

# Scales of coastal heterogeneity: influence on intertidal community structure

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**ABSTRACT:** The effect of 3 spatial heterogeneity scales on benthic community species richness, diversity, total biomass, biomass of dominant taxa (Fucaceae, littorinids and *Mytilus edulis*) and *M. edulis* recruitment was investigated in the intertidal zone over a 90 km portion of the south shore of the St. Lawrence Estuary, Québec, Canada. Three scales of coastline heterogeneity and cascade (interaction) of these scales were examined using a nested and crossed design with replication. Large-scale heterogeneity (LSH) was determined with a shore heterogeneity index (SHI) which was the ratio of the length of the coastline, measured on a 1:20 000 map, over the 1 km linear distance between end points. The SHI were classified as low, medium, and high. Within each of the 3 categories of LSH, 2 levels of medium-scale heterogeneity (MSH) were examined: linear coasts (100 m linear portions of the shore) and headlands (mean length  $52 \pm 5$  m). Within each of the MSH sections, small-scale heterogeneity (SSH) was investigated by sampling twenty  $10 \times 10$  cm quadrats at positions upstream, apex and downstream. SSH was represented as 2 types of rock surfaces, flat exposed surfaces and crevices ( $n = 540$ ). LSH did not influence the community characteristics considered, MSH had only a minor influence on them but SSH had a major influence on them. LSH explained 1% or less of biomass variance of taxa encountered; MSH explained at most 11% of biomass of littorinids, SSH explained 30% of variance in total biomass, 28% of biomass of *M. edulis*, and 21% of biomass of Fucaceae and littorinids. We also observed that some scale combinations affected the diversity and biomass of littorinids.

**KEY WORDS:** Spatial scale · Coastal heterogeneity · Small-, medium- and large-scale heterogeneity · Species richness · Diversity · Biomass · Intertidal

## INTRODUCTION

Spatial heterogeneity may influence community structure through a variety of factors and patterns (Palmer & Poff 1997). For example, topographical heterogeneity may influence intertidal community structure by modifying diversity (Eadie & Keast 1984, Menge et al. 1985, Bourget et al. 1994, Guichard & Bourget 1998), biomass (Archambault & Bourget 1996, Cusson & Bourget 1997, Guichard & Bourget 1998) and distribution and abundance of dominant organisms (Raffaelli & Hughes 1978, Genin et al. 1986, Bourget et al. 1994). Topographical heterogeneity may also influence processes such as predation intensity (Menge et al. 1985, Gosselin & Bourget 1989), competition

(Menge 1976) and larval dispersal and recruitment (Lauga 1997, Archambault & Bourget 1999).

However, the observation scale may influence perceptions of the community patterns and processes (Levin 1992). New emerging properties may appear at different observation scales (Dayton & Tegner 1984, Allen & Hoekstra 1991, Kolasa & Rollo 1991). Some community members may experience the environment over a unique range of scales (Levin 1992) and physical and biological properties may change with scale. Thus, multi-scale investigations are needed to understand how scales influence community structure in complex systems.

Examining how community characteristics are influenced by the scales used by the observer is considered necessary to understand better communities processes. Although there have been multi-scale studies in the pelagic environment (Schneider 1994), few stud-

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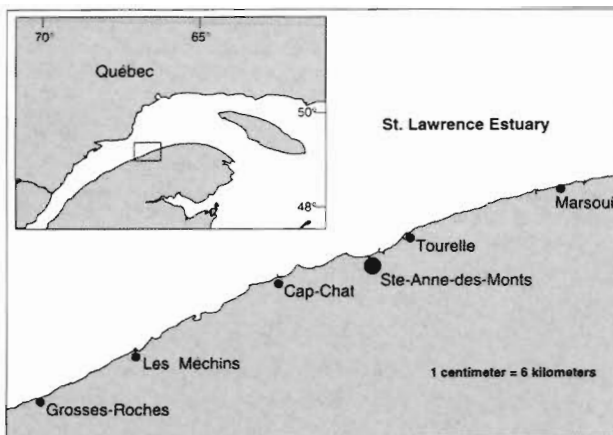


