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Scales of coastal heterogeneity and benthic intertidal species richness, diversity and abundance

Philippe Archambault, Edwin Bourget*

GIROQ, Département de Biologie, Université Laval, Québec, PQ, Canada G1K 7P4

ABSTRACT: Species richness, diversity, total biomass of the benthic macrofauna and macroflora, and the biomass of the 2 dominant taxa (*Fucus* spp. and *Mytilus edulis*) were examined in relation to coastal heterogeneity at different scales in the intertidal zone. The sampling design included randomness at all scales and replication of treatments. A 103 km portion of the south shore of the St. Lawrence Estuary, Canada, was divided into 1 km stretches of shore (stations)—the large scale—which were classified using a shore heterogeneity index (SHI) into 3 categories (low, medium and high). Species richness was qualitatively evaluated for each station and substratum heterogeneity on a 100 m (medium scale) was measured as covariate. At the smallest scale 4 types of surface (smooth, crevices of 1, 10 and 20 cm) were quantitatively sampled. Species richness tended to increase with SHI category but this tendency was not statistically significant. A multiple regression analysis was carried out to find which scale of heterogeneity was the most significant for defining species richness. Diversity in types of surface did not vary significantly among SHI categories. Our results show that large-scale heterogeneity explained a higher proportion of the variance in species richness than substratum heterogeneity on a 100 m scale. No statistically significant difference was found in total biomass, *M. edulis* and *Fucus* spp. biomass or percent cover among the SHI categories. At the small scale (types of surface), the abundance increased significantly from smooth surfaces to 20 cm crevices except for mussels, where abundance was higher in 10 cm crevices. The types of surface explained 42% of the variation in total biomass and 21% of that in *Fucus* spp. biomass. Variation in percent cover was explained by the types of surface (40%) and to a lesser extent by the SHI (7%). The present study showed that the scales which influenced abundance were smaller than 20 cm in the intertidal zone. Thus, our results indicated that 2 distinct spatial scales explained the variability within the same marine intertidal community, i.e. variability in species richness (scale of 1 km) and in abundance (types of surface; scale of ≤20 cm).

KEY WORDS: Shore heterogeneity · Topographical heterogeneity · Small- and large-scale heterogeneity · Species richness · Diversity · Abundance · Benthos · Sampling design

INTRODUCTION

Ecologists have recognized topographical heterogeneity as a major factor regulating species distribution and abundance within a community (Emson & Faller-Fritsch 1976, Raffaelli & Hughes 1978, Genin et al. 1986, Bourget et al. 1994). Community characteristics such as diversity and richness are also modified by topographical heterogeneity (MacArthur & MacArthur 1961, Simpson 1964, Menge et al. 1983, Menge et al. 1985). The role of topographical heterogeneity may change with scale. It is known to alter predator-prey relationships at small scale (Gosselin & Bourget 1989, Hixon & Beets 1993) while at larger scales, topographical heterogeneity probably does not modify this interaction. Furthermore, what may be homogeneous at a particular spatial scale of observation may be considered heterogeneous at another spatial scale (Kolasa & Rollo 1991). Other authors have referred to such scale effects as the grain or the extent (Allen & Hoekstra 1991). The grain of an observation is the smallest entity

*Addressee for correspondence.
E-mail: edwin.bourget@giroq.ulaval.ca

(resolution of the observer) that can be detected in the data, while the extent is the largest entity. In this study, the scale is a topographical one which corresponds to a shore development or rugosity ranging from grain sizes of ≤20 cm to an 'extent' of 1 km. There are few *in situ* benthic studies which have identified the relative importance of different spatial scales on community characteristics. Most studies have examined one spatial scale, and its effects on a variety of community characteristics. Recently, Bourget et al. (1994) examined the influence of 4 scales of heterogeneity (≤10 cm) on the establishment of an epibenthic community. Lindergarth et al. (1995) investigated the influence of spatial variability on abundance and age distribution in 2 bivalve species over several scales (between 1 m and 10^5 m). Multi-scale investigations should be carried out in community studies since different scales may influence community characteristics differently (Levin 1992). The relative importance of factors influencing marine benthic communities could therefore be substantially altered when scale is considered.

Biogeographical information has traditionally been the focus of previous large-scale studies. Topographical heterogeneity (e.g. mountainous areas) has been shown to increase species richness for mammals (Simpson 1964) and birds (Cook 1969). Currie & Paquin (1987) have also shown that topographical heterogeneity influences species richness of trees. In the marine benthic environment, studies at the landscape scale have focused on biogeographical patterns (Ardisson et al. 1990, Ardisson & Bourget 1992, Thiébaut et al. 1994). To our knowledge, no *in situ* studies have investigated the influence of topographical heterogeneity at large scales (≥1 km) on community characteristics, species richness and diversity, in marine benthic habitats.

