Hydrobiologia **445:** 27–35, 2001.

Recruitment preferences of blue mussel spat (*Mytilus edulis*) for different substrata and microhabitats in the White Sea (Russia)

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Received 15 November 1999. in revised form 25 September 2000; accepted 7 December 2000

Key words: recruitment, microhabitats, fouling, attraction, repellence, small scale variability of colonisation, *Mytilus edulis*, blue mussel

Abstract

We tested the assumption that fouling pressure by the blue mussel *Mytilus edulis* on a small spatial scale – especially onto a given substratum type – is homogeneous. Artificial substrata were exposed to natural recruitment within and outside different microhabitats. These microhabitats were monospecific patches (diameter in the meter range) in a mixed subtidal community composed of the brown algae *Laminaria saccharina*, and *Chorda tomentosa*, the green filamentous alga *Cladophora rupestris*, and the blue mussel *Mytilus edulis*. While mussel spat settled in all microhabitats, recruitment was far from homogeneous. Within microhabitats, artificial substrata were preferred over living surfaces. Recruitment also differed between microhabitats exhibiting identical preference gradients on living surfaces and associated artificial substrata: recruitment preference for microhabitats increased in the order *Laminaria saccharina* < control area (stone or mud) < *Chorda tomentosa* < *Cladophora rupestris*< *Mytilus edulis*. In a second experimental approach on a smaller spatial scale (cm range), we assessed mussel recruitment in the vicinity of identical aliquots of some of the microhabitat-constituting species. Again, *Laminaria* proved to be of least, *Cladophora* of highest attractiveness. We conclude that primary settlement of mussel spat is not only influenced by the structure of the substratum (e.g. filamentous forms) but additionally by nearby macroorganisms – presumably by exuded chemical cues as suggested by the second experiment.

Introduction

The blue mussel *Mytilus edulis* is a conspicuous and highly competitive component of inter- and subtidal communities on many circumpolar coasts of both hemispheres (e.g. Suchanek, 1985; Petraitis, 1990). In many habitats, mussels of the genus *Mytilus* outcompete other species if insufficiently controlled by predators (e.g. Seed, 1969a, b; Suchanek, 1985; Wootton, 1993; Ardizzone et al., 1996; Reusch & Chapman, 1997; Dürr & Wahl, submitted). In Kiel Fjord (Western Baltic), recruitment and growth capacity of *Mytilus edulis* are such that in the absence of its main predators, the shore crab *Carcinus maenas* and the starfish *Asterias rubens*, mussels completely dominate newly submerged substrata within 6 months (Dürr & Wahl, submitted) and would, if unchecked, monopolise the entire fjord benthos within 1–2 years (Reusch & Chapman, 1997). A similar situation is found in the White Sea (Oshurkov & Oksov, 1983; Dobretsov & Railkin, 1996; Maximovich et al., 1996). Enhanced by local losses of predator species (decreasing mussel mortality), eutrophication (increasing mussel growth rates) and world-wide spreading of mussels in bulk water, on ship hulls or by aquaculture, ever more autochthonous communities seem to turn into mussel monocultures (e.g. Hockey & Schurink, 1992).

The competitive dominance of mussels in general and *Mytilus edulis* in particular is built on three pillars: wide ecological tolerance, enormous reproductive potential and fast growth (e.g. Seed, 1969a,b; Wootton, 1993; Reusch & Chapman, 1997).

While predatory and competitive interactions, ecology and physiology of adult mussels are well understood (e.g. contributions in Gosling, 1992), studies on the recruitment preferences have mostly focused on the physical aspects of settlement substrata. Thus, it seems well established that *Mytilus* postlarvae prefer to settle first onto artificial or natural filamentous structures such as hydroids or certain algae (Bayne, 1964, 1976; Seed, 1969; King et al., 1990; McGrath et al., 1994; Hunt & Scheibling, 1996; Pulfrich, 1996). In some cases, however, larvae seem to directly settle into blue mussel beds (McGrath et al., 1988). Due to a secreted mucus thread, the larvae may be trapped by these filaments rather than actively 'choosing' them (Caceres-Martinez et al., 1994; Bourget & Harvey, 1998). A strong physical (passive) component in the process of primary settlement would explain why rates of settlement are enhanced by water movement (Eyster & Pechenik, 1987). Also, it does not seem to matter much what kind of biofilm these substrata bear (McGrath et al., 1994) or whether they are of living or artificial nature (King et al., 1990).

