Physical and biological factors influencing mussel (*Mytilus trossulus, M. edulis*) settlement on a wave-exposed rocky shore

Heather L. Hunt*, Robert E. Scheibling

Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada B3H 4J1

ABSTRACT: Settlement rates of mussels *Mytilus trossulus* and *M. edulis* on artificial collectors (aquarium filter wool) and natural substrata were measured in tidepools and on emergent rock in recently ice-scoured and non-scoured regions of a rocky shore near Halifax, Nova Scotia, Canada. Patterns of abundance and size distribution of mussel settlers differed markedly between artificial collectors and natural substrata. Settlement rate on artificial collectors was directly related to water flux, and was highest on ice-scoured emergent rock and lowest in non-scoured tidepools. Settlement rate on natural substrata was related to a suite of biological (macroalgal/barnacle cover) and physical factors (water flux, tidal height, flushing time), and was highest in ice-scoured tidepools and lowest on ice-scoured emergent rock. Large postlarval mussels (>5 mm shell length) were common on natural substrata but rare on artificial collectors. Recruitment patterns of mussels on natural substrata reflected the distribution of settlers, suggesting that settlement patterns are important in determining the distribution and abundance of mussels in this population.

KEY WORDS: Ice-scour · Intertidal zone   Larval supply · Mussels · *Mytilus* · Recruitment · Settlement · Tidepools

INTRODUCTION

Spatial variation in settlement of larvae of benthic marine invertebrates arises through a combination of passive (hydrodynamic) and active (behavioural) processes operating at various scales (reviewed by Butman 1987). Larvae tend to be passively deposited at large spatial scales (tens of metres to tens of kilometres) since horizontal advection usually exceeds larval swimming speeds, although some larvae can vertically migrate between water masses. Active habitat selection becomes important at smaller scales (centimetres to metres) as larvae respond to various abiotic (e.g. surface texture and chemistry) and biotic (e.g. microbial films, conspecifics, and other macrobenthic species) cues associated with the substratum (reviewed by Pawlik 1992). However, hydrodynamic processes, such as turbulent eddies around biotic roughness elements, may also influence the small-scale distribution of settlers (e.g. Eckman 1983, 1987, Havenhand & Svane 1991, Harvey et al. 1995). Settlement patterns may be reflected in recruitment patterns, depending on the intensity and spatial variation of early post-settlement mortality (Keough & Downes 1982).

In their natural habitat, recently settled mussels (*Mytilus* spp.) are usually associated with filamentous substrata (primarily macroalgae) or small crevices and depressions in the bottom (reviewed by Seed 1976, Seed & Suchanek 1992). Laboratory studies have shown that larvae of *M. edulis* and postlarvae of *M. galloprovincialis* settle almost exclusively on filamentous substrata (Bayne 1965, Petersen 1984, Eyster & Pechenik 1987, Cáceres-Martínez et al. 1994). A variety of artificial substrata (including rubberized hair pads, plastic panels, ropes, jute pads, shag rugs, and plastic pot scrubbers) have been used to collect mussel settlers (Menge 1978, King et al. 1990 and references therein, Petraitis 1991, Cáceres-Martínez et al. 1994,

*E-mail: hlhunt@is2.dal.ca

Menge et al. 1994, Molares & Fuentes 1995), since they provide a standardized surface which is easy to sample. The abundance of mussel settlers on artificial substrata probably reflects larval supply, as observed for freshwater zebra mussels (Martel et al. 1994) and estuarine Dungeness crabs (Eggleston & Armstrong 1995). King et al. (1990) observed that the temporal pattern of mussel settlement on an artificial substratum (nylon pot scrubbers) was similar to that recorded on filamentous algae and adult mussels at the same site.

Along the Atlantic coast of Nova Scotia, Canada, 2 species of mussels (*Mytilus trossulus* and *Mytilus edulis*, hereafter *Mytilus*) co-occur in the low and mid intertidal zones, but they cannot be distinguished visually at small sizes (Pedersen 1991, Mallet & Carver 1995). Mussels in tidepools generally occur in centimetre-scale patches (Hunt & Scheibling 1995), whereas mussels on emergent rock tend to form more extensive beds (authors' pers. obs.). This pattern may reflect greater settlement and/or lower post-settlement mortality on emergent rock. Tide-pools and emergent rock differ in several aspects which may influence mussel settlement rate: (1) they have different macroalgal assemblages (reviewed by Metaxas & Scheibling 1993) which are the substrata for settlement; (2) they are differentially affected by ice-scour which occurs sporadically along the Atlantic coast of Nova Scotia (McCook & Chapman 1991, Minchinton et al. in press) and generally disturbs the biota of tidepools less than that of emergent rock; and (3) settlement may continue during the period of tidal isolation in tidepools but not on emergent rock.

In this study, we examine patterns of settlement of *Mytilus* in tidepools and on emergent rock, both in ice-scoured and non-scoured regions of an exposed shore. Comparisons of settlement rates on artificial collectors and natural substrata enable us to examine the relative roles of larval supply (as reflected by settlement on collectors) and substratum type in shaping settlement patterns of mussels. We relate the observed patterns of settlement to physical and biological characteristics of the local environment, and examine the relationship between settlement and recruitment of mussels on this shore.

MATERIALS AND METHODS

Physical environment. This study was conducted in September and October 1994 on a rocky shore at Cranberry Cove (44° 28' N, 63° 56' W) near Halifax, Nova Scotia, Canada The shore is composed of granite platforms and outcrops, and exposed to southerly swells of up to 10 m (significant wave height) in fall and winter For further description of the site see Metaxas et al. (1994) and Hunt & Scheibling (1995).

