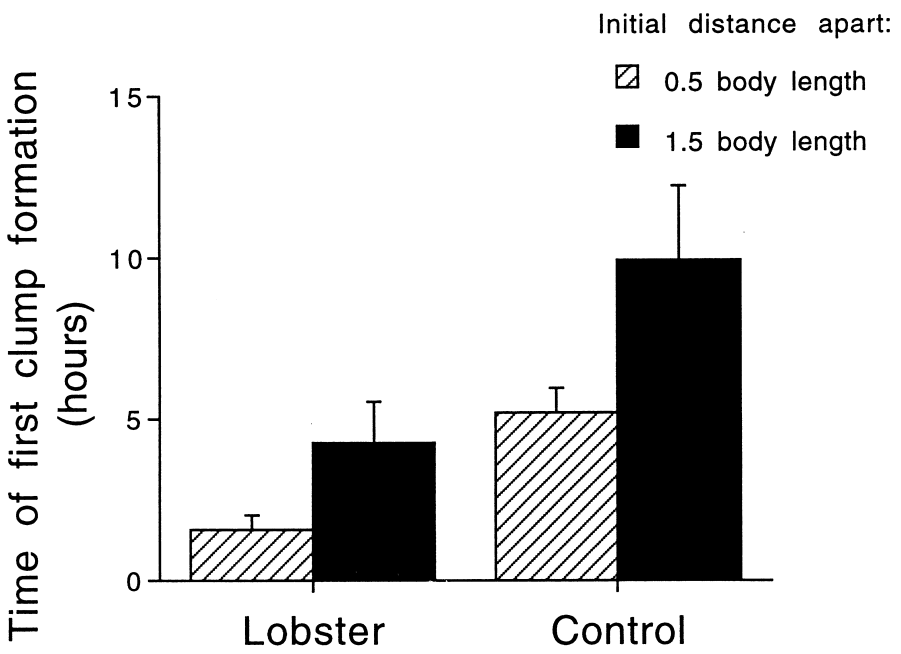

Fig. 3. The speed of first clump formation, expressed as hours elapsed since the onset of the experiment, by mussels held in lobster effluent and in control water. Means are shown + 1 S.E. $n = 15$ for each of the four groups.

no speed differences between mussels in either treatment after the first hour of the experiment.

4. Discussion

Mussels tend to aggregate under natural conditions. Upon settlement, *Mytilus* larvae crawls and forms clumps that may be permanent unless the larvae are disturbed (Bayne, 1964; Caceres-Martinez et al., 1994). Solitary individuals, which may have become dislodged from a bed, also tend to move more than aggregated ones (Tan, 1975). Our results show that the tendency for blue mussels to clump is enhanced under risk of predation. In the simulated presence of a predatory lobster, mussels formed more clumps more rapidly. Mussels also travelled at a greater speed, at least during the first hour of the experiment, and a greater proportion of mussels formed clumps under threat of predation than under control conditions.

The general mechanism of clump formation in bivalves remains unclear. There is evidence from other mussel species that aggregations may result from the random movement of individual mussels. Urya et al. (1996), for example, showed that the freshwater mussel *Limnoperna fortunei* tended to aggregate into small clumps, and the pattern of clumping largely mirrored the results of a computer simulation in which all