Smaller scales have received much more attention than larger scales. Substratum heterogeneity (physical or biotic) has been shown to modify competition (Buss & Jackson 1979, Walters & Wethey 1986), predation (Russ 1980, Keough & Downes 1982, Gilinsky 1984, Holt 1984, Menge et al. 1985, Gosselin & Bourget 1989, Hixon & Menge 1991, Hixon & Beets 1993), larval settlement (Eckman 1983, Chabot & Bourget 1988, Havenhand & Svane 1991, Miron et al. 1996), and community characteristics (diversity, richness and abundance; Emson & Faller-Fritsch 1976, Raffaelli & Hughes 1978, Menge et al. 1983, Menge et al. 1985, Chapman & Underwood 1994). Our observations in the St. Lawrence Estuary, Canada, suggested that a linear shoreline was less colonized by benthic organisms than bays and headlands. In the present study we tested the hypothesis that intertidal benthic sessile community characteristics (species richness, diversity and abundance) were related to shore heterogeneity and that the array of shore heterogeneity scales influence these characteristics differently. The specific objectives were to observe species richness, diversity, and abundance in relation to increasing shore heterogeneity.

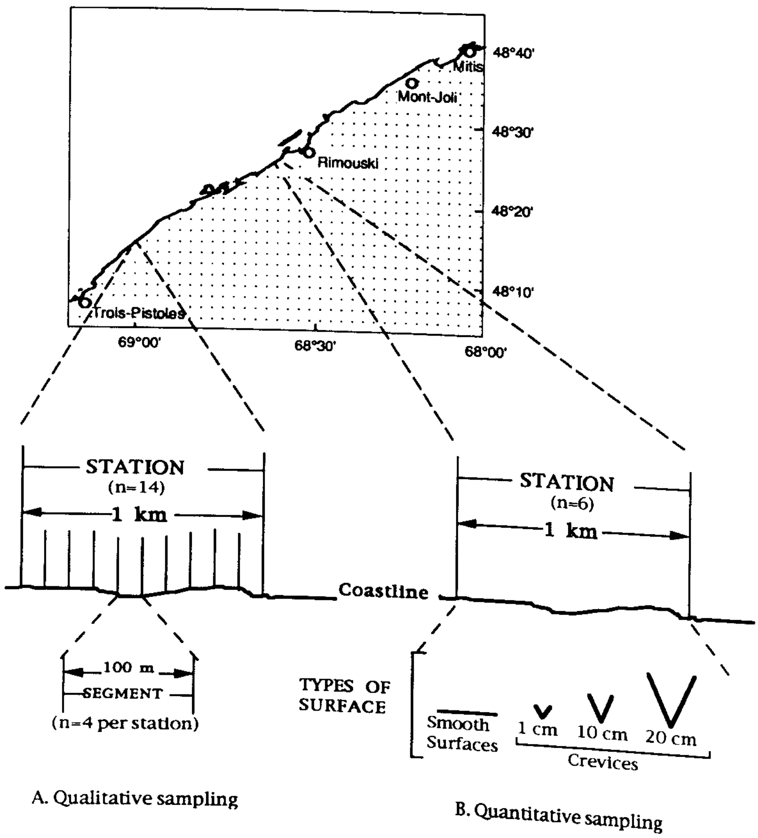

Fig. 1. Study area on the south shore of the St. Lawrence Estuary, Canada, and schematic view of the (A) qualitative and (B) quantitative sampling procedures

METHODS

Study area and large-scale heterogeneity measurement. The present study was carried out on a 103 km portion of the south shore of the St. Lawrence Estuary (Fig. 1; between Trois-Pistoles and Mitis) from 8 June to 17 August 1992. This area was chosen for its relatively linear shoreline which is broken up by bays and headlands. In addition, this part of the estuary is characterized by a small gradient in physico-chemical conditions (El-Sabh 1979, Fradette & Bourget 1980, Ardisson & Bourget 1992). Within this area, sites with significant freshwater tributaries and high human activity (e.g. harbors) were excluded.

Shore heterogeneity was defined as the coastline contour (see below), estimated using topographic maps (scale 1:20 000; Energie & Ressources, Québec). A shore heterogeneity index (SHI) which corresponded to the ratio between points 1 km apart and the measured shoreline distance between these points (modified from Bergeron & Bourget 1986) was calculated. Shore heterogeneity was measured directly from topographic maps using a curvimeter (Alvin model 1112). The starting point for estimating the SHI was determined at random from among all possible 1 km stretches of shore (stations) on the maps. The 1 km scale was considered to be large-scale and resulted in sufficient 1 km stations with relatively high heterogeneity (>3 stations; see below) over the studied coastline. The SHI values varied from 1.0 to 5.2 and were grouped into 3 arbitrarily determined categories on the basis of the frequency distribution plot: low (L = 1.0 to 1.79), medium (M = 1.8 to 3.59), high (H = 3.6 to 5.2).

Qualitative sampling, species richness. Within the SHI categories, 4 high SHI, 5 medium SHI and 5 low SHI 1 km stations (stretches of shore) were randomly chosen for in depth study (Fig. 1A). Each of these stations was subdivided into ten 100 m shoreline segments. Within each station, 4 segments were randomly chosen for sampling. The following *a priori* criteria, determined acceptance of the segments: (1) >60% rocky substratum; (2) absence of a freshwater tributary; (3) shore slope <20°; (4) wave exposed areas; and (5) intertidal zone wider than 15 m, in order to sample 3 shore levels. Whenever the randomly selected segment did not meet these criteria, the one adjacent on the left was inspected using the same criteria until an appropriate segment was found.