We examined settlement and recruitment of mussels in 2 habitats (tidepools and emergent rock) within each of 2 strata (areas scoured by ice during winter 1992–93 and non-scoured areas). Emergent rock surfaces were scoured bare except for the scattered thalli of crustose macroalgae, whereas some upright macroalgae remained in scoured tidepools. By September 1994, foliose macroalgae had become re-established in ice-scoured areas, and mussels were abundant in all areas except ice-scoured emergent rock. We selected 12 sampling locations along a horizontal distance of ~1 km of shoreline to make up 3 replicates of each of the 4 combinations of habitat and stratum. Tidepool locations ranged from 2.7 to 7.2 m in length, 1.1 to 2.8 m in width, and 0.3 to 0.6 m in depth; locations on emergent rock were similar in area. We measured the height of each location above a chart datum using a transit level in May 1995. We measured flushing time for each of the 6 tidepools in August 1993 and June 1994 as the time taken for a fluorescent red dye (Rhodamine B, Sigma Chemicals), added at low tide at an initial concentration of 1.4 to 6.4 mg l^{-1}, to become undetectable in a spectrophotometer (Perkin-Elmer, Lambda 3B, Oak Brook, IL, USA). We measured isolation time of tidepools (the period during which there is no sea water input) on the same dates as flushing time.

We measured relative water flux at each location as the dissolution rate of dental stone (calcium sulfate) (Yund et al. 1991). The dental stone (Denstone® Golden, Miles Dental Products, South Bend, IN, USA) was cast in cylindrical molds 2 cm high and 11 cm in diameter. After drying at room temperature for at least 24 h and then at 40°C for an additional 24 h, the sides and bottom of the cylinders were coated with polyurethane so that only the top surface was exposed to flow. The cylinders were then dried for a further 24 h at room temperature. The cylinders were fastened to 11×15 cm rectangles of galvanized mesh (0.6 cm mesh size) with epoxy putty (Z-Spar A-788 Splash Zone Compound®, Kop-Coat Inc., Los Angeles, CA, USA), dried at 40°C for 24 h, and then weighed. We measured relative water flux for two 5 to 6 d periods (May 15 to 20 and June 30 to July 6, 1995). During each period, 2 cylinders were bolted to the substratum at each location; another 2 cylinders were deployed above the tidal range as controls for losses not due to water flow, such as transport and rain. After each period, the cylinders were returned to the laboratory, rinsed in fresh water, dried at room temperature for 48 h and then at 40°C for an additional 24 h, and then weighed. In July, dissolution rate was not measured for 1 location because both cylinders were abraded by macroalgae. However, the missing value was estimated from a regression equation relating dissolution rates in July (J) to those in May (M) at all other locations: $J = 0.933M - 12.719$

$(r^2 = 0.802; F_{1,9} = 36.344; p < 0.001)$. The ranks of dissolution rates in May and July were strongly correlated (Spearman Rank Correlation: $r_s = 0.944; p < 0.001$); these ranks were averaged to give an index of water flux for multiple regression and principal components analysis (see 'Statistical analysis').

Significant wave heights (SWH: average height of the largest third of all waves measured) were recorded at a station (44° 50' N, 63° 25' W) ~40 km from the study site (data provided by Department of Fisheries and Oceans, Canada).

Larval/postlarval abundance. We measured the availability of *Mytilus* larvae and postlarvae in sea water at high tide on September 24 and October 8, 1994, the same dates that artificial collectors were deployed (see 'Settlement and recruitment'). Three 30 l samples of sea water were collected at each of 3 (September) or 4 (October) positions separated by 100 to 400 m along ~1 km of shoreline. We hand-pumped the water with a bilge pump through a hose fastened to the substratum at the same height on the shore as our artificial collectors. The water sample was filtered through a 60 μm filter, which was rinsed with filtered sea water and preserved in 70% ethanol. Larvae and postlarvae were enumerated and measured in the laboratory under a dissecting microscope.

Settlement and recruitment. For benthic marine invertebrates with dispersing larvae, settlement includes attachment to the substratum and metamorphosis, while recruitment refers to survival until the organism is counted by an observer (Keough & Downes 1982). Defining settlement and recruitment in terms of sampling period is more problematic for *Mytilus*, which remains mobile for some time after settlement (reviewed by Seed & Suchanek 1992), than for truly sessile species. In this study, we define settlers as mussels collected after a period of hours to days, and recruits as those collected after a period of 5 mo. In this region, settlement of *Mytilus* is protracted, occurring over a 9 mo period, with an annual peak in late summer or early fall (Pedersen 1991, authors' unpubl. data).

Genetic analysis was used to identify the species of mussels present at the study site. A sample of 27 older juvenile and adult mussels [4 to 44 mm shell length (SL)] was collected in March 1996 and analysed by polymerase chain reaction/restriction fragment length polymorphism assays using a marker for the female mitochondrial DNA lineage (Rawson & Hilbish 1995a, b) and a nuclear DNA marker for the adhesive foot protein (Rawson et al. in press). The analysis revealed that ~80% of mussels in both tidepools and emergent rock were *Mytilus trossulus*. At another wave-exposed shore in Nova Scotia (ca 30 km away), Pedersen (1991) found that 77 to 91% of settlers (<1 mm SL) and 76 to 90% of older individuals (from 6, 10, and 24 mo old mussel patches) were *M. trossulus*. Therefore, it is likely that most of the settlers that we sampled were *M. trossulus*.