These findings seem to indicate a predominantly passive ensnarement of mussel larvae. On the other hand, it seems that even suitable substrata exposed to similar larval densities on an intermediate spatial scale (tens of meters) are not always homogeneously colonised as should be the case if larvae were collected by these filamentous structures like passive sticky particles (e.g. Bourget & Harvey, 1998). In an unpublished study, we noted that recruitment by mussels and other sessile species on a given hydroid species or a monofilament pad was much less intense next to *Laminaria saccharina* than on the same substrate in the vicinity of the seagrass *Zostera marina*. This pattern could have been produced by repellents exuded by *Laminaria* and/or attractants exuded by *Zostera*.

Such an interaction between an established constituent of a community and a new coloniser should have decisive implications for local succession , especially when the recruiting species in question is the invasive and highly competitive blue mussel.

In this context, we experimentally tested whether: (i) mussel recruitment on identical substrata differed between microhabitats constituted of different macroorganisms; (ii) observed recruitment patterns on artificial substrata correlated with mussel recruitment onto nearby living surfaces; and (iii) whether mussel larvae exhibit preferences for living vs. artificial substrata.

Methods

Microhabitat recruitment

Experiments were carried out in the White Sea (Kandalakshsky Gulf, Chupa Bay, 66° 18′ N, 33° 40′ E, July 26th until August 20th, 1995). In this region, larvae of *M. edulis* are observed in the plankton from late June to late August (Oshurkov & Oksov, 1983; Maximovich et al., 1996). Settlement of larvae (size 250–300 μm) usually occurs on the filamentous green alga *Cladophora rupestris* (Dobretsov & Railkin, 1996; Dobretsov, 1999). The experimental area (depth 3–6 m) was characterised by a patchy distribution of the brown algae *Laminaria saccharina*, *Fucus vesiculosus* and *Chorda tomentosa*, the filamentous green alga *Cladophora rupestris* and the blue mussel *Mytilus edulis* (hereafter referred to by their generic names). Each monospecific patch constituted a 'microhabitat'.

Recruitment of mussel postlarvae (<0.35 mm: first settlement) was monitored simultaneously on artificial substrata suspended near a given microhabitat and on the living surfaces of the species constituting the microhabitat. Patches devoid of large sessile epibenthos served as control areas. For artificial substrata, we used monofilament lines with a diameter of 0.4 mm. These were suspended from an anchored buoy within 1–2 m from a given control area or monospecific patch (20 replicate patches per microhabitat type). Depth over-ground varied with tides (amplitude 1–2 m). After 4 weeks, artificial substrata were collected, bagged individually, and preserved in formalin (4%). At the same time, from the same locations thalli and holdfasts of *L. saccharina*, *C. tomentosa* and *C. rupestris* ('living substrata') from 25 random sites were collected and treated as described above. Prior to the experiment, these parts of algae had been devoid of macroorgnisms. (Because this was not the case for *Mytilus* shell surfaces, larval recruitment onto these was not assessed.) Thus, macrofouling was of comparable age on artificial and living surfaces. In the laboratory, numbers of settled postlarvae of *Mytilus edulis* were counted under a stereomicroscope, and transformed into recruitment abundances per cm^2.