Substratum heterogeneity within each selected 100 m segment of rocky shoreline was measured directly on the shore using a method analogous to that used to calculate the SHI. A graduated chain (±5 cm precision) haphazardly placed on the substratum parallel to the shoreline in the mid intertidal zone was used to measure total distance and profile and a rope stretched above the chain was used to measure the linear distance between the 2 ends of the chain. The ratio of these 2 values was used as the index of medium-scale heterogeneity (MSHI).

Within the 100 m segments of shoreline selected, as many sessile species of flora (macroalgae) and fauna (macrofauna) as possible were recorded at low tide (lower than 0.75 m, maximal amplitude = 4.7 m; Department of Fisheries and Oceans Canada) by the same 2 trained observers over a 2 h period (standardized method). Species observed within and outside tidepools were recorded separately. The sampling schedule was established to minimize variability among stations due to sampling period; that is, when a low SHI station was sampled first, the next low SHI station was sampled at the end of the sampling season (7 June to 17 August) and so on. Furthermore, to control for biases which may have been associated with the duration of the sampling period, the first station examined was resampled at the end of the season and the number of species compared. Only 1 additional species was found.

Quantitative sampling, diversity and abundance. Quantitative sampling was carried out to compare species diversity and abundance among the 3 SHI categories (1 km scale). Two stations (stretches of shore) were sampled for each SHI category. These 6 stations were selected randomly from the 14 stations used in the qualitative sampling. The sampling procedure ensured that stations contained comparable small-scale heterogeneity (Fig. 1B). Four types of surface were sampled at smaller scales: smooth surfaces (15 × 40 cm), and crevices with depths of 1, 10–13 and 20–25 cm. These were nominally designated as 1, 10 and 20 cm crevices. The sampling areas for each type of surface was 600 cm^2 for smooth surfaces and 20 cm crevices, 300 cm^2 for 10 cm crevices, and 30 cm^2 for 1 cm crevices. Sampling area had no significant influence on the estimated total biomass over the range of the sampling sizes used in this study, as indicated by the ANOVA on the biomass estimated for the same 38 areas from quadrats of 30, 300 and 600 cm^2 ($F_{2,38}$ = 0.318, p = 0.718). For diversity, only comparisons within surface types were carried out, hence results of the analyses are independent of the sampling area. Only crevices >15 cm long were sampled. Selection criteria for surfaces sampled were determined *a priori*, and correspond to: (1) smooth surfaces, 10 and 20 cm deep crevices with irregularities not deeper than 1 cm; (2) surfaces with an horizontal angle <10° and closely parallel to the general shoreline (angle <45°); and (3) crevice angle openings between 60° and 90° to the horizontal.

All surfaces examined were located in the mid littoral zone, between the upper and lower limits of *Fucus vesiculosus*. Surfaces inside tidepools were not considered for the quantitative sampling. Each station was sampled over 2 tidal periods. During the first tidal period, 2 persons marked all surfaces fitting the above criteria. The surfaces used for sampling were then randomly selected from among all surfaces marked during the first tidal period. For a given station, the total number of surfaces of each type sampled depended on the total number of surfaces labelled. At least 1 surface for every 5 marked surfaces was sampled (e.g. if 50 smooth surfaces were labelled at a station, then 10 surfaces were randomly chosen and sampled). Where there were less than 20 marked surfaces, a minimum of 4 surfaces was selected per station. Samples were collected by scraping the crevices and the smooth surfaces bare. Wet weight (towel-dried) and % cover of each sessile species present (fauna and flora) were determined. Weighing was carried out in the laboratory using a Mettler balance (model PE, ±0.001 g) and the total % cover of encrusting species was independently estimated visually by removing canopy and smothering organisms when necessary. Percent cover was estimated by the same 2 observers.

Species diversity was calculated using Shannon's Index ($H' = -\Sigma p_i \ln p_i$, where p_i is the proportional abundance of the ith taxon; Magurran 1988). Because of the large size differences observed between individuals of the same species, biomass (wet weight) was used to determine the proportion of each species present, rather than the number of individuals (Wilhm 1968, Magurran 1988). To reduce variability due to growth, all quantitative data were collected over a 19 d period from 15 July to 2 August 1992.

Statistical treatment. ***Qualitative sampling:*** The response variables used in the analyses of the qualitative sampling were total species richness (total number of species counted during 2 h observation periods) and that of the fauna and flora separately, recorded (standardized method) within and outside tidepools. An ANCOVA with MSHI as the covariate was used to analyze species richness (total, faunal and floral number of species) from the stations to account for variations among: (1) SHI categories, (2) stations within SHI categories and (3) an error term (see Table 1). The 3 variables were tested for normality using Shapiro-Wilk's test (SAS 1982; $p > 0.34$). Homogeneity of variances was confirmed by graphical examination (Scherrer 1984). The assumption of independence among stations and segments was met since stations and segments were randomly selected (Sokal & Rohlf 1981, see also Bourget & Fortin 1995).

Quantitative sampling, species diversity: The model used to analyze the diversity index was the same as that used in the qualitative sampling analysis (see Table 3). The 4 types of surface were analyzed separately since species diversity (H') is affected by the sampling area (Frontier 1983, Magurran 1988). Normality (all variables, $p > 0.2$) and homogeneity of variance were tested as for qualitative sampling.