We deployed artificial collectors to sample *Mytilus* settlers on September 24 and October 8, 1994. The collectors [similar to those used by Pearce & Bourget (1996) for scallop spat] were made of 9×11 cm pouches of plastic Vexar mesh (3 mm mesh size), filled with ~1.5 g of polyester wool for aquarium filters ('Poly' Filter Wool®, Rolf C. Hagen Inc., Montreal, Quebec, Canada). The collectors were placed in running sea water in the laboratory for ~1 wk before use to allow colonization by microflora. At each location, 4 collectors were bolted to the substratum (through a grommet in the center of the pouch) before tidal immersion, and removed after 6.5 to 10 h when the tide receded. A second set of collectors was placed in the tidepools at this time, and removed after 2.5 to 5.5 h, before immersion by the incoming tide. The collectors were returned to the laboratory and frozen until they were processed. Mussels from each collector were counted and SL was measured using an ocular micrometer (accuracy: ±30 μm). Mussels on both filter wool and Vexar mesh were counted, but those on the mesh were rare.

At each location, we also sampled settlement of *Mytilus* in three 10×10 cm quadrats on the natural substratum. We prepared these quadrats by removing the existing mussels with forceps or a pipette to avoid disturbing the rest of the macrobenthic community. We also removed mussels (with a paint scraper) from a 10 cm border around each quadrat to limit migration into the quadrat. The quadrats were spaced at least 10 cm apart at each location and marked by stainless steel screws in plastic anchors. We collected recently settled mussels from each quadrat after two 5 d intervals (September 22 to 26 and October 7 to 11, 1994). Three other quadrats at each location were similarly prepared on May 20 and 21, 1994 and sampled after ~5 mo (October 17 to 29) to estimate mussel recruitment. The mussel samples were returned to the laboratory and frozen until they were processed as described above.

In October 1994, we estimated the cover of macroalgae and barnacles (*Semibalanus balanoides*, the only sessile macrofaunal species besides *Mytilus*) in each of the settlement quadrats. A plexiglass panel with 20 random points was placed over a quadrat and the number of points overlying each species/group were counted and expressed as a percentage of the total. Macroalgae were assigned to functional form groups after Littler (1980) and Littler & Littler (1984): filamentous, coarsely branched, thick leathery, jointed calcareous, and crustose forms.

Statistical analysis. We used 3-way analysis of variance (ANOVA) to analyze the settlement/recruitment rate of *Mytilus* on artificial collectors and natural substrata. Habitat (tidepool and emergent rock) and Stratum (scoured and non-scoured) were fixed factors, each with 2 levels, and Location was a random factor nested within Habitat × Stratum, with 3 levels. If Location was non-significant at $\alpha = 0.250$, we removed this term from the analysis and calculated a pooled estimate of the residual error (Winer 1971). If Location was significant at $\alpha = 0.05$, we examined the Location effect within each combination of Habitat × Stratum. We used Student-Newman-Keuls (SNK) tests ($\alpha = 0.05$) for post hoc comparisons of means. If necessary, counts of mussels (x) were $\ln(x+1)$ transformed to homogenize variances (Cochran's C-test: $\alpha = 0.05$).

We used Kolmogorov-Smirnov tests (Seigel & Castellan 1988) to compare size distributions of mussels among habitats and strata for samples from both artificial collectors and natural substrata.

We used forwards stepwise multiple regression to examine the relationship between settlement rate of *Mytilus* settlers on artificial collectors and the physical characteristics of the locations (water flux index, tidal height, and flushing time). We did regressions for tidepools and emergent rock separately, as well as for the 2 habitats combined. For analysis of settlement on natural substrata, we used principal components analysis (PCA), based on both the physical and the biological (cover of macroalgal groups/barnacles) characteristics of the locations, to reduce the number of variables needed to explain the total variance in the data (Kleinbaum et al. 1988). Only PCA factors with eigenvalues >1 were used in stepwise regression. Also, we analyzed 2 size classes of mussels (<2 and >2 mm SL) separately because the larger settlers (post-larvae >2 mm) may have different substratum preferences than smaller ones (Seed 1969). Counts of mussel settlers on natural substrata were $\ln(x+1)$ or square transformed, if necessary, to homogenize variances (as detected in plots of residuals).

RESULTS

Environmental variability

The height of the sampling locations ranged from 0.80 to 2.33 m above the chart datum (Fig 1a), and did not differ significantly between tidepool and emergent rock habitats ($F_{1,8} = 1.01$; $p = 0.344$) or between ice-scoured and non-scoured strata ($F_{1,8} = 3.04$; $p = 0.119$), and there was no significant interaction between Habitat and Stratum ($F_{1,8} = 1.22$; $p = 0.301$). Ice-scoured tidepools were flushed within 2.8 to 3 h after low tide,
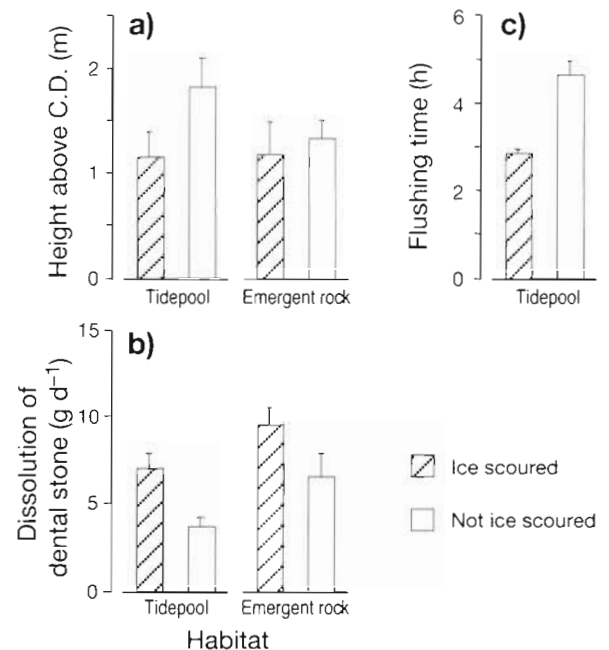

Fig. 1. Physical characteristics of the sampling locations at Cranberry Cove, Nova Scotia, Canada. Mean ± SE (n = 3 locations per Habitat × Stratum combination): (a) height of locations above chart datum (m); (b) water flux index: dissolution of dental stone (g d⁻¹) (average of 2 sampling periods); (c) flushing time: number of hours required after low tide for the pool to be flushed with new sea water (average of 2 sampling dates)

significantly faster ($t_4 = 5.329$; $p = 0.006$) than non-scoured tidepools which were flushed in 4.0 to 5.0 h (Fig. 1c). Average isolation times during low tide were 3.8 to 4.8 h for scoured tidepools and emergent rock and 6.5 to 8 h for non-scoured tidepools.