Fig. 1. Study region along the south shore of the St. Lawrence Estuary, Québec, Canada

ies have been carried out in the benthic environment. Thrush et al. (1996) tested how differences in aerial extent (0.203, 0.81, 3.24 m<sup>2</sup>) of disturbance influenced macrofaunal colonization on a sandflat. Lindergarth et al. (1995) investigated the effect of spatial scales between 1 and 10<sup>5</sup> m on abundance and age structure of 2 infaunal bivalves. Archambault & Bourget (1996) examined the influence of 3 spatial scales, large- (1 km), medium- (100 m) and small-scale (≤20 cm) heterogeneity, and studied their influence on some characteristics of an intertidal benthic community. They showed that small-scale heterogeneity influenced some community characteristics more (e.g. abundance) while others (e.g. diversity) were best explained by the medium scales. Little information is available on the influence of scales between km (large) and cm (small). In the present study, we examine the influence of 3 spatial scales (large, medium, small) of coastal heterogeneity on the intertidal benthic community characteristics (biomass, diversity, richness and recruitment) in the St. Lawrence Estuary, Québec, Canada. We test the null hypothesis that indices of community structure were not modified by the spatial scale and topographical heterogeneity considered.

## METHODS

This study was carried out over a 90 km portion of the south shore of the St. Lawrence Estuary between Grosses-Roches and Marsoui (Fig. 1). Three scales of coastline heterogeneity and combinations of these scales were examined (Fig. 2): large-scale heterogeneity (LSH, km scale with 3 levels, see below), medium-scale heterogeneity (MSH) represented by headlands (ca 52 ± 5 m, 2 levels) and small-scale heterogeneity (SSH, <10 cm, 2 levels).

**Large-scale heterogeneity (LSH).** The 90 km long shore was divided in linear sections of 1 km and, for each section, a shore heterogeneity index (SHI) was determined. SHI can be expressed as  $SHI = LCT/LD$ , where LCT represents the length of the coastline measured on a 1:20 000 topographical map (Energie & Ressources, Québec) and LD is the linear distance (1 km) separating the end points of the section of coastline (Bergeron & Bourget 1986, Archambault & Bourget 1996). The SHI values (n = 90) were classified into 3 group levels, based on the SHI frequency distribution plot: low (L = 1.0 to 1.2, n = 67), medium (M = 1.3 to 1.6, n = 14) and high (H = 1.7 to 2.8, n = 9).

**Medium-scale heterogeneity (MSH).** Headlands and linear coasts were used as MSH sources. A headland was loosely defined as any portion of rocky shore longer than wide, emerging at high tide, and extending into the sea perpendicular to the shoreline. A linear coast corresponds to a 100 m linear portion of the shore. Within each of the 3 levels of LSH (L, M, H), 2 levels of MSH were examined: linear coasts (LC) and headlands (HD) (mean length = 52 ± 5 m). Three replicates (REP) of each treatment combination (MSH × LSH) were examined for a total of 18 sections. Because of the limited availability of headlands in the high category (H) of LSH, we used 2 different headlands at one site, but treated them as 2 separate sections. We felt

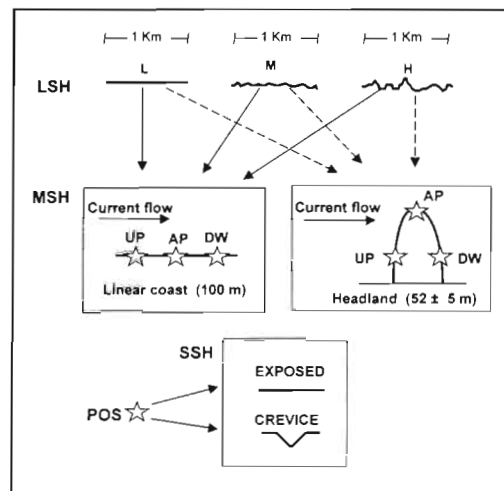


Fig. 2. Sampling design used in this study. LSH is large-scale heterogeneity with 3 levels with 3 replicate samples for each level: low (L), medium (M), high (H). MSH is medium-scale heterogeneity with 2 levels with 3 replicate samples for each level, 52 ± 5 m headlands and linear coasts (100 m linear portions of the shore). These were further divided into 3 positions (POS): upstream (UP), apex (AP), downstream (DW), which are represented by stars. SSH is small-scale heterogeneity divided into 2 levels with 5 replicate samples for each, crevices (CR) and exposed flat surfaces (EX)