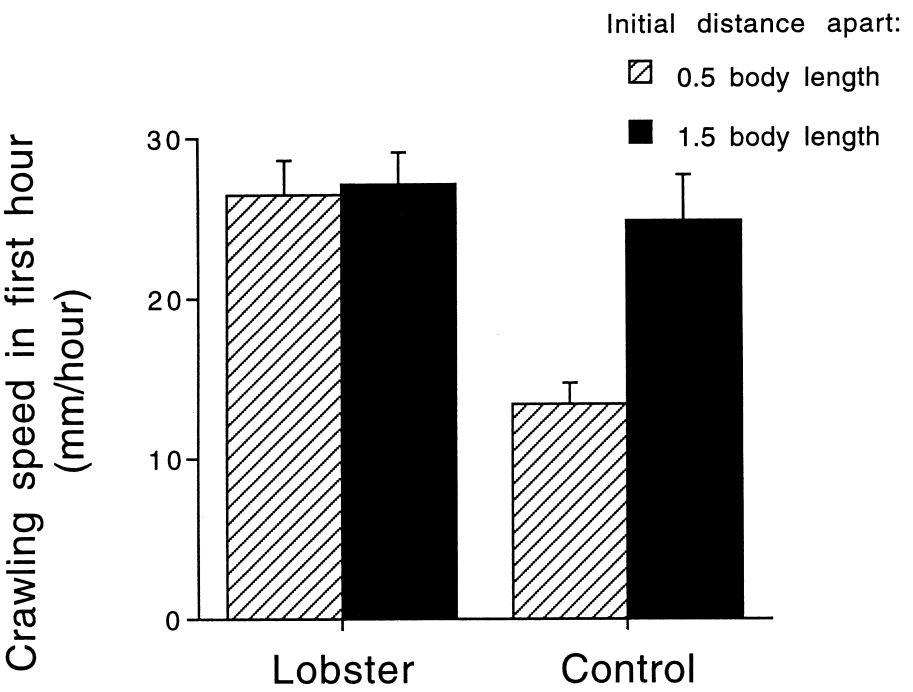

Fig. 4. The crawling speed of mussels held in lobster effluent and in control water in the first hour of the experiment. Means are shown + 1 S.E. $n = 15$ for each of the four groups.

mussels moved with random walks. Aggregations of *Hormomya mutabilis* also appear to be the result of random movements (Senawong, 1970). An alternative mechanism which has been documented in other, more mobile bivalves is clumping through chemical attraction to conspecifics. Morton (1960) suggested chemotaxis as a potential cause for reproductive aggregations in *Lasaea rubra*. Chemical means were also invoked in the intraspecific interactions of the scallop *Pedum spondyloideum* (Kleeman, 1990).

Although chemical attraction has never previously been suggested for *Mytilus edulis*, our results are consistent with this possibility. Mussels under threat of predation exhibited enhanced locomotion, which may have led to a greater chance of encountering other individuals. Indeed, clumps were formed more rapidly by mussels in lobster effluent. However, in both lobster and control effluents, mussels initially set far apart also showed a similar increase in locomotory speed, yet those in the control treatment formed clumps 5 h later, on average, than mussels in the lobster treatment. Enhanced speed and random movement can therefore not explain fully the aggregation behaviour observed here, and an additional mechanism, such as chemotaxis, may have been involved.

Regardless of the mechanism used, clumping under threat of predation should be adaptive for mussels since the likelihood that any individual will be preyed upon decreases with increasing group size. This leads to the prediction that mussels should form larger clumps when faced with a risk of predation. Interestingly, the number of mussels per clump in this study was small (2.5 mussels on average compared with a

theoretical maximum of seven) and did not differ between mussels held in control water or lobster effluent. Urya et al. (1996) also found smaller clump sizes in *Limnoperna fortunei* than expected from a random walk simulation. Mussels may be sensitive to the costs of group living, such as reduced growth and reproductive output (Bertness and Grosholz, 1985; Okamura, 1986), and there is evidence that small mussels, such as those used in our study, may incur relatively greater costs than larger individuals (Fréchette et al., 1992; Stiven and Gardner, 1992). Limited clump size may therefore be a trade-off between reducing the risk of predation and the costs of living near conspecifics, but whether this trade-off occurs in clumps as small as those observed in our study remains untested.

Predation enhances the aggregation behaviour of mussels in the laboratory. Can it also be responsible for the formation of the large, conspicuous mussel beds that characterise many rocky shores? At present, there is limited evidence for this suggestion. Paine (1974) and Okamura (1986) failed to find any movement of mature mussels either toward the centre of natural mussel beds, where predation rate is reduced, or toward the edges, where growth and reproduction are enhanced. However, McGrorty and Goss-Custard (1995) provided evidence of widespread density-dependent immigration of adult mussels, especially in the summer and in the younger age-classes. Mussels can therefore, at least under some circumstances, track environmental conditions in their vicinity and modify their position within a bed accordingly. Despite this, it is expected that in typical, dense beds, movements by mussels may be difficult since mussels become covered with and retained by the byssus threads of neighbours. In such cases, predation may play a relatively minor role in bed formation, and other factors such as space limitation (Jackson, 1977) or the ability to withstand strong water currents (Witman and Suchanek, 1984) may be more important. However, in a more sparsely populated bed composed of small, discrete clumps in softer substrata, such as our collection site at Stiffkey, migration would be relatively easier, and mussels could potentially respond more readily to local changes in predation pressure. Field experiments are now underway to determine whether mussels at Stiffkey can detect and react to the presence of a predator under natural conditions.

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