The water flux index, measured as the dissolution rate of dental stone, differed significantly with Habitat ($F_{1,16} = 37.55$; $p = 0.0001$), Stratum ($F_{1,16} = 48.14$; $p = 0.0001$), and Sampling Date ($F_{1,16} = 91.79$; $p = 0.0001$), but there were no significant interactions between these factors ($p > 0.40$). Water flux was higher on emergent rock than in tidepools and in ice-scoured than non-scoured areas (Fig. 1b). Although water flux and mussel settlement were measured at different times of the year, SWH were similar during both measurement periods: mean SWH (±SD) were 1.62 ± 0.54 and 0.73 ± 0.18 m during water flux measurements in May and June 1995, respectively, and 0.97 ± 0.23 and 0.86 ± 0.17 m during sampling of mussel settlement in September and October 1994, respectively.

The macrobenthic assemblage varied markedly between habitats and strata (Fig. 2). Filamentous and jointed calcareous macroalgae were found only in tidepools. Conversely, thick leathery macroalgae were
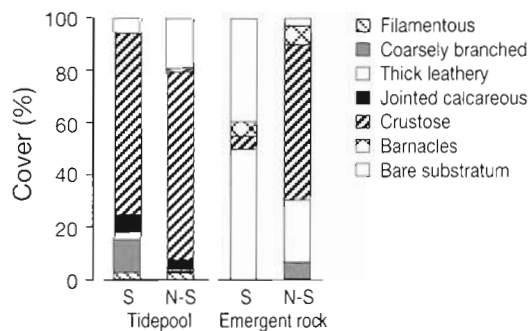
Fig. 2. Mean percentage cover of 5 functional form groups of macroalgae and of bare substratum and barnacles in ice-scoured (S) and non-scoured (N-S) tidepools and emergent rock in October 1994

rare (<3% cover) in tidepools, but common on emergent rock (24 and 50% for scoured and non-scoured strata, respectively). Ice-scoured emergent rock lacked coarsely branched macroalgae and had a much lower cover (5%) of crustose macroalgae than other Habitat × Stratum combinations (59 to 72%). Barnacle cover was somewhat higher on emergent rock (6 and 7% for scoured and non-scoured strata, respectively) than in tidepools (<1%).

Larval/postlarval availability

The abundance of *Mytilus* larvae and postlarvae >250 µm (the size at competency, Bayne 1965) in the sea at high tide (Fig. 3) did not vary significantly along ~1 km of shoreline within our study site, in either September ($F_{2,6}$ = 1.750; p = 0.252) or October ($F_{3,8}$ = 2.465; p = 0.137). However, the mean proportion of mussels >250 µm in these samples increased from 16% (n = 37) to 92% (n = 91) between the 2 sampling periods (Fig. 3).
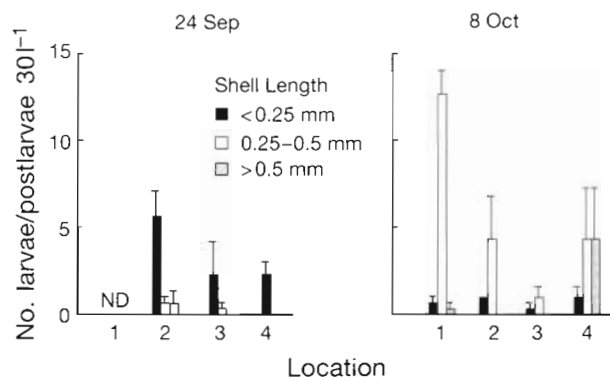

Fig. 3. Mean (±SE) concentration of *Mytilus* larvae and post-larvae [no. (30l)$^{-1}$] in sea water at high tide at 4 positions along ~1 km of shoreline on September 24 and October 8, 1994. n = 3 samples at each location. ND = no data

Settlement on artificial collectors

In September 1994, settlement rate of *Mytilus* on the artificial collectors did not vary significantly with Location (within Habitat × Stratum), Stratum or Habitat (Table 1 & Fig. 4a). In October 1994, settlement rate also did not vary significantly with Location, but it was significantly higher in the ice-scoured than non-scoured stratum and significantly higher on emergent rock than in tidepools; there was no significant interaction between Stratum and Habitat (Table 1 & Fig. 4a). In September, 33 and 38% of mussels in scoured and non-scoured tidepools, respectively, settled during the