justified to use this procedure as the variance among headlands at a single section was similar to that among headlands at different sections. For each of these individual sections, 3 sampling positions (POS) were selected in relation to residual current flow in the St. Lawrence: upstream (UP) facing the residual current flow, apex (AP) at the tip of the headland where the residual current was tangential to this position and downstream (DW) below and protected from the residual current. The distance between positions on headlands and those on the linear coast were identical. All sections consisted of similar rock types and were not influenced by human activity or major freshwater tributaries.

**Small-scale heterogeneity (SSH).** The area available for sampling at the apex of the headland was limited by the width of the headland, so to achieve the same sampling protocol at all positions (upstream, downstream and apex positions), we limited the length of the sampling area. Similarly, since there are differences in bathymetry between the tip and the base of the headland, which influence immersion time and thus community growth and structure, the height of the sampling area was fixed. Thus, for each position (POS) of the MSH, a sampling area of 0.5 m wide by 3 m long was selected halfway along the length of the headland, in the midshore zone between the upper limit of *Mytilus edulis* and the lower limit of Fucaceae algae. Within this area 2 types of rock surfaces (SSH) were sampled: flat exposed surfaces (EX) and crevices (CR) between 2 and 4 cm depth. For each potential preselected and prenumbered site of each type of surface POS within each area, 5 quadrats (10 × 10 cm) were randomly selected ( $n = 540$  samples). EX surfaces had irregularities smaller than 1 cm and CR surfaces contained a 2 to 4 cm crevice over 40% of the quadrat area.

**Sampling procedure.** Samples were collected by removing organisms from the crevices and exposed surfaces. The algae were collected only if their holdfasts were located within the 10 × 10 cm quadrat. To minimize the variance due to recruitment and growth, all collections were made over a 2 wk period from 27 July to 10 August 1995. Organisms in all samples were identified to species, when possible (Table 1). The samples were sieved to 500  $\mu$ m and the macrofauna (>1 mm) was counted and weighed to the nearest mg using a Mettler PE balance. Recruitment for *Mytilus edulis* was estimated by the number of recently settled young *M. edulis* (between 500 and 1000  $\mu$ m). Two Shannon-Weaver species diversity indices were calculated ( $H' = -\sum p_i \ln p_i$ , where  $p_i$  is the proportion of individuals (100 cm<sup>2</sup>) of the  $i$ th taxon; Magurran 1988).  $H'_a$  (abundance) diversity was determined using the number of individuals of each species

per quadrat and  $H'_b$  (biomass) using biomass data for each species in each quadrat.  $H'_b$  is a useful index when there are a range of sizes observed among individuals of the same species (Wilhm 1968, Magurran 1988).

The relationship between small-scale topographical heterogeneity and some biological response variables (total biomass, biomass of Fucaceae algae, littorinids and *Mytilus edulis*) was examined using the following technique. For each quadrat, a topographical heterogeneity index (THI) and a fractal index (FRI) were estimated. THI was determined from the ratio of the actual measured length of a quadrat cross-section and 10 cm linear distance between the end points of the section. The THI index for each quadrat was determined by the mean of 4 cross sections, 2 horizontal and 2 vertical. To calculate FRI we used the following procedure. For each quadrat, 4 surface profiles (2 horizontal and 2 vertical) were taken using a woodworker's profile gauge (1 mm resolution), the profiles were graphed onto paper in the field and digitized with a scanner in the laboratory. Fractal dimensions of the profiles were determined using a box-counting method (Liebovitch & Toth 1989). This technique compares grid sizes and numbers of squares containing any part of the profile. The fractal dimension is given by the regression slope of  $\log[N(S)]$  to  $\log(1/S)$ , where  $S$  is the box size and  $N$  is the number of mesh boxes that contained part of the profile.