Quantitative sampling, biomass and percent cover: Biomass data were standardized over the same unit area. An ANOVA was performed on the total biomass data (g 10 cm^{-2}) and % cover data from the different types of surface to account for variations among: (1) SHI categories (1 km), (2) stations within SHI categories, (3) types of surface, (4) types of surface by SHI categories, (5) types of surface by stations within SHI categories, and (6) an error term (see Table 4). When a source of variation was significant, multiple pairwise comparison tests using least square means (Lsmeans; SAS 1982) were carried out to specify the differences.

Response variables used in the analysis were total biomass, total % cover and total biomass of the 2 dom-

Table 1. Analysis of covariance (ANCOVA) showing the effect of shore heterogeneity index (SHI) categories, stations within SHI categories, and the heterogeneity of the substratum (MSHI) as covariate, on the total, floral and faunal species richness (within and outside of tidepools)

Source of variation	df	MS	F	p
Within tidepools				
Total number of species				
MSHI	1	12.1	0.001	0.981
SHI categories	2	127.6	1.3	0.311
Stations (SHI categories)	11	98	8.07	<0.0001
Error	40	12.1		
Flora				
MSHI	1	0.19	0.04	0.836
SHI Categories	2	52.8	1.28	0.317
Stations (SHI Categories)	11	41.3	9.25	<0.0001
Error	40	4.5		
Fauna				
MSHI	1	0.01	0.01	0.964
SHI Categories	2	29.8	1.42	0.283
Stations (SHI Categories)	11	21	3.58	0.002
Error	40	5.9		
Outside of tidepools				
Total number of species				
MSHI	1	0.55	0.06	0.814
SHI Categories	2	85.7	0.99	0.403
Stations (SHI Categories)	11	86.7	8.84	<0.0001
Error	40	9.8		
Flora				
MSHI	1	1.2	0.34	0.562
SHI Categories	2	74.8	2.53	0.125
Stations (SHI Categories)	11	29.5	5.04	<0.0001
Error	40	5.9		
Fauna				
MSHI	1	0.45	0.08	0.777
SHI Categories	2	8.3	0.31	0.74
Stations (SHI Categories)	11	26.7	4.78	<0.0001
Error	40	5.6		

inant taxa: *Mytilus edulis* and *Fucus* spp. Only 2 types of surface (10 and 20 cm deep crevices) were used in the analysis of *M. edulis* biomass, since no mussels were observed on smooth surfaces and only 1 individual was found in the 1 cm crevices. Total biomass, biomass of *M. edulis* and biomass of *Fucus* spp. were log(x+1) transformed and total % cover data were cube root transformed. Normality and heteroscedasticity assumptions were not met after transformation of biomass data for these 2 dominant taxa. We used ANOVA on the raw data as suggested by Conover (1980) when results of the ANOVAs are the same for the raw and the rank transformed data.

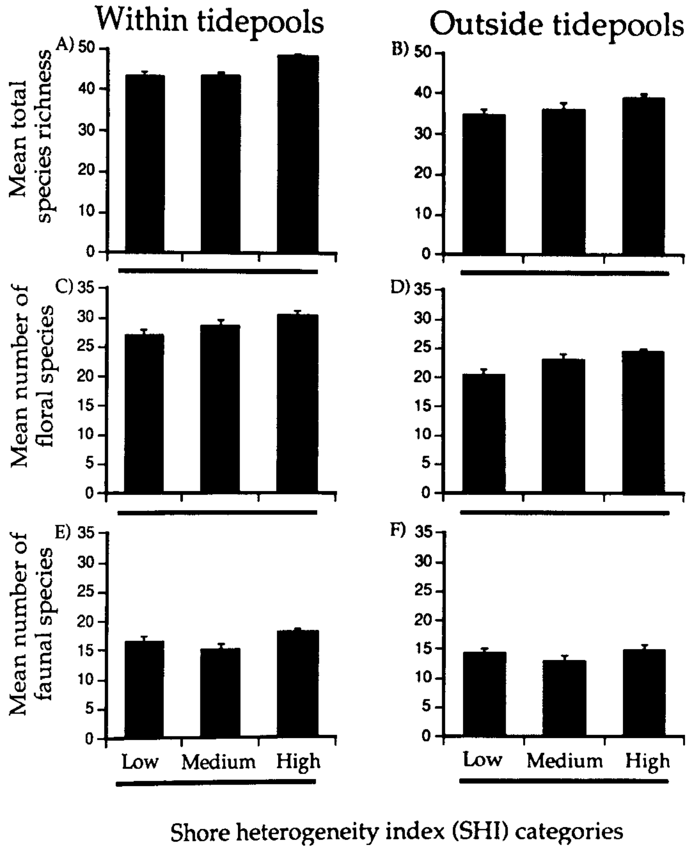

Fig. 2. Mean (A, B) total, (C, D) floral and (E, F) faunal species richness within and outside of tidepools for 3 shore heterogeneity index categories. The lines below the SHI categories indicate there is no significant difference among the 3 categories. Error bars are SE

RESULTS

Qualitative sampling

For all fourteen 1 km stations, the species richness was higher within tidepools compared to outside. A total of 86 species (48 species of macroalgae and 38 species of benthic invertebrates) were observed. Within tidepools, there was a maximum of 56 species (31 spp. of macroalgae and 25 spp. of invertebrates), at a high SHI station. By comparison, the lowest number of species within tidepools was observed at a low SHI station (20 spp. of macroalgae and 13 spp. of invertebrates). Outside of the tidepools, the richest station (27 spp. of macroalgae and 22 spp. of invertebrates) was a high SHI station, and the lowest number of species (16 spp. of macroalgae and 10 spp. of invertebrates) was observed at a low SHI station.