Table 1 Three-way ANOVA of abundance of *Mytilus* settlers on artificial collectors (no. collector^{-1} tidal cycle^{-1}) and natural substrata [no. (100cm)$^{-2}$ (5d)$^{-1}$] in September and October 1994, and of *Mytilus* recruits on natural substrata [no. (100cm)$^{-2}$] between May and October 1994. Factors are Habitat (H), Stratum (S), and Location (L) (nested within H × S). For artificial collectors, degrees of freedom are: L (H × S) = 8,36; H, S and H × S = 1,8 if $p_{L(HXS)}$ < 0.25 and df = 1,44 if $p_{L(HXS)}$ > 0.25. For natural substrata, degrees of freedom are: L (H × S) = 8,24; H, S and H × S = 1,8 if $p_{L(HXS)}$ < 0.25 and df = 1,32 if $p_{L(HXS)}$ > 0.25. Pooled error is the estimate of experimental error when L is removed from the model (when $p_{Log(HXS)}$ > 0.25). *p < 0.05; **p < 0.01; ***p < 0.001

| Source	MS	F	p
Settlement on artificial collectors			
Sep Location (H × S)	1.50	1.07	0.41
Habitat	0.33	0.23	>0.25
Stratum	3.00	2.11	0.10 < p < 0.25
Habitat × Stratum	2.08	1.47	0.10 < p < 0.25
Residual	1.40		
Pooled error	1.42		
Oct Location (H × S)	11.52	1.93	0.086
Habitat	133.33	11.57	0.009 **
Stratum	225.33	19.56	0.002 **
Habitat × Stratum	24.08	2.09	0.186
Residual	5.97		
Settlement on natural substrata			
Sep Location (H × S)	23.97	3.19	0.013 *
Habitat	56.25	2.35	0.164
Stratum	0.03	0.001	0.974
Habitat × Stratum	90.25	3.77	0.088
Residual	7.53		
Oct Location (H × S)	1.50	0.42	0.898
Habitat	34.03	11.12	<0.005 **
Stratum	0.03	0.01	>0.25
Habitat × Stratum	14.69	4.80	<0.05 *
Residual	3.58		
Pooled error	3.06		
Recruitment on natural substrata			
Location (H × S)	6.17	8.87	0.000 ***
Habitat	7.47	1.21	0.303
Stratum	0.012	0.002	0.963
Habitat × Stratum	57.67	9.35	0.016 *
Residual	0.70		
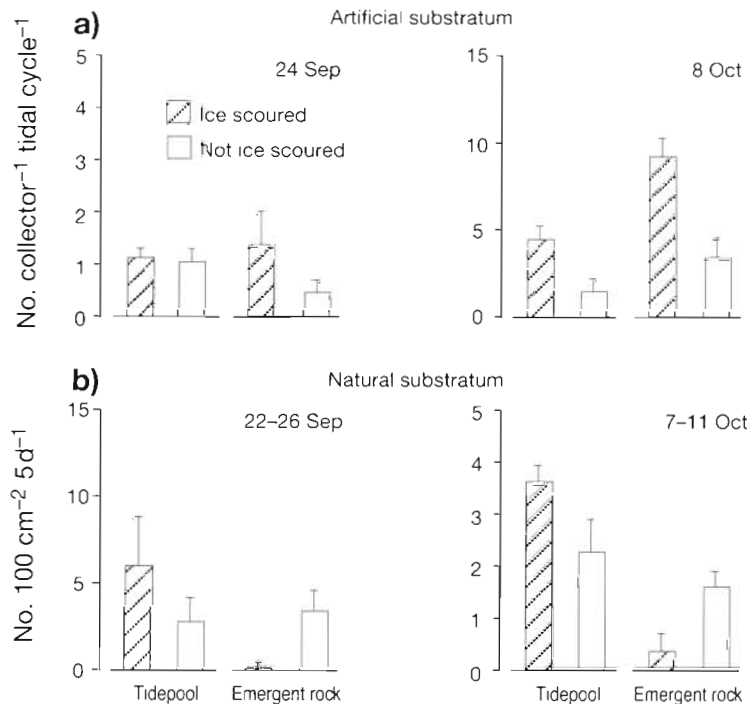
Fig. 4. Mean (±SE) settlement rate of *Mytilus* in ice-scoured and non-scoured tidepools and emergent rock (n = 3 locations per Habitat × Stratum combination): (a) settlement on artificial collectors (no. collector^{-1} tidal cycle^{-1}) on September 24 and October 8, 1994 (averaged for 4 collectors per location); and (b) settlement on natural substrata [no. (100 cm)$^{-2}$ (5 d^{-1})] on September 22 to 26 and October 7 to 11, 1994 (averaged for 3 quadrats per location)

were combined ($D_{25,21}$ = 0.316; p = 0.178; Fig 5). In October, >76% of mussels in all Habitat × Stratum combinations (n = 17 to 110) were <0.5 mm SL (Fig. 5). The size distribution of mussels did not differ significantly between scoured and non-scoured tidepools ($D_{52,17}$ = 0.182; p = 0.758) or emergent rock ($D_{110,40}$ = 0.241; p = 0.069). There was a statistically significant difference in size distribution ($D_{69,150}$ = 0.233; p = 0.012) between tidepools and emergent rock when these strata were combined, although the distributions were very similar (Fig. 5).

Regression analysis showed no significant relationship between mussel settlement rate on artificial collectors and the physical characteristics of locations (water flux, tidal height, and flushing time) when tidepools and emergent rock were analyzed separately. However, when locations in both habitats were included in the same regression analysis, there was a significant positive relationship between settlement rate and water flux in October ($F_{2,9}$ = 9.653; p = 0.006; water flux p = 0.002, tidal height p = 0.074).

period of tidal isolation (combining counts for all collectors: n = 12 and n = 13, respectively). In October, however, no mussels in non-scoured tidepools and only 8% (n = 69) in scoured tidepools settled during tidal isolation.