**Statistical treatment.** Nested ANOVAs with crossed factors and replication were used to examine the effect of LSH (L, M, H), MSH (LC, HD), POS (UP, AP, DW) and SSH (EX, CR) on total biomass and biomass of *Mytilus edulis*, Fucaceae and littorinids. Fucaceae data

Table 1. List of taxa present in the samples. Proportion of the total biomass of the dominant taxa is given in parentheses

Fauna	Flora
<i>Mytilus edulis</i> (33%)	Fucaceae (61%)
Littorinids (3%)	
<i>Acmæa testudinalis</i>	<i>Acrosiphonia arcta</i>
<i>Balanus balanoides</i>	<i>Dictyosiphon</i> sp.
<i>Buccinum undatum</i>	<i>Ectocarpus siliculosus</i>
<i>Cingula aculeus</i>	<i>Elachista fucicola</i>
<i>Dendronotus frondosus</i>	<i>Enteromorpha</i> sp.
<i>Fabricia sabella</i>	<i>Petalonia fascia</i>
<i>Hiatella arctica</i>	<i>Porphyra</i> sp.
<i>Lacuna vincta</i>	<i>Ulvaria obscura</i>
<i>Mya arenaria</i>	
Nematoda	
Nemertinea	
Oligochaeta	
Platyhelminthes	
<i>Skenopsis planorbis</i>	
<i>Thais lapillus</i>	





square root transformed, biomass of Fucaceae and *M. edulis* biomass was log transformed and littorinid biomass was  $1/(x + 1)$  transformed. There was a high correlation between THI and FRI and we did not introduce FRI into the multiple regression analysis. Relationships between dependent variables (total biomass, biomass of Fucaceae, littorinids and *M. edulis*) and the FRI, were tested using a simple regression model.

**Wave force at study sites.** Waves intensity at each site was estimated as the percentage of plastic Vexar bags at each POS of each site remaining 2 mo after installation (mid-July to mid-September). Five  $5 \times 10$  cm Vexar bags were initially fastened to the rock substrata in the midshore zone at each POS by 2 stainless steel screws (3 cm, no. 8) with 1.5 cm diameter stainless steel washers. An ANOVA with crossed factors and replicates was used to examine the effect of MSH (LC, HD) and POS (UP, AP, DW) on the percentage of bags remaining after 2 mo.

## RESULTS

### Biomass

Among possible direct or indirect interaction effects between factors likely to influence total biomass at all scales, only SSH had a significant effect (Table 2). Total biomass was approximately  $10\times$  higher per unit area in crevices compared to exposed surfaces (Fig. 3). A clear pattern emerged when individual taxa were examined more closely (Table 2). LSH had no significant effect on biomass of individual taxa. There was some influence by MSH (headland or linear coasts) with a significant heterogeneity effect on biomass of littorinids and Fucaceae (Table 2). There was higher Fucaceae biomass on headlands than at linear coasts, and the opposite for littorinids (Fig. 3). Within headlands and linear coasts, influences were minor; position influenced littorinid biomass only (Table 2).

A significant MSH-POS-SSH interaction was observed for littorinid biomass (Table 2). Littorinids were significantly more abundant at linear coasts than around headlands (Fig. 4) and, within headlands, biomass was higher in both crevices and exposed surfaces downstream and lowest at the apex (Fig. 4).

For SSH, however, there was a significant heterogeneity influence on all variables examined (Table 2). Total biomass as well as biomass of each taxon examined was significantly higher in crevices than on exposed surfaces (Fig. 3).

Multiple regression using LSH, MSH and SSH as independent variables, and total biomass and biomass of Fucaceae, littorinids and *Mytilus edulis* was carried out to test the relative influence of each heterogeneity

