

# Influence of topographic heterogeneity and spatial scales on the structure of the neighbouring intertidal endobenthic macrofaunal community

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**ABSTRACT:** The influence of topographic heterogeneity (boulders of different sizes: 0.75, 1.5, 2.25 m) on intertidal soft-bottom community characteristics [diversity ( $H'$ ) richness, and biomass] was examined in the St. Lawrence Estuary, Canada. The macrofauna, sediment characteristics, and flow regime in the zones surrounding boulders were examined in 6 orientations (directions) and at 3 distances from boulders. Flow around boulders and control sites (no boulders) was estimated by the rate of plaster dissolution of standard plaster cylinders. Control sites (no boulders) showed the highest species diversity ( $H'$ ; based on density) and richness. These parameters decreased significantly with boulder size and increased significantly with distance from boulders. For both small and large boulder sizes, highest and lowest diversities were generally observed in opposite orientations. Overall, biomass was not influenced by boulder size. Plaster dissolution explained more variability in diversity, richness and biomass (up to 35, 30 and 25%, respectively) than did sediment characteristics (8, 6 and 27%, respectively). Species dominance was strong and probably explained the relative constancy of diversity among treatments.

**KEY WORDS:** Topographical heterogeneity · Scale heterogeneity · Species richness · Diversity · Soft bottom · Macrofauna · Intertidal community · Biomass · Flow rate · Sediment

## INTRODUCTION

The topographic heterogeneity (TH) of hard substrata is known to provide protection to a variety of benthic organisms against wave action (Denny et al. 1985), ice scouring (Bourget et al. 1985, Bergeron & Bourget 1986), and desiccation (Garrity 1984). It also affects the organisms indirectly by changing local currents and food abundance (Genin et al. 1986, Abelson et al. 1993, Abelson & Loya 1995) and affects biological interactions by providing refuge from predators (Menge & Lubchenco 1981, Menge et al. 1985, Hixon & Menge 1991, Bourget et al. 1994). Topographic heterogeneity has been considered unimportant on sandflats (Rhoads 1974), and few studies have examined its influence on soft-bottom community structure. Moreover, the effect of TH on hydrodynamic (flow rate) and

sediment transport processes over soft bottoms has been investigated primarily on scales of cm in studies examining microtopographic heterogeneity. Microtopography of sand ripples (Sun et al. 1993, Fleeger et al. 1995) or biogenic structures (e.g. crab burrows, polychaete tubes, and faecal mounds) (Rhoads 1974, Woodin 1978, Eckman et al. 1981, Woodin 1981, Eckman 1983, Thrush 1988) have been investigated. At larger scales (100 m to km), fewer studies have explored the influence of topographic heterogeneity on the distribution of soft-bottom fauna (Levin & Thomas 1989, Levin & DiBacco 1995). This is the first study, to our knowledge, to examine the influence and potential mechanisms of topographic heterogeneity on natural soft-bottom benthic community structure on a scale of meters. While there have been studies on the effect of predation on communities adjacent to artificial reefs, they are not analogous (Davis et al. 1982, Ambrose & Anderson 1990, Posey & Ambrose 1994).

Hydrodynamic conditions often determine the distribution of larvae, juveniles, and adults of soft-bottom

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organisms (Butman 1987). Bottom heterogeneity, at all scales, modifies water flow patterns by varying the roughness of the bottom sediments. In turn, flow patterns influence larval settlement (Eckman 1983, 1990, Butman 1987, Breitburg et al. 1995), food availability (Muschenheim 1987, Marinopoulos 1991, Abelson et al. 1993, Abelson & Loya 1995), sediment transport and deposition (Eckman et al. 1981, Jumars & Nowell 1984), and eventually infaunal distribution (Rhoads & Young 1970, Eckman 1979, 1983).

The present study examines the influence of topographical heterogeneity, i.e. glacially deposited intertidal boulders, which are a common feature of subarctic shore environments (Dionne 1972, Drapeau 1990), on the soft-bottom intertidal community characteristics (diversity, richness, and biomass) on a scale of meters. We examined the effects of boulder sizes on benthic macrofauna, hydrodynamic flow regime, the grain size distribution and composition of sediments.