Mytilus sampled on the artificial collectors were <7 mm SL and the size distribution was highly skewed to the right (Fig. 5). In September, 0.5 to 1 mm mussels were the most abundant size class (Fig. 5), and size distributions did not differ significantly between scoured and non-scoured tidepools ($D_{13,12}$ = 0.378; p = 0.281), strata were not compared for the emergent rock habitat because of the small sample size (n = 5) for non-scoured areas. There was no significant difference between tidepools and emergent rock when strata
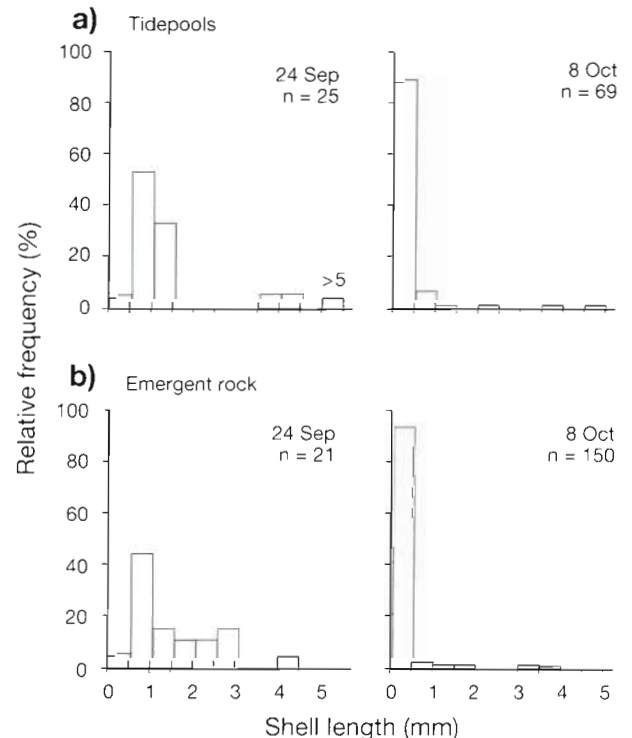

Fig. 5. Size-frequency distributions of *Mytilus* on artificial collectors in (a) tidepools and on (b) emergent rock on September 24 and October 8, 1994. Mussels from all collectors (n = 24; 4 collectors per location × 6 locations) from a habitat, including those from both ice-scoured and non-scoured strata, are pooled. In tidepools in September, mussels in the last bar are 5.05 to 7 mm SL

Settlement on natural substrata

The settlement pattern of *Mytilus* on natural substrata differed markedly from that on the artificial collectors. In September 1994, settlement rate varied significantly with Location, mainly because of differences among ice-scoured tidepools ($F_{2,24}$ = 3.792; p = 0.037); differences among locations for other Habitat × Stratum combinations were non-significant (Table 1 & Fig. 4b). There were no significant differences in settlement rate with Habitat or Stratum, and no significant interaction between Stratum and Habitat (Table 1 & Fig. 4b). In October 1994, however, there was no significant variation in settlement rate among locations but there was a significant interaction between Habitat and Stratum (Table 1): settlement rate was significantly higher in ice-scoured tidepools than on the scoured emergent rock (SNK, p < 0.05), but did not differ significantly among the other Habitat × Stratum combinations (Fig. 4b).

In contrast to artificial collectors, the size distributions of *Mytilus* on the natural substratum were relatively uniform and the mussels were larger (Fig. 6). In October, only 4 % (n = 52) of mussels in tidepools and no mussels on emergent rock were <0.5 mm SL, the dominant size class on artificial collectors. We only found 1 mussel >5 mm SL on artificial collectors; however, mussels sampled on the natural substratum were up to 12 mm SL, and 31 % (n = 109) in September and 20 % (n = 69) in October were >5 mm SL. The size distributions of mussels did not differ significantly between ice-scoured and non-scoured pools for either sample period (September: $D_{53,24}$ = 0.152; p = 0.803; October: $D_{32,20}$ = 0.262; p = 0.321); strata were not compared for the emergent rock because of the small sample sizes in scoured areas (n = 2 and 3 in September and October, respectively). The size distributions of mussels in tidepools and on emergent rock were similar in September ($D_{77,32}$ = 0.241; p = 0.131), but differed significantly in October ($D_{52,17}$ = 0.519; p = 0.002) when mussels <1 mm SL were absent on emergent rock but comprised the most abundant size class in tidepools (Fig. 6).

To examine the relationship between mussel settlement rate on the natural substratum and the physical and biological characteristics of locations, we used 3 PCA factors for tidepools (94.9 % of variance) and emergent rock (92.8 % of variance) and 4 PCA factors for the combined habitats (87.7 % of variance) (Table 2). There was no consistent relationship between settlement rate and PCA factor scores between sample periods and mussel size classes (Tables 2 & 3). In September, mussels <2 mm SL on emergent rock varied significantly with a factor (Factor 1) with high positive
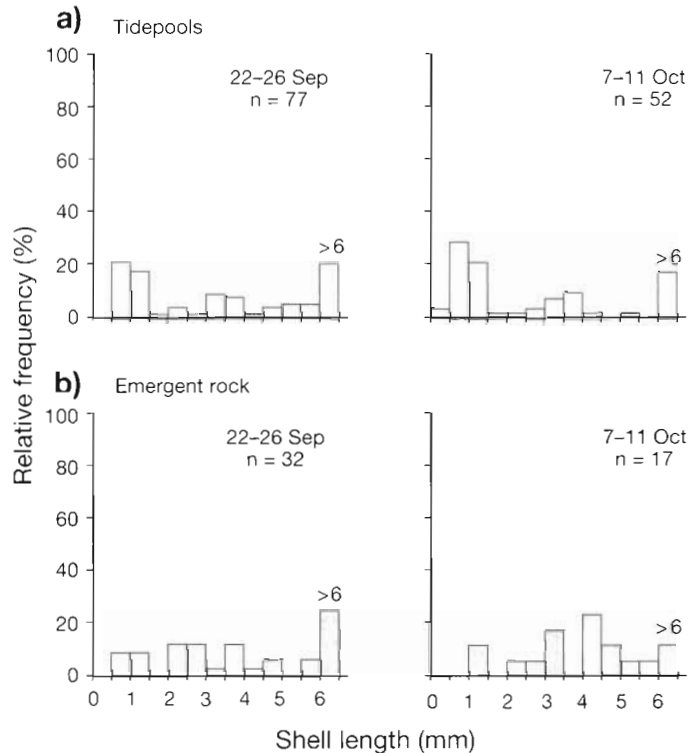