No statistically significant difference in total number of species (TNS), floral and faunal species richness was observed within and outside of tidepools among SHI categories (Table 1; $p > 0.05$). However, although not statistically significant, TNS and floral species richness tended to increase with shore heterogeneity (Fig. 2). The mean TNS and mean number of macroalgae increased from low to high SHI categories, but the mean number of faunal species decreased in the medium SHI category and increased in the high SHI category. For TNS, floral and faunal species richness, the highest average number of species was observed in the high SHI category (Fig. 2).

A multiple regression using MSHI and SHI as independent variables and species richness as the response variable was carried out to identify which scale better explained the variations in species richness (Table 2). The variation in TNS and floral species richness within and outside of tidepools was closely related to SHI. The influence of SHI on faunal richness was not significant (within and outside of tidepools). Heterogeneity of substratum (MSHI) explained only a small part of the variation of TNS, and floral richness within tidepools. However, the MSHI explained no significant variation of the faunal richness within tidepools. Outside tidepools, the MSHI explained more variation in TSN and faunal richness than SHI. The resulting models explained 23 and 34% of the variation in TSN within and outside tidepools, respectively. The total variation in macroalgae richness explained by both SHI and MSHI was 28% within tidepools and 38% outside tidepools. In contrast, for the fauna the same variables explained either a small ($r^2 = 0.13$, outside tidepools) or negligible (non-significant, inside tidepools) proportion of the variance in species richness.

Table 2. Partial correlation analyses between species richness and heterogeneity indices. Equations of the models are shown for total, floral and faunal species richness within and outside of tidepools. SHI: shore heterogeneity index; MSHI substratum heterogeneity index; NS: not significant

Source of variation	Partial correlation	p
Within tidepools		
Total number of species (TNS)		
SHI	0.419	0.002
MSHI	0.281	0.04
Model: TNS = 12.4 + 1.65 SHI + 25 MSHI; $r^2 = 0.23$, $p = 0.001$		
Flora		
SHI	0.476	0.002
MSHI	0.284	0.038
Model: Flora = 8.23 + 1.15 SHI + 15.96 MSHI; $r^2 = 0.28$, $p = 0.0002$		
Fauna		
SHI	0.228	0.98
MSHI	0.184	0.184
Model: $p = 0.101$, NS		
Outside of tidepools		
Total number of species (TNS)		
SHI	0.409	0.002
MSHI	0.475	0.0003
Model: TNS = −15.48 + 1.47 SHI + 44.03 MSHI; $r^2 = 0.34$, $p < 0.001$		
Flora		
SHI	0.525	<0.001
MSHI	0.436	0.001
Model: Flora = −7.65 + 1.23 SHI + 24.63 MSHI; $r^2 = 0.38$, $p < 0.001$		
Fauna		
SHI	0.112	0.419
MSHI	0.342	0.011
Model: Fauna = −7.83 + 0.24 SHI + 19.4 MSHI; $r^2 = 0.13$, $p = 0.028$		

Table 3. Analysis of variance showing the effect of shore heterogeneity index (SHI) categories and stations within SMH categories on the diversity (H') of the 4 types of surface: smooth surfaces and 1, 10 and 20 cm crevices

Source of variation	df	MS	F	p
Smooth surface				
SHI categories	2	0.03	0.1	0.9
Stations (SHI categories)	3	0.32	4.38	0.01
Error	30	0.07		
1 cm crevices				
SHI categories	2	0.04	2.11	0.27
Stations (SHI categories)	3	0.02	0.36	0.78
Error	30	0.06		
10 cm crevices				
SHI categories	2	0.13	0.89	0.5
Stations (SHI categories)	3	0.15	2.22	0.12
Error	30	0.07		
20 cm crevices				
SHI categories	2	0.08	0.54	0.63
Stations (SHI categories)	3	0.14	2.6	0.08
Error	30	0.05		