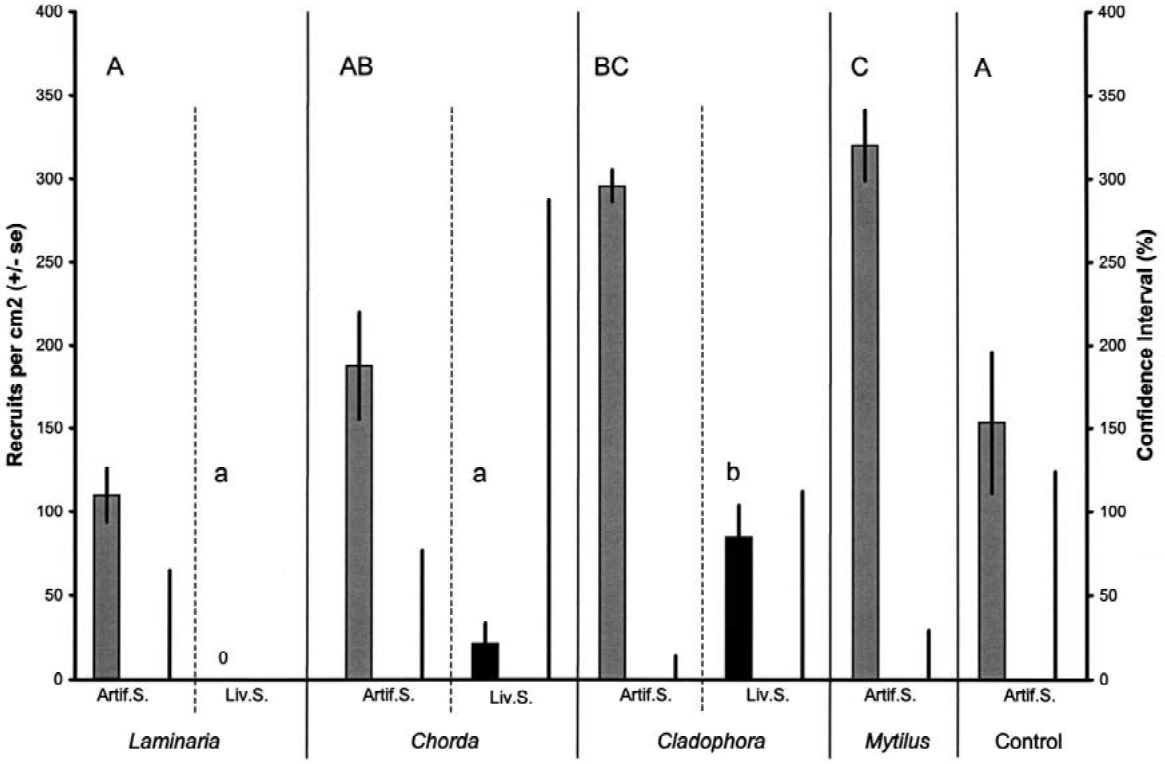

Figure 1. Natural Microhabitats: Recruitment (columns with SE-bars) and its Confidence Intervals (bar beside a column) by mussel spat on artificial ('Artif.S.') and living substrata ('Liv.S') exposed side by side in different microhabitats. Means + s.e. Within microhabitats, recruitment was always significantly lower on living surfaces. Significant differences among microhabitats are indicated separately for artificial and for living substrata by letter code (capital and small letters, resp.): treatments sharing at least one letter do not differ significantly.

Small scale recruitment preferences

For the 2 species having exhibited the most extreme effects on mussel recruitment during experiment 1, we assessed effects on an even smaller scale (cm) and in a low-flow environment. Under these conditions, any heterogeneous distribution of settlers presumably reflects an active choice of the larvae. The experimental set-up consisted of a settlement box (65 cm × 39 cm × 35 cm) subdivided into 3 vertical compartments in its central part (Fig. 2). Top and bottom of the box remained open. Side-walls cut off most of the external currents. Prior flow measurements showed that the central part of the boxes was current-free during the entire tidal cycle. Within each compartment, six settling panels were fixed to the side walls and a gauze bag (mesh 50 μm, size 5.5 × 7.5 cm) was suspended centrally. Per box, 2 gauze bags held equivalent amounts of *Cladophora* and *Laminaria*, respectively, one remained empty (control). Quantities of macroorganisms in the gauze bags were matched by algal surface (35 cm^2/bag) rather than weight, because exudation rates were considered surface-dependent. The algal material was loosely packed to avoid squeezing. Distribution of gauze bags among compartments was random. The design corresponds to a randomised block design with 3 blocks (boxes) each containing 3 treatments (*Laminaria*, *Cladophora*, control). Once penetrated into the upper or lower part of the box, larvae could enter one of the three compartments before settling on panels next to one of the gauze bags (or elsewhere and escape census). In situ, boxes were suspended between a buoy and an anchor at a depth of 1.5 m in the experimental area. Swivels allowed for free rotation. Three boxes were exposed for 2 weeks. Subsequently, mussel recruitment numbers on the settlement panels were counted under a stereomicroscope. Values for the six panels in a given compartment were averaged to avoid pseudoreplication.