Fig. 6. Size frequency distributions of *Mytilus* on natural substrata in (a) tidepools and on (b) emergent rock on September 22 to 26 and October 7 to 11, 1994. Mussels from all quadrats (n = 18; 3 quadrats per location × 6 locations) from a habitat, including those from both ice-scoured and non-scoured strata, are pooled. Mussels in the last bar are 6.05 to 12 mm SL

component loadings for water flux and crustose macroalgae. In October, mussels <2 mm SL in tidepools varied significantly with a factor (Factor 1) with high negative component loadings for flushing time, bare space, tidal height, and water flux index. When both habitats were combined in the same analysis, mussels >2 mm SL in September varied significantly with one factor (Factor 3) with a positive loading for coarsely branched algae and a negative loading for bare space, and another (Factor 4) with a positive loading for thick leathery macroalgae and a negative loading for coarsely branched macroalgae. In contrast, mussels <2 mm SL in October varied significantly with one factor (Factor 1) with positive loadings for crustose macroalgae, water flux, and jointed calcareous and filamentous algae, and another (Factor 2) with a positive loading for tidal height.

Recruitment

On natural substrata, the pattern of recruitment of *Mytilus* after 5 mo reflected the pattern of settlement (Fig. 7). Recruitment rate varied significantly with
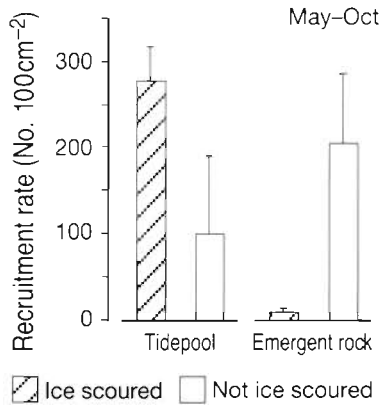
Fig. 7. Mean (±SE) abundance of *Mytilus* recruits on natural substrata [no. (100 cm)$^{-2}$] in ice-scoured and non-scoured tidepools and emergent rock (n = 3 locations per Habitat × Stratum combination) sampled in October 1994 from quadrats cleared of mussels in May 1994 (averaged for 3 quadrats per location)

Location: there was significant variation among scoured tidepools ($F_{2, 24}$ = 30.336; p < 0.001) but not among locations in the other Habitat × Stratum combinations. There was a significant interaction between Habitat and Stratum (Table 1). Mussel recruits were significantly more abundant in ice-scoured tidepools than on scoured emergent rock (SNK, p < 0.05); there was no significant variation among the other Habitat × Stratum combinations.

DISCUSSION

Settlement rate of *Mytilus* on artificial collectors was directly related to water flux, and was highest on the ice-scoured emergent rock and lowest in non-scoured tidepools. This pattern probably reflects an increase in larval supply with increased water flux. Bushek (1988) found a similar positive relationship between barnacle settlement rate and water motion which he attributed to both larval supply and selective settlement. In our study, settlement on collectors placed on ice-scoured emergent rock may also have been enhanced by the apparent unsuitability of the surrounding substratum (where settlement rate was low). A similar effect has been reported by Pineda (1994), who found that barnacles settled at higher densities at sites surrounded by unsuitable sandy substratum. Horizontal variability in the availability of settlers did not contribute to the pattern, since the abundance of competent larvae in the surrounding sea water did not vary significantly over the 1 km of shore spanning our sampling locations.

Artificial collectors have been widely used in studies monitoring the abundance of mytilid larvae (King et al. 1990 and references therein, Cáceres-Martínez et al. 1994, Molares & Fuentes

Table 2. Results of PCA of physical and biological characteristics of locations at Cranberry Cove, Nova Scotia. Only factors with eigenvalues >1 and components with loadings >0.5 or < –0.5 are shown. Components are listed in order of descending loadings. n = 6 locations for tidepools or emergent rock, and n = 12 when the habitats are pooled. Functional form groups of macroalgae: FIL = filamentous; CB = coarsely branched; JC = jointed calcareous; TL = thick leathery; CR = crustose; BA = barnacles; BE = bare substratum. Physical characteristics: TID = tidal height; WFI = water flux index; FLU = flushing time

Habitat	Eigenvalue	% Variance explained	Components
Tidepool			
Factor 1	3.801	47.51	–FLU, –BE, –TID, –WFI, FIL, JC, CB
2	2.724	34.05	–CB, FIL, JC, CR, WFI
3	1.068	13.35	–CR
Emergent rock			
Factor 1	2.945	42.07	WFI, CR, –BE, TID
2	2.202	31.46	–TL, BA, BE
3	1.347	19.24	CR, –TID
Combined habitats			
Factor 1	3.571	39.68	CR, WFI, JC, FIL, –TL, –BA, –BE
2	1.839	20.43	TID, –FIL
3	1.444	16.05	CB, –BE
4	1.039	11.54	TL, –CB

Table 3. Significant forwards stepwise multiple regressions relating abundance of *Mytilus* <2 and >2 mm SL on natural substrata in September and October 1994 to factor scores obtained by PCA on physical and biological characteristics of locations at Cranberry Cove, Nova Scotia. F1 to F4 = PCA factors from Table 2. Independent variables with significant partial *F*-values are shown in bold

Habitat	Month	Size (mm SL)	Model	R^2	F	p
Tidepool	Oct	<2	3.093 + 2.194(**F1**)	0.925	49.25	0.002
Emergent rock	Sep	<2	0.333 + 0.248(**F1**)	0.692	8.98	0.040
Combined habitats	Sep	>2	1.972 + 1.141(**F3**) – 1.013(**F4**)	0.672	9.21	0.004
	Oct	<2	0.861 + 0.634(**F1**) – 0.485(**F2**) – 0.287(**F4**)	0.800	10.68	0.007