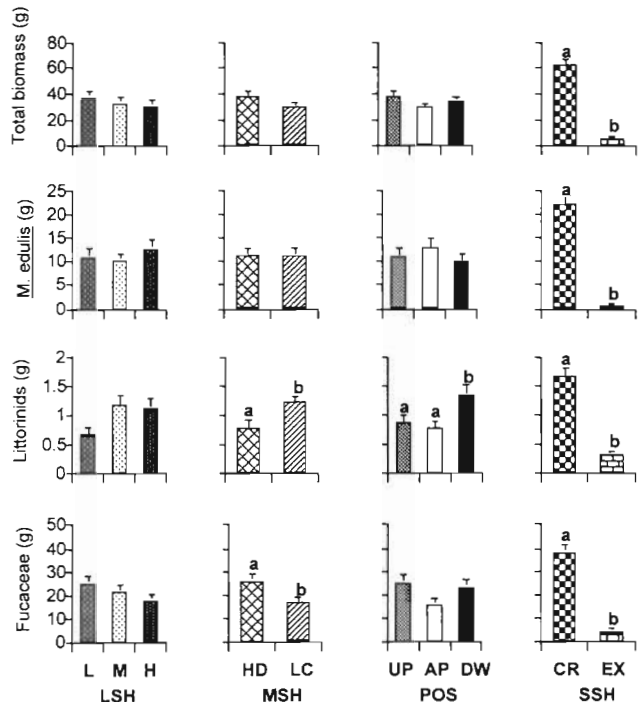


Fig. 3. Mean total biomass and biomass of *Mytilus edulis*, littorinids and Fucaceae for 3 scales of heterogeneity. LSH is large-scale heterogeneity with 3 levels: low (L), medium (M), high (H). MSH is medium-scale heterogeneity with 2 levels; 52 m headlands (HD) and linear coasts (LC) (100 m linear portions of the shore). These were further divided into 3 positions (POS): upstream (UP), apex (AP), downstream (DW). SSH is small-scale heterogeneity divided into 2 levels: crevices (CR) and exposed flat surfaces (EX). Values ( $\pm$  SE) differing significantly from one another are indicated by different letters

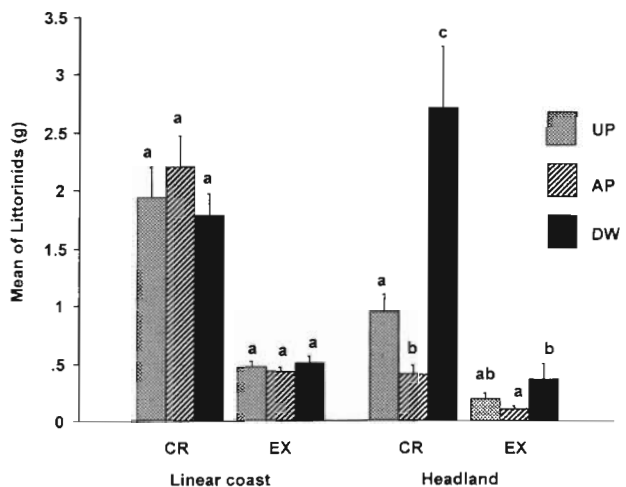


Fig. 4. Mean biomass of littorinids for medium-scale heterogeneity with 2 levels: linear coast and headland; small-scale heterogeneity with 2 levels: exposed (EX) and crevice (CR); and position with 3 levels: upstream (UP), apex (AP) and downstream (DW). Within position (small-scale heterogeneity); values ( $\pm$  SE) differing significantly from one another are indicated by different letters



### Recruitment

Recruitment of *Mytilus edulis* was not influenced by LSH or MSH, nor by position around headlands or linear coasts (Table 5). However, for SSH, recruitment was significantly higher in crevices (13×) than on exposed surfaces.

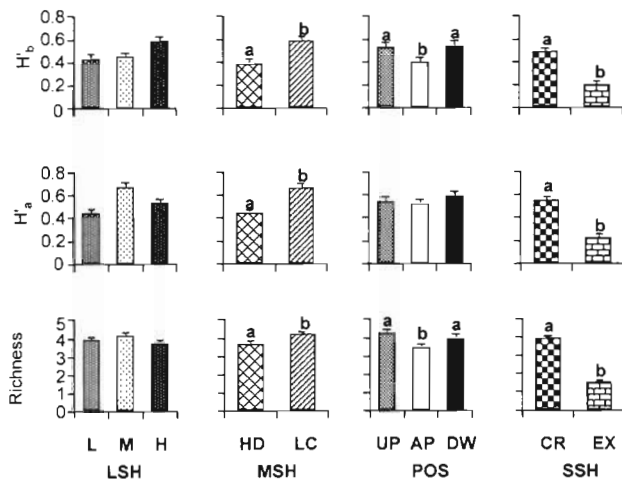


Fig. 5. Mean of  $H'_b$  and  $H'_a$  diversity and richness for 3 scales of heterogeneity. Large-scale heterogeneity (LSH) with 3 levels: low (L), medium (M), high (H); medium-scale heterogeneity (MSH) with 2 levels: linear coasts (LC) and headlands (HD); small-scale heterogeneity (SSH) with 2 levels: crevices (CR) and exposed flat surfaces (EX); and position (POS) with 3 levels: upstream (UP), apex (AP), downstream (DW). Values ( $\pm$ SE) differing significantly from one another are indicated by different letters