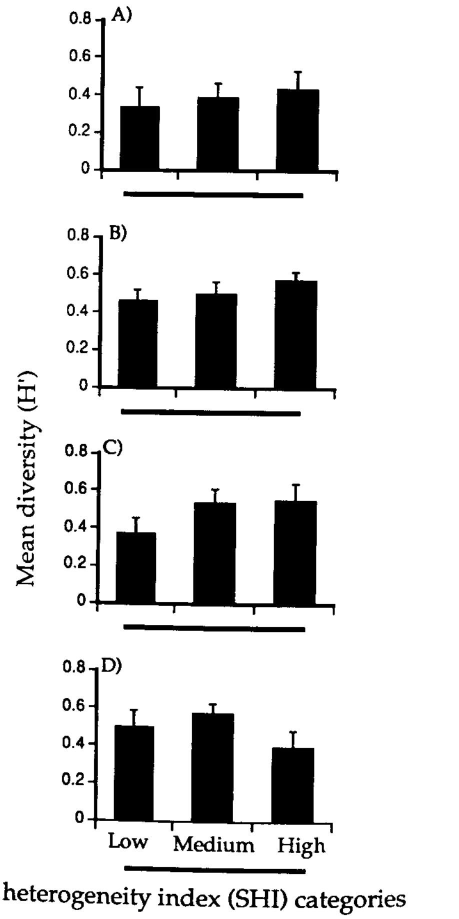

Fig. 3. Mean diversity (H') for (A) smooth surfaces and (B) 1 cm, (C) 10 cm, and (D) 20 cm crevices for 3 shore heterogeneity index categories. The line below SHI categories indicates that there were no significant differences among the 3 categories. Error bars are SE

Quantitative sampling

Species diversity

Diversity (H') on the different types of surface did not vary significantly among SHI categories (Table 3). There was a tendency, however, for diversity to increase with SHI category on smooth surfaces, 1 cm and 10 cm crevices (Fig. 3A, B, C). Average diversity in the 20 cm crevices was high in the medium SHI category and slightly lower in the low and high SHI categories (Fig. 3D).

Biomass and percent cover

No statistically significant difference in total and *Fucus* spp. biomass and % cover was observed among the SHI categories (Table 4), though 3 of 4 variables showed greater mean values for the high SHI category than for the low SHI category. Lowest biomass and % cover were in the medium SHI category (Fig. 4A, B, D). In contrast, maximum biomass of mussels was observed in the medium SHI category (Fig. 4C).

There was a significant effect of surface types on total and *Fucus* spp. biomass and % cover. This effect was similar for the total and *Fucus* spp. biomass (see below; Fig. 4E, H). In these 2 cases the 10 and 20 cm crevices showed no difference, but there was increased biomass from smooth surfaces to 20 cm deep crevices. The same pattern was observed for the % cover (Fig. 4F) but no difference was observed between abundance on smooth surfaces and the 1 cm crevices.

The ANOVA performed on abundance of *Mytilus edulis* used only 2 types of surface (10 and 20 cm crevices) because no mussels were found on smooth surfaces and only 1 individual was observed in 1 cm crevices. Thus, although differences could not be confirmed statistically given the large number of zero values, there were obvious positive type-of-surface effects for *M. edulis* (Fig. 4G).

Multiple regression analysis was carried out on the total and *Fucus* spp. biomass and % cover using SHI and type of surface as independent variables. Total biomass was fourth root transformed and % cover was cube root transformed to meet normality and heteroscedasticity assumptions. Of the 3 variables considered the types of surface explained the highest proportion of residual variation (Table 5). Types of surface explained 41 % of the total biomass and 21 % of *Fucus* spp. biomass. Over 40 % of the variance in % cover was explained by types of surface and 7 % by the SHI. Thus, the scale at which the types of surface influences the total biomass, % cover and *Fucus* spp. biomass was ≤20 cm.

Table 4. Analysis of variance showing the effect of shore heterogeneity index (SHI) categories, stations within SHI categories and types of surface (TS) on total biomass, % cover, total biomass of *Mytilus edulis* and total biomass of *Fucus* spp. Note that ANOVA performed on total biomass of *M. edulis* used only 10 and 20 cm crevices since no *M. edulis* was found on smooth surfaces and only one was found in the 1 cm crevices

Source of variation	df	MS	*F*	p
Total biomass				
SHI categories	2	0.45	0.5	0.65
Stations (SHI categories)	3	0.89	3.57	0.06
TS	3	13.86	55.7	<0.001
TS × SHI categories	6	0.55	2.22	0.14
TS × Stations (SHI categories)	9	0.25	1.06	0.4
Error	114	0.23		
Corrected total	137			
% cover				
SHI categories	2	9.94	1.47	0.36
Stations (SHI categories)	3	6.78	4.69	0.03
TS	3	39.81	27.54	<0.001
TS × SHI categories	6	1.48	1.02	0.47
TS × Stations (SHI categories)	9	1.45	1.66	0.11
Error	114	0.87		
Corrected total	137			
Total biomass of *Mytilus edulis*				
SHI categories	2	0.54	1.52	0.35
Stations (SHI categories)	3	0.35	2.27	0.26
TS	1	0.002	0.01	0.93
TS × SHI categories	2	0.11	0.69	0.57
TS × Stations (SHI categories)	3	0.15	0.45	0.72
Error	51	0.34		
Corrected total	62			
Total biomass of *Fucus* spp.				
SHI categories	2	1.32	1.77	0.31
Stations (SHI categories)	3	0.75	2.08	0.17
TS	3	9.73	26.87	<0.001
TS × SHI Categories	6	0.88	2.42	0.11
TS × Stations (SHI categories)	9	0.36	1.43	0.18
Error	114	0.25		
Corrected total	137			

DISCUSSION

Variations in intertidal community characteristics (species richness, abundance and diversity) in relation to coastal heterogeneity (over a scale of 1 km of coastline) and substratum heterogeneity (scale ≤20 cm) were examined. Species richness was weakly explained by large-scale shore heterogeneity while abundance differences were substantially explained by smaller-scale (≤20 cm) heterogeneity.