1995), but such studies cannot fully explain settlement patterns between habitats or sites because they do not account for the spatial variability of the natural substratum. In our study, the settlement patterns of *Mytilus* differed markedly between artificial collectors and natural substrata. In contrast to the collectors, settlement on natural substrata was greatest in ice-scoured tidepools and minimal on scoured emergent rock. This difference in settlement patterns between artificial and natural substrata is probably related to variation in the macrobenthic assemblage between habitats and strata. In this study, ice-scoured emergent rock was devoid of filamentous or coarsely branched macroalgae, which are known to promote settlement of *Mytilus* (reviewed by Seed 1976, Seed & Suchanek 1992), and had less crustose macroalgae than the other habitat and stratum combinations. Multiple regression did not reveal a consistent relationship between settlement rate on natural substrata and any particular macroalgal group, but there were some associations between either small or large settlers and a suite of biological and physical factors.

In October, mussels <1 mm SL on natural substrata were common in tidepools but absent on emergent rock. Filamentous and jointed calcareous algae, which were found only in tidepools, may be more suitable settlement sites for mussel larvae and early postlarvae than thick leathery macroalgae, the predominant erect form on emergent rock. Also, mussels <1 mm SL settle in tidepools during the period of tidal isolation, although only a small proportion of mussels settled on our artificial collectors during tidal isolation in October.

The relationship between the settlement rate of *Mytilus* and macroalgal substrata may depend upon both active substratum choice and passive hydrodynamic processes, and the processes and cues involved probably vary with spatial scale. Active substratum choice by *Mytilus* was suggested by Bourget et al. (1994) who examined the establishment of an epibenthic community on panels with various combinations of scales of substratum heterogeneity (1, 10, and 100 mm wide grooves). Bivalve settlers, including *M. edulis*, were aggregated at particular scales of heterogeneity, suggesting they are active settlers; in contrast, bryozoans were uniformly distributed, suggesting they are passive settlers. However, Harvey et al. (1995) found that passive settlement processes were sufficient to explain settlement patterns at decimetre scales (on plastic filamentous substrata) of several species of bivalves, including *M. edulis*. Cáceres-Martínez et al. (1994) have suggested that the association of postlarvae of *M. galloprovincialis* with filamentous substrata results from passive ensnarement of these substrata by byssus threads secreted by the postlarvae, rather than active selection.

Most *Mytilus* settlers in our study (with the exception of those on artificial collectors in October) were >0.5 mm SL and were probably not settling for the first time. Secondary settlement of postlarvae of *M. edulis* on adult mussel beds, after a second pelagic phase following detachment from initial settlement sites on filamentous algae, was first described by Bayne (1964). Subsequent studies have shown that movement of postlarval mussels, either by drifting in the water column on mucous threads (Sigurdsson et al. 1976, De Blok & Tan-Maas 1977, Lane et al. 1985) or by crawling along the substratum (Harger 1968, Seed & Suchanek 1992, Cáceres-Martínez et al. 1994), may be important in determining distributional patterns of recruits. However, settlement behaviour of *Mytilus* appears to vary considerably among populations: mussels may settle directly onto adult beds (reviewed by Seed & Suchanek 1992), or they may repeatedly settle on various substrata and disperse until they die or reach a suitable settlement site (Cáceres-Martínez et al. 1994).

In our study, the size of mussel settlers was much smaller on artificial collectors than on natural substrata. We found only 1 mussel >5 mm SL on a collector, which is consistent with the small sizes reported in previous studies using artificial collectors (e.g. Bayne 1964, Bohle 1971, King et al. 1990). In contrast, 20 to 30% of settlers on natural substrata were >5 mm SL, suggesting that postlarval mussels in this area move repeatedly. Paine (1974) also observed that relatively large (>3 cm SL) *M. californianus* colonized cleared plots in the intertidal zone in Washington, USA. The filamentous substrata generally used in artificial collectors may be more suitable for smaller, early postlarvae than for the larger, later stages (Seed 1969). Also, mussels >5 mm SL may disperse by crawling but are probably too heavy to drift on byssal threads, reducing the likelihood of sampling them in studies which use collectors suspended in the water column.

The pattern of recruitment of *Mytilus* that we observed on natural substrata after 5 mo reflected the pattern of settlement after 5 d, suggesting that spatial variations in settlement are important in determining the abundance and distribution of mussels in this population. However, the recruitment that we measured between May and October may largely reflect a fall peak in primary settlement, as was evident from the increase in settlement rate between September and October (see also Pedersen 1991). Recruitment patterns of a number of groups of benthic invertebrates have been related to their settlement patterns, particularly in cases where settlement rate is low (reviewed by Rodríguez et al. 1993). However, little is known about recruit-settler relationships in mussels.

The settlement and recruitment patterns of *Mytilus* that we observed on natural substrata correspond to

the patterns of distribution and abundance of mussels on ice-scoured but not non-scoured regions of the shore. On non-scoured substrata, mussels occur in smaller patches in tidepools than on the emergent rock. The rates of settlement and recruitment (after 5 mo) that we measured did not differ significantly between non-scoured tidepools and emergent rock, suggesting that this pattern is generated by later post-settlement processes. In contrast, mussels are rare on ice-scoured emergent rock, which probably reflects low settlement rates, as indicated by our low counts of both settlers and recruits on the natural substratum in these areas. Settlement rate is clearly not limited by larval supply to these areas, since the highest settlement rates were recorded on artificial collectors on ice-scoured emergent rock. Our study underscores the importance of measuring settlement on both a standardized artificial substrate and the natural substratum to compare the relative roles of larval supply and substratum type in determining patterns of settlement in a spatially variable environment.

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