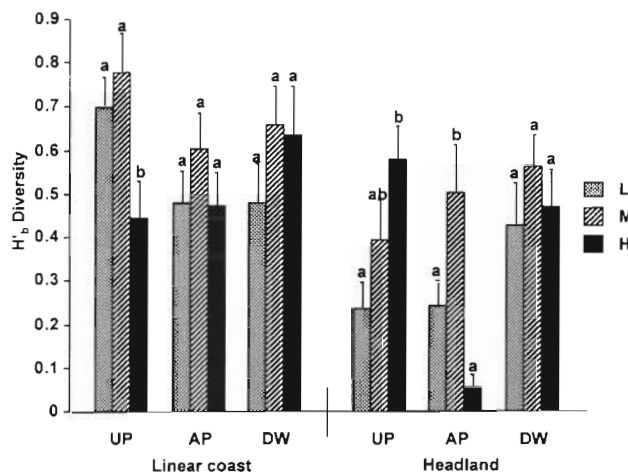


Fig. 6. Mean  $H'_b$  diversity for large-scale heterogeneity with 3 levels [low (L), medium (M) and high (H)] and medium-scale heterogeneity with 2 levels (linear coast and headland). Position with 3 levels: upstream (UP), apex (AP) and downstream (DW). Within large-scale heterogeneity (Position) values ( $\pm$ SE) differing significantly from one another are indicated by different letters

Table 5. Nested and crossed ANOVA with replication showing the effect of heterogeneity on recruitment of *Mytilus edulis*. Recruitment values were log + 1 transformed. LSH = large-scale heterogeneity, MSH = medium-scale heterogeneity, POS = positions. Small-scale heterogeneity (SSH) was not included in the model because of the low recruitment on exposed surfaces. Error 1 = Replicate(LSH\*MSH), Error 2 = Replicate\*POS(LSH\*MSH)

Source of variance	df	MS	F	p
LSH	2	2.5608	0.2812	0.760
MSH	1	0.3494	0.0384	0.848
LSH*MSH	2	26.9580	2.9599	0.090
Error 1	12	9.1078		
POS	2	6.1278	1.1807	0.324
LSH*POS	4	6.5522	1.2624	0.312
MSH*POS	2	2.7063	0.5214	0.600
LSH*MSH*POS	4	3.6505	0.7034	0.597
Error 2	24	5.1901		
Error model	216	1.2093		
Corrected total	269			

### Wave force

More bags remained at linear coast than at headland sites, except in the downstream headland positions. Differences among sites were not statistically significant except for the downstream headland site where nearly all bags remained (Fig. 7).

### DISCUSSION

Our results support the hypothesis that indices of community structure (recruitment, diversity and biomass) were modified by (1) spatial scale, (2) topo-

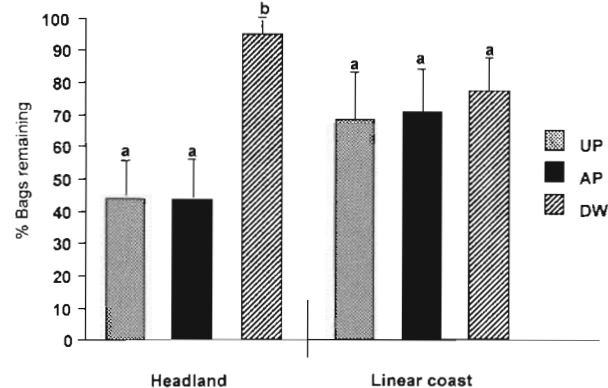


Fig. 7. Mean proportion of bags remaining for positions upstream (UP), apex (AP), downstream (DW), at medium-scale heterogeneity for linear coast (LC) and headland (HD) sites. Within position (medium-scale heterogeneity) values ( $\pm$ SE) differing significantly from one another are indicated by different letters

graphical heterogeneity, and (3) interaction among scales of heterogeneity. They showed that SSH influenced all community characteristics examined, MSH had a minor effect on the same characteristics, and LSH had no influence on the community characteristics. Two scale combinations (MSH-POS-SSH, LSH-MSH-POS) did influence littorinid biomass and diversity respectively.