Statistics

The fact that not a single mussel larva settled on living *Laminaria* (zero variance) produced a hetero-

geneity of variances (F_{max}-test) which prohibited the use of parametric ANOVA for analyses. Consequently, multiple-sample-analyses (e.g. between microhabitat preferences) were done by a Kruskal–Wallis–ANOVA followed by an advanced multi-comparison *U*-Statistic (STP, Sokal & Rohlf, 1995). Recruitment differences between artificial and living substrata of the same microhabitat (dependent pairs of data) were assessed by a Wilcoxon Paired Sign test. Variances of paired substrata were compared by *F*-test. Distribution patterns were tested by a Chi-squared dispersion test (Heath, 1995).

Preferential recruitment into different compartments of the boxes was analysed by a Friedman's Anova. To graphically represent *relative* recruitment preferences, numbers of settled larvae per compartment were transformed to *proportions* (number of larvae per compartment/number of larvae per compartment expected under the null-hypothesis). The null-hypothesis was that equal proportions of larvae, i.e. 33% of total number of settled larvae per box, settle in each of the 3 compartments. 95%-confidence intervals were used to confirm preferences.

In all cases, the threshold for significance was 5%.

Results

Recruitment on artificial vs. living substrata

Artificial substrate (monofilaments) were consistently preferred over the various living surfaces of algae (*Chorda, Cladophora, Laminaria*, Wilcoxon $p>0.001$, Table 1, Fig. 1). In the *Laminaria* microhabitats, larvae recruited onto artificial substrata but consistently avoided the kelp thalli. *Chorda* was colonised 9 times less than artificial substratum only a meter away. Finally, artificial substratum was preferred 3.5 times over neighbouring *Cladophora* thallus.

Table 1A. Raw data of recruitment on living substrata in different microhabitats. se = standard error, CV = coefficient of variation (%), 'ChiDisp' = Chi-squared value of the dispersion test ($X^2=s^{2*}(n-1)$/mean, $X^2_{crit(n=25,upper)}= 39.36$, $X^2_{crit(n=20,upper)}= 32.85$).

Replicates	Recruits on LIVING Surfaces (# cm^{-2})		
	Laminaria	Chorda	Cladophora
1	0	0	21
2	0	0	121
3	0	0	13
4	0	0	298
5	0	0	301
6	0	0	0
7	0	0	15
8	0	0	0
9	0	0	103
10	0	75	0
11	0	0	90
12	0	0	176
13	0	0	1
14	0	0	140
15	0	0	12
16	0	43	123
17	0	0	11
18	0	0	30
19	0	0	0
20	0	144	106
21	0	0	200
22	0	0	202
23	0	0	1
24	0	268	2
25	0	0	155
mean	0.0	21.2	84.8
se	0.0	12.2	19.0
variance	0	4624	11342
ChiDisp	-	5235	3208
CV	-	287	112

Microhabitat preferences

Between microhabitats, mussel recruitment differed both on living and on artificial substrata (Kruskal–Wallis $p < 0.001$ in both cases, Fig.1).

The surface of *Laminaria* was completely avoided. *Chorda* thalli exhibited intermediate mean mussel recruitment (21 /cm^2), however only 4 out of 25 plants were fouled at all. The branching filamentous *Cladophora* was regularly and on average most densely covered (85/cm^2). Mussels significantly preferred *Cladophora* over the two other algal species (STP $p<0.01$). Larval distinction between *Laminaria* and *Chorda* as settling sites was just non-significantly (STP $p=0.055$) in favour of *Chorda*.

Recruitment preferences for artificial substrata exposed in different microhabitats mirrored those observed on living surfaces: identical substrata (polymer monofilaments) became least colonised when exposed close to *Laminaria* (115 postlarvae / cm^2, on average), moderately so near *Chorda* (188 / cm^2) and most densely close to *Cladophora* and *Mytilus* (296 and

Table 1B. Recruitment on artificial substrata in different microhabitats. se = standard error, 'CV' = coefficient of variation (%), 'ChiDisp' = Chi-squared value of the dispersion test ($X^2=s^{2*}(n\text{-}1)$/mean, $X^2_{crit(n=25,upper)}= 39.36$, $X^2_{crit(n=20,upper)}= 32.85$)