Species richness

Studies in terrestrial environments have highlighted the importance of large-scale topographical heterogeneity for species richness (Simpson 1964, Cook 1969, Currie & Paquin 1987). Our results showed that medium- (substratum) and large-scale (shore) topographical heterogeneity explained little of the variance in species richness in the intertidal zone examined. At the large scale (SHI categories) there was a non-significant but consistent increase in total number of species and floral richness both inside and outside of tidepools

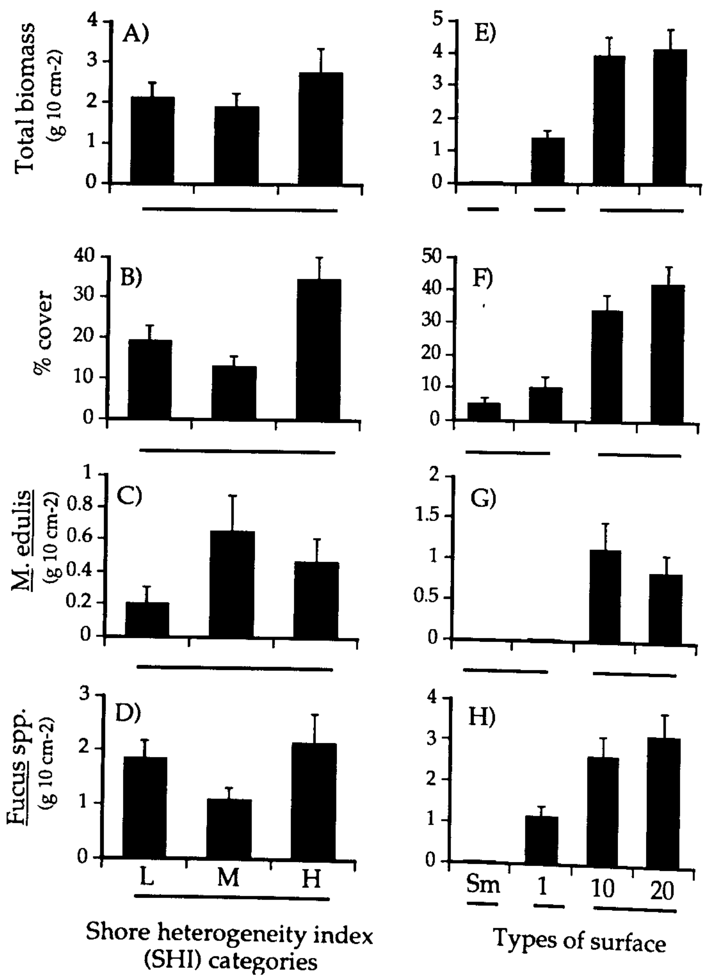

Fig. 4. Influence of scale of heterogeneity on mean (A, E) total biomass, (B, F) % cover, (C, G) biomass of *Mytlis edulis* and (D, H) and biomass of *Fucus* spp., among the shore heterogeneity index categories (L = low, M = medium, H = high) and types of surface (Sm = smooth surface; and 1, 10, and 20 cm crevices). SHI categories and types of surfaces that were not significantly different are underlined. Error bars are SE

with increasing shore heterogeneity (Fig. 2). A consistent pattern was also observed for the fauna where richness decreased at the intermediate SHI category. The influence of topographical heterogeneity at large and medium scales was probably reduced by the effect of other factors such as ice scouring in this environment (Bergeron & Bourget 1984, 1986). There is evidence in the literature that when there are recurrent disturbances, the number of species remains low (Connell 1978, Sousa 1979a, b, Davis & Wilce 1987, Kautsky & Kautsky 1989, Kilar & McLachlan 1989, Petraitis et al. 1989).

For each spatial scale, a much greater percentage of the variance in species richness was explained for the algae than for the fauna. A possible explanation for this result may be that many littoral algae, when affected by ice scouring or grazers, are able to recover by regenerating from the basal disc (Printz 1956, Archambault & Bourget 1983), while all non-colonial sessile invertebrate species abraded by ice or attacked by predators are likely to be killed. Hence, algal richness may be less affected by physical and biological perturbations than animals. The fact that large-scale heterogeneity (SHI) explained significantly more variance in algal richness than MSHI, while the opposite was observed for the fauna (Table 2), may lie in differences in the dispersal, retention or settling mechanisms of these 2 groups of organisms, but further work would be required to validate this hypothesis.

Higher values of mean total number of species, floral and faunal species richness were observed within tidepools than outside of tidepools (Fig. 2). This difference between emergent substrata and tidepools may arise because of smaller physical fluctuations in tidepools (Metaxas & Scheibling 1993), and reduced annual ice scouring within substratum depressions (Bergeron & Bourget 1986).