### Influence of large-scale heterogeneity

Biogeography traditionally examined species distribution at large scales (> km) (Ardisson et al. 1990, Ardisson & Bourget 1992, Sanvicente-Añorve et al. 1996). There have been few attempts to quantify levels of coastal heterogeneity and examine their influence on community characteristics. The current LSH did not influence biomass, diversity or richness of an intertidal community, results consistent with those of Archambault & Bourget (1996). In contrast, Lindergarth et al. (1995) showed that spatial scales of 1 to 10 km were important in explaining variability in infaunal bivalves distribution, but large scales of 10 to 100 km did not influence abundance and age structure of the same community. The different conclusions could be explained by differences in community type. In our study, LSH did not influence *Mytilus edulis* recruitment, contrary to previous reports of LSH influencing recruitment on artificial substrata and larval dispersion in the same area (Archambault & Bourget 1999). In that study, carried out in the subtidal zone, *M. edulis* recruitment was significantly greater within bays than on a straight coast. The influence of LSH has been reported for spatial distribution and abundance of *Acanthaster planci* on scales of about 0.5 to 10 km (Black & Moran 1991), where a close correspondence was found between regions of highest larval retention and the adults location. In that case, hydrodynamics at the reef scale (km) had a major influence on larval dispersal and possibly on initial recruitment. Further studies are needed to understand precisely the influence of LSH on recruitment and settlement of *M. edulis* in the intertidal zone of the St. Lawrence.

### Influence of medium-scale heterogeneity

Physical phenomena (e.g. fronts, eddies) are well documented at large scales, but little information is available on physical characteristics at medium scales (Wolanski & Hamner 1988). Physical processes are likely to be important at medium scales where currents interact with local topography to produce complex flows, e. g. near headlands (Wolanski & Hamner 1988,

Geyer & Signell 1990, Geyer 1993, Laval 1996), islands (Wolanski & Hamner 1988), bays (Bang et al. unpubl.), boulders (Cusson & Bourget 1997, Guichard & Bourget 1998) and reefs (Wolanski & Hamner 1988, Black & Moran 1991). Modification of circulation patterns around headlands has been shown to affect larval distribution (Shepherd et al. 1992), recruitment (Caffey 1985, Rankin et al. 1994, Lauga 1997), zooplankton (Murdoch 1989, Lauga 1997) and size structure in purple sea urchins (Ebert & Russell 1988).

We found that MSH did influence diversity ( $H'_a$  and  $H'_b$ ), richness and biomass of 2 taxa (Fucaceae and littorinids). Since  $H'_b$  diversity and the biomass of littorinids at MSH interacted with other scales, these parameters will be discussed later. In general, diversity  $H'_a$  and richness were higher at the linear coasts than at headlands. Seed & Brotohadikumo (1994) observed a higher diversity within mussel mats in higher shore pools of wave-exposed rocky promontories than on higher shore pools of more sheltered sites in Hong Kong, but there were no significant differences in richness between these sites. In the St. Lawrence region, the intertidal community is strongly affected by ice scouring (Archambault & Bourget 1983, Bergeron & Bourget 1984), which affects structure and succession stages (Archambault & Bourget 1983). Diversity increases with age and structural complexity of the mussel matrix (Seed & Suchanek 1992). Since exposed shores are presumably more easily ice scoured and wave exposed than sheltered ones (Bergeron & Bourget 1984), the regular disruption of mussel beds in exposed areas may explain the observed low diversity in exposed sites compared to high diversity in linear coasts and sheltered sites. We found that Fucaceae biomass was greater on headlands than at linear coasts. It is possible that headlands, which are sites of increased water motion and possibly increased nutriment and gaseous exchanges, may promote Fucaceae growth rates (Norton et al. 1981).