Replicates	Recruits on ARTIFICIAL Surfaces (# cm^{-2})				
	Laminaria	Chorda	Cladophora	Mytilus	Control
1	110	199	300	367	102
2	53	392	291	306	23
3	68	19	270	319	244
4	111	92	297	398	201
5	98	385	278	390	65
6	20	47	281	332	109
7	230	329	287	314	79
8	180	280	279	315	18
9	121	254	293	319	366
10	78	36	288	321	42
11	257	305	275	310	9
12	123	358	395	322	448
13	157	17	310	319	30
14	4	51	340	219	12
15	9	294	200	324	115
16	135	23	394	610	19
17	199	29	295	215	97
18	120	390	281	284	99
19	100	154	271	318	210
20	21	100	295	100	779
mean	109.7	187.6	295.9	320.1	153.4
se	15.9	32.4	9.4	21.1	42.5
variance	5056	20995	1767	8904	36125
ChiDisp	876	2127	113	529	4476
CV	65	77	14	29	124

Table 1C. Recruitment on artificial substrata in different compartments of the settlement boxes. 'Treatments' designates the different compartments equipped with *Laminaria* or *Chorda* or empty (control), CI = confidence interval, 'expected' = total larval numbers per box divided by 3 (number of compartments per box) giving expected recruits per compartment for random recruitment

Treatments	Boxes				
	1	2	3		
Observed postlarvae/cm2 (se)					
Control	32.8 (0.8)	5.2 (0.9)	5.1 (0.7)		
Laminaria	24.8 (2.3)	2.6 (0.4)	2.3 (0.3)		
Cladophora	59.2 (5.0)	9.8 (1.3)	10.7 (1.2)		
Expected	38.9	5.9	6		
	Preference (observed / expected)			mean	CI
Control	0.84	0.88	0.85	**0.86**	**0.80 – 0.90**
Laminaria	0.64	0.44	0.38	**0.49**	**0.15 – 0.82**
Cladophora	1.52	1.7	1.8	**1.67**	**1.32 – 2.03**

320/cm^2, respectively). Most of these differences are significant as shown in Figure 1.

Artificial substrata near *Cladophora* and *Mytilus* attracted significantly more mussel spat (STP $p<0.01$ in both cases) than in control areas. *Chorda* and *Laminaria* seemed non-significantly attractive and repulsive, respectively, when comparing artificial substrata near these species to artificial substrata in the control area (Fig. 1, Table 1). Thus, living surfaces and associated artificial substrata exhibit identical and consistent recruitment preference gradients: *Laminaria* < *Chorda* < *Cladophora* (< *Mytilus*).

Variability of recruitment differed between treatments (Fig. 1) but was generally high (Table 1). In all instances, the dispersion test indicated patchy recruitment ($p < 0.05$). Variances were significantly higher on living substrata than on artificial substrata exposed close to them (*F*-test). Postlarvae generally recruited at comparable densities on the 20 artificial substrata associated with a given type of macroorganism (coefficient of variation CV: 14 – 77%). Recruitment on the 25 thalli of *Chorda* and *Cladophora*, however, was highly variable. Per cm^2 of *Cladophora*, recruitment ranged from 0 to 301, and CV was 112%. Among all 25 *Chorda* plants, 21 were not colonised at all (the nearby artificial substrata invariably were) and the remaining 4 exhibited relatively high numbers of postlarvae (mean: 132/cm^2), comparable to artificial substrata in the control area. Recruitment-CV on *Chorda* was 287%. The high variability of mussel recruitment onto different algal conspecifics does not necessarily reflect spatial patchiness of pelagic larvae, as this would have caused similar variability among the artificial substrata exposed near these plants. It more likely points at inter-individual plant differences in susceptibility to fouling. The relatively high variability of recruitment onto artificial substrata in the control area will be discussed later.