Diversity

Diversity has been shown to increase with small-scale (<50 cm) substratum heterogeneity (Menge et al. 1983, Menge et al. 1985). Bourget et al. (1994) found no increase in diversity with small-scale heterogeneity in the early (<4 mo) phases of colonization. To our knowledge, no other study has been carried out in the intertidal zone which has examined the influence of large-scale (1 km) heterogeneity on species diversity (H'). Our results have shown that while diversity was not significantly different among SHI categories (large-scale; Table 3), there was a trend of increasing diversity with increasing heterogeneity for 3 types of surface out of the 4 investigated (smooth surfaces, 1 and 10 cm crevices; Fig. 3). This trend suggests a possible weak influence of large-scale heterogeneity on diversity which may not reach statistical significance due to the low number of SHI categories and replicates used here.

Abundance

Our results showed that small-scale (≤20 cm) topographic shore heterogeneity is more important than

Table 5. Partial correlation analysis of total biomass, % cover, and total biomass of *Fucus* spp. versus shore heterogeneity index (SHI) and type of surface (TS). General equations of the models are also shown

Source of variation	Partial correlation	p
Total biomass (TB)		
SHI	0.064	0.457
TS	0.644	<0.001
Model: Fourth root TB = 0.83 + −0.02 SH + 15.17 TS; $r^2 = 0.42$, $p < 0.0001$		
% cover		
SHI	0.272	0.001
TS	0.631	<0.001
Model: Cube root % cover = 0.66 + 0.21 SHI + 0.12 TS; $r^2 = 0.44$, $p < 0.0001$		
Total biomass of *Fucus* spp. (TBF)		
SHI		0.485
TS		<0.001
Model: TBF = 0.4 + 0.09 SHI + 0.14 TS; $r^2 = 0.21$, $p < 0.0001$		

large-scale (1 km) heterogeneity in determining the abundance of organisms in the intertidal community in the St. Lawrence Estuary (Tables 4 & 5). It is hypothesized that this is related to the fact that small-scale topographic heterogeneity offers suitable refuges for organisms against prevailing physical stress (e.g. ice scouring) in a subarctic environment. Many studies have shown that small-scale heterogeneity (crevices) protects organisms against different physical stresses, such as desiccation (Garrity 1984), and disturbances such as drift logs (Dayton 1971) and ice scouring (Bergeron & Bourget 1984, 1986, Bourget et al. 1985). The abundance of predators has been shown to increase in crevices (Underwood & Denley 1984), but predators are seldom encountered in the mid intertidal zone of the St. Lawrence Estuary (Bourget et al. 1985). When present, their efficiency can be considerably reduced due to small-scale heterogeneity (Menge et al. 1985, Gosselin & Bourget 1989, Hixon & Menge 1991).

Protection from disturbance is consistent with the higher total biomass, % cover and *Fucus* spp. biomass found with increasing crevice depth observed (Fig. 4). The lower values observed for *Mytilus edulis* biomass in 20 cm crevices (Fig. 4G) may be explained by the fact that communities in this microhabitat, which has opening angles of 60 to 90°, are more vulnerable to physical factors (e.g. ice scouring and wave action) than those in smaller crevices. Indeed, Bergeron & Bourget (1986) showed that in small crevices, animals are all directly attached to the substratum, while in larger crevices, mussel mud accumulates on the bottom of the crevice and the mussel community gradually becomes unstable.

Our study shows a strong small-scale (≤20 cm) heterogeneity effect on abundance. This result contrasted with that of Lindergarth et al. (1995), where scales of 1 km and 100 m were important in explaining spatial variability in abundance of some infaunal bivalves. Both their study and ours were carried out in subarctic environments; however, it may be that epibenthic intertidal populations are more strongly affected by physical factors than the subtidal infaunal populations. The sampling scale was 1 m in Lindergarth et al. (1995) and less than 20 cm in our study, which would also influence the relative importance of large-scale and smaller-scale effects.

Spatial scale

A trend that emerges from this study is that different spatial scales explain the variability of different community characteristics. Species richness is best explained by the 1 km scale, while abundance is best explained by the ≤20 cm scale. Bourget et al. (1994) suggested that in the sublittoral zone the effect of topographical heterogeneity on diversity and % cover may occur at a spatial scale larger than 10 cm, a conclusion which was indirectly supported by results of Lindergarth et al. (1995). In the present study, species richness increased with large-scale heterogeneity but processes by which large-scale heterogeneity could influence diversity and abundance were apparently not sufficiently marked in the intertidal zone to induce significant differences among SHI categories. An alternative hypothesis may be that the annual regulation of intertidal populations by physical stress in this harsh intertidal environment (see Bergeron & Bourget 1984, 1986, Bourget et al. 1985) is sufficient to limit potential large-scale (1 km) effects on the community. In the intertidal zone, small-scale topographical heterogeneity creates refuges from environmental disturbances on populations (Menge et al. 1985, Gosselin & Bourget 1989, Hixon & Menge 1991). Other studies have shown that small-scale heterogeneity provided by holes and crevices positively affected diversity and abundance (Emson & Faller-Fritsch 1976, Raffaelli & Hughes 1978, Menge et al. 1983). Thus, the results relating spatial scales to community characteristics suggest that small-scale topographical heterogeneity significantly influences some intertidal community characteristics (e.g. abundance). Large scales of heterogeneity may influence intertidal community characteristics such as richness, and possibly also sublittoral community characteristics, at least in subarctic environments (see Bourget et al. 1994, Lindergarth et al. 1995).

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