## METHODS

**Study area.** The study was carried out in June and July 1994 at Baie des Milles Vaches on the north shore of the St. Lawrence Estuary, Québec, Canada (Fig. 1). The study area, an intertidal sandflat (0.5 km wide and 2 km long) with no freshwater tributaries (salinity = 25‰), has homogeneous edaphic characteristics except for numerous glacially deposited boulders of various sizes. The study zone was located between 1.4 and 2.4 m above the zero water level. Tidal maximum amplitude was 5.0 m (Dept of Fisheries and Oceans, Canada, 1994). Water circulation was dominated by a

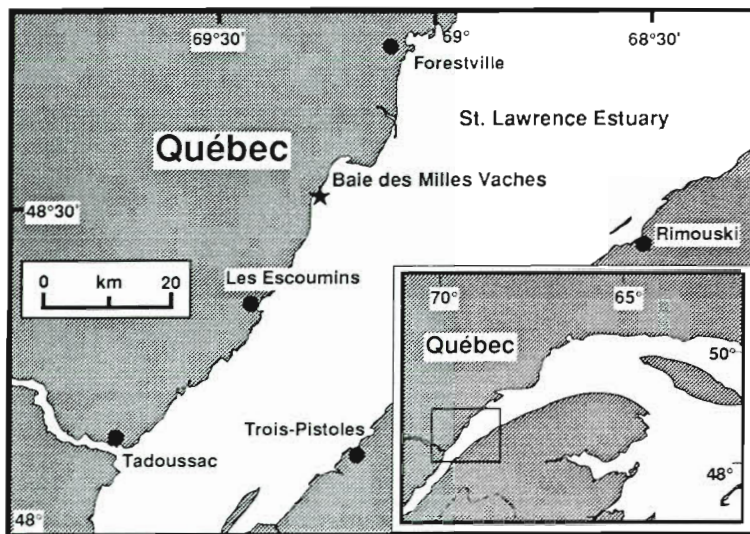


Fig. 1 Study area (★) at Baie des Milles Vaches, Lower St. Lawrence Estuary (Québec, Canada)

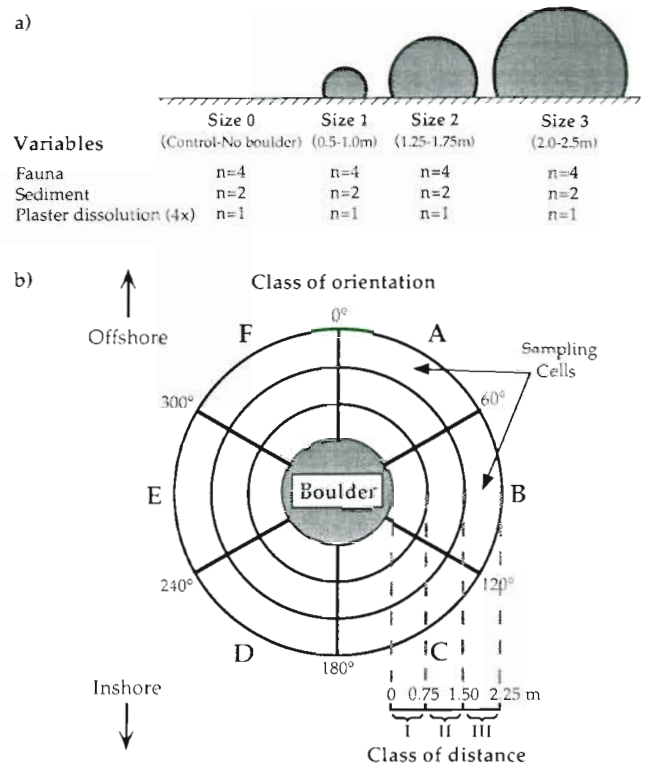


Fig. 2. (a) Substratum heterogeneity (boulder size) considered in this study with number of treatments and samples or measurements for each variable considered. (b) Schematic showing the 18 sampling cells around boulders and control sites. Classes of orientations are A–F and distances I–III. In each cell, 3 cores (6 cm interior diameter, 5 cm depth) were collected at random coordinates to examine the fauna ( $n = 2$ ) and sediment characteristics ( $n = 1$ ). A plaster cylinder was installed in the center of each cell to examine the rate of plaster dissolution as a surrogate measure of flow

bi-directional tidal flow. The layer of the sediment (up to 15 cm) available for colonization by the organisms overlies hard Goldthwait sea clay deposit (Dionne 1977).

**Field sampling and sample processing.** Three boulder size-classes were selected: small (diam. 0.5 to 1.0 m), medium (1.25 to 1.75 m) and large (2.0 to 2.5 m). Zones without boulders were used as control sites (Fig 2a). Boulder and control sites were randomly chosen in the study area among a number (4 to 9 per size category) of predetermined sites corresponding to the following *a priori* criteria: (1) boulders were totally submerged at high tide, (2) algal cover on boulder sides did not exceed 50%, (3) boulders were rounded and slightly embedded in the sediment, (4) boulders were without any shallow

depression and sediment push ridge (indicative of periodic ice-pressures (Dionne 1972), and (5) the selected sites (boulders and controls) were free of extraneous boulders within a 15