Active choice results

Mussel recruitment patterns in the boxes (small spatial scale, absence of directional currents) were similar to those observed on artificial and living surfaces in natural microhabitats. In all replicate boxes, highest recruitment occurred in compartments containing aliquots of *Cladophora*, while in the *Laminaria* compartments recruitment was lowest (Table 1, Fig. 2). Differences in recruitment among the three compartments were marginally significant (Friedman $X^2= 6$, $X^2_{crit}= 5.991$, $p<0.05$). In each of the replicates, recruitment was lowest in the *Laminaria* compartment, intermediate in the control compartment and highest in the *Cladophora* compartment. Thus, compared to expected frequencies, mussel larvae were attracted by *Cladophora* and repelled by *Laminaria*. This is consistent with the results from the microhabitat comparisons. Recruitment densities in the absence of algae (control compartments) was close to expected densities. Ninety five percent-confidence intervals for proportional recruitment in *Cladophora* compartments (1.32–2.03) do not overlap with those in *Laminaria* (0.15–0.82) or in the control compartments (0.80–0.90) (Fig. 2).

Discussion

In this study, we assessed recruitment patterns of mussel spat on different spatial scales with regard to substratum type (living vs. artificial) and microhabitat (patches of several benthic macroorganisms).

Recruitment rates differed between microhabitats (range: tens of meters), between artificial and living substratum (meter range) and between artificially created micropatches (box compartments: cm range).

In all microhabitats, mussel larvae significantly preferred artificial over living algal substrata. For the time being, we have no explanation for this pattern.

Additionally, rates of recruitment differed between microhabitats. Among living substrata, *Laminaria* thalli were avoided. The surfaces of *Chorda* were of low, those of *Cladophora* of high preference. The artificial substrata exposed close to these plants showed a parallel recruitment pattern: low, intermediate and high recruitment densities on monofilaments suspended near *Laminaria*, *Chorda* and *Cladophora*, respectively. In the control area, recruitment onto the monofilaments was comparable to *Chorda* and *Laminaria* patches, while near beds of adult mussel and *Cladophora* postlarvae recruited in much higher densities. When assessing recruitment in the immediate vicinity of the least and the most preferred algae (*Laminaria* and *Cladophora*) but in calm water (active choice boxes), postlarvae once again recruited more densely near *Cladophora* than near *Laminaria* or in the absence of macroorganisms (controls).

These results suggest that mussel recruitment even in restricted areas is neither homogeneous nor random. This pattern could be caused by (i) a patchy distribution of competent larvae, (ii) by heterogeneities in the current regime, (iii) by passive en-