We found that MSH had no effect on recruitment of *Mytilus edulis*. This result was in contrast with an analogous study around different size piers along the same coast; in that case barnacle recruitment and growth in the subtidal zone was greater close to the piers (100 to 1200 m) compared to control zones with no pier (Lauga 1997).

### Influence of small-scale heterogeneity

Many studies have examined direct and indirect influences of SSH topographic (crevices and exposed surfaces) on the structure of rocky benthic communities. Topographical heterogeneity directly influences benthic community structure by offering protection



against ice scouring (Bergeron & Bourget 1984, Bourget et al. 1985, Bergeron & Bourget 1986), wave action (Delafontaine & Flemming 1989), desiccation (Garrity 1984), drift logs (Dayton 1971) and predators (Menge 1976). It also has an indirect influence on community structure by modifying local hydrodynamics (Eckman 1983, Grégoire et al. 1996), competition (Menge 1976) and predation intensity (Menge et al. 1985, Gosselin & Bourget 1989).

We observed that SSH influenced all variables examined. Total biomass, biomass of individual taxa, diversity and richness increased with heterogeneity level, from exposed surfaces to crevices. Archambault & Bourget (1996) also showed that diversity, biomass and richness were greater in crevices than on exposed surfaces on the shore of the St. Lawrence Estuary, as did Menge et al. (1985) on the coast of Panama. In the Panama study, diversity was correlated with substratum heterogeneity (>25 cm); the more heterogeneous the substrata, the higher the average diversity. We found *Mytilus edulis* recruitment was higher in crevices, analogous to results of Chabot & Bourget (1988), who showed that barnacle cypris larvae, in the same area of the Gulf of St. Lawrence, settled about 13× more frequently in crevices (> 10 cm) than on flat exposed surfaces.

### Examining the influence of different scales of heterogeneity

The majority of studies in marine benthic ecology have been carried out ignoring spatial scales or over narrow spatio-temporal scales. Levin (1992) and Butman (1987) emphasized the importance of integrating different scales to better understand ecological systems. In those few studies which have considered spatial and temporal scales, most have concluded that scales were important (Dayton & Tegner 1984, Eadie & Keast 1984, Lindergarth et al. 1995, Archambault & Bourget 1996). The present study found LSH had no effect on the variables considered, MSH had a minor effect and SSH had a major influence on some of the community characteristics (biomass, richness and diversity). Indeed, SSH explained 30% of the variance in total biomass, 28% of the biomass of *Mytilus edulis*, and 21% of the biomass of the Fucaceae and littorinids. MSH explained, at the most, 11% of the biomass of littorinids, while the LSH explained 1% or less of the variance of the biomass of the taxa analyzed.

The hierarchical experimental design, which incorporated MSH—not included in Archambault & Bourget's (1996) study—helps us consider the relative importance of a large combination of scales for a num-

ber of species. Littorinid biomass showed variable responses to combinations of heterogeneity scales: position, medium scale and small scale. Biomass of littorinids was higher in linear coast crevices than around promontories. No differences among positions at linear coasts were found, but there were significantly more littorinids in crevices downstream than at other positions on headlands. As noted earlier, crevices are microhabitats offering protection against biotic and abiotic elements. Relative wave forces at the study sites might explain the variations in biomass of littorinids observed at MSH. The wave energy index (bags remaining) suggested that waves were stronger in the upstream and apex positions of the headlands, while there was a tendency for wave energy to be weaker along linear coasts. The biomass of littorinids was significantly lower on the wave-exposed positions of the headlands, possibly because littorinids are more easily dislodged from exposed sites (Lewis 1964, Boulding & Van Alstyne 1993). Lewis (1964) suggested that the sizes of *Littorina saxatilis* differed between exposed and sheltered sites and that large individuals survived better in sheltered sites. No clear pattern emerged from our study of  $H'_b$  diversity (large scale, position and medium scale). There was only tendency for  $H'_b$  diversity to be higher at linear coasts compared to headlands. The higher abundance of *Mytilus edulis* on headlands suggests that this species outcompetes other groups in this habitat.

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