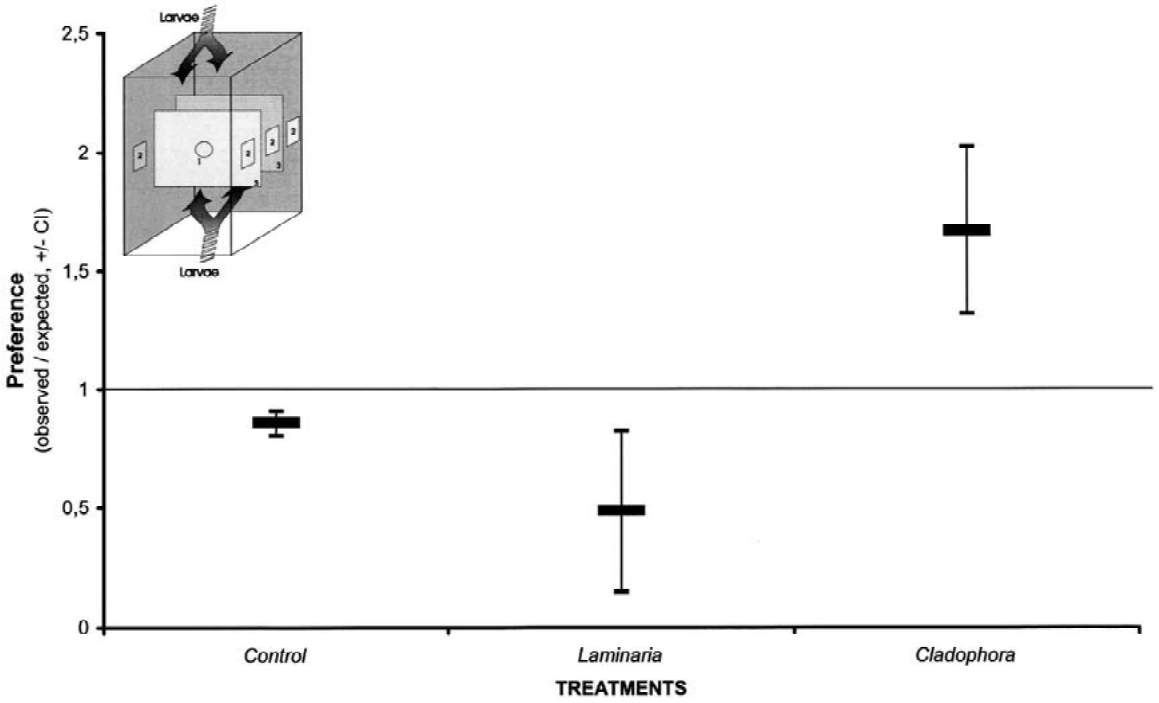

Figure 2. Settlement Box Experiment: Recruitment preferences by mussel spat onto artificial substrata in box sections containing samples of *Laminaria* or *Cladophora* or empty gauze bags (controls) as compared to expected recruitment. A ratio of 1 (reference line) indicates that observed numbers equal expected numbers of larvae. Means of treatment/expected ± confidence intervals.Letter code for significant differences as in Figure 1. Insert of Settlement Box: side walls solid, open at top and bottom with current-breaking devices not shown. (1) Suspended gauze bag containing algae or empty (control). (2) Settlement panels (6 per compartment). (3) Inner subdivisions separating the three compartments.

tanglement of larvae by filamentous structures, (iv) by microhabitat-specific postsettlement mortality (e.g. predation) and/or v. by an active preference behaviour of the larvae.

Spatial patchiness of presettlement larvae should produce high variability among replicates. This was the case for *Chorda* thalli and to a much lower extent for *Cladophora* thalli and monofilaments in the control area. In the latter case, patchy distribution of pelagic larvae indeed seems to be the most plausible cause. Additional factors must, however, account for the variability between *Chorda* and *Cladophora* replicates, since artificial substrata exposed aside these plants exhibited conspicuously lower CVs. It seems inconceivable that larval patchiness should affect living but not artificial substrata positioned side by side.

Differences of hydrodynamics among patches can not account for observed differences of recruitment between artificial and living substrata paired within the same patch. On the other hand, they could contribute to recruitment differences among microhabitats. However, the fact that in the no-flow regime within the boxes very similar patterns of recruitment preferences were observed largely discounts hydrodynamics as a major causal factor.

Besides exudates, surface chemistry, consistency and colour, artificial and living substrata differed with regard to structure. *Laminaria* thalli are broadly leafy and smooth, *Chorda* resembles a long, flexible whip (up to 4 mm in diameter) covered with fine hair (diameter ca 10 μm), *Cladophora* is a branching filamentous form with filament thickness ranging between 40 and 220 μm, artificial substrata were unbranched polymer filaments 400 μm thick.

Passive entanglement of mussel larvae possessing a sticky mucus thread has been suggested to explain their enhanced recruitment onto filamentous living or artificial structures (e.g. Caceres-Martinez et al., 1994; Dobretsov & Railkin, 1996). The observation that blue mussel spat 'preference' for filaments is more conspicuous in moving water than in the absence of currents seems to support this view (Eyster & Pechenik, 1987). We noted that first-settlement larvae would adhere to a preparation needle from a distance of 2–3 mm and could be moved around by it (Dobretsov, Railkin,

1996). This hints at the existence of a sticky thread (byssus or mucus) at this larval stage.

On the other hand, our results show that passive entanglement alone can not account for all of the observed recruitment patterns. On living substrata, densities of recruits do coincide with 'filamentousness' of the algae: the avoided *Laminaria* grows broadly foliose, the moderately preferred *Chorda* features as a thick thread covered with fine hair and the highly attractive *Cladophora* belongs to the typical branching filamentous type repeatedly described as the primary settling site for mussel larvae (Seed, 1969a; McGrath et al., 1994; Suchanek, 1995; Pulfrich, 1996; Ardizzone et al., 1996; Hunt & Scheibling, 1996). The monofilaments used were intermediate both in diameter as in subjectively assessed 'branchiness' as compared to available living structures.

However, mussel spat clearly discriminated between identical artificial substrata which only differed by their organismic neighbourhood. There is no reason why larvae should become entangled by filaments suspended above a *Cladophora* stand and not by identical filaments above a *Laminaria* patch. Additionally, differential recruitment onto otherwise unfouled smooth plastic panels in the boxes could not have been engineered by entanglement at all.

Postsettlement mortality of mussels is mainly caused by browsing starfish and juvenile crabs (McGrorty et al., 1990; Reusch & Chapman, 1997; Dolmer, 1998). Neither species had access to the suspended artificial substrata or the boxes. Predation by fishes was not observed. While predation may have occurred on the thalli, it can not be responsible for the recruitment patterns on artificial substrata.

Recruiting mussel spat seems not to differentiate between biologically filmed and unfilmed surfaces (McGrath et al., 1994). This may be either because they do not select substrata chemotactically (also suggested by the 'passive entanglement model') or because the biofilm studied did not emit the relevant cues. In contrast to the cited work, in a recent investigation biofilms were identified as one of the main factors inducing blue mussel settlement on artificial substrata (Dobretsov & Railkin, 1996).

The results of the present investigation, also suggest that the distinct recruitment preferences at least on artificial substrata may best be explained by a chemotactic selection of certain microhabitats. Artificial substrata of high or low attractiveness differed consistently only by their organismic neighbourhood: whether they happened to be near *Cladophora* or near *Laminaria*, for instance. We speculate that secondary metabolites exuded by the macroorganisms act as settlement cues for mussel larvae. Under this hypothesis, exudates from *Cladophora* attracted mussel larvae, while those from *Chorda* were neutral and those from *Laminaria* repulsive. Indeed, it has been shown that 'wash-outs' of *Laminaria saccharina* and its microbial film repel mussel larvae, while 'wash-outs' of *Cladophora rupestris* and its associated microbial film attract mussel larvae (Dobretsov, 1999). Interestingly, recruitment was also enhanced in the vicinity of mussel beds which contrasts with the postulated larval avoidance of adult conspecifics during first settlement (Bayne, 1964, 1976; Seed, 1969a; McGrorty et al., 1990, but see McGrath, 1988 for a contrasting view). The attractive and/or repulsive effects of algal exudates seem the most plausible explanation for the recruitment patterns in the box experiment.

The fact that in the present investigation larval preference for *Cladophora* as compared to *Chorda* and *Laminaria* was more conspicuous on living than on artificial surfaces could be caused by higher concentration of cues close to the thalli, by more intense predation especially on *Laminaria* surfaces or by trapping of the larvae in the filamentous morphology of *Cladophora* once the larvae have approached this substratum.

Recruitment rates of sessile benthic organisms with planktonic larvae depend on the sequential phases of (i) arrival of competent larvae, (ii) approach to a given substratum, (iii) attachment, and (iv) postsettlent mortality. We found that macroorganisms may influence recruitment rates of *Mytilus edulis* in their vicinity – presumably by acting on phases (ii) and (iii). During the approach phase, blue mussel larvae seem to chemotactically select microhabitats on a spatial scale of meters or tens of meters. Possibly they react to the attractive exudates of, for instance, *Cladophora rupestris* by actively swimming or sinking into this microhabitat along a chemical gradient. Other exudates (e.g. *Laminaria*) may repel larvae. Small scale approach (cm range) and attachment may be enhanced by the larva's sticky filament attaching best to filamentous structures. But even in the absence of such entanglement, chemical cues play an important role (box results here, biofilming results of Dobretsov & Railkin, 1996).

The present results suggest that different communities are not equally sensitive to mussel invasion. Thus, the presence of *Laminaria* (or other non-attractive, foliose forms) may protect a habitat from

massive first settlement, whereas the occurrence of *Cladophora* (or other attractive, branching filamentous forms like the red algae *Ceramium* or hydroids) may increase the risks of mussel spat invasion. After a growth phase, young mussel of 0.5 – 1.5 mm shell length usually leave the substratum of first settlement and drift or crawl to a more definitive habitat. It is known that during this phase of secondary and rather small scale dispersal, young mussels preferentially select existing mussel beds for settlement. Which cues control their preference behaviour in the absence of mussel beds, or whether under these circumstances they do not switch settlement sites at all, remains to be investigated.

In view of the blue mussel's invasive capacities, modulation of mussel recruitment by pre-existing macroorganisms, as suggested here, may have far-reaching effects on the further development of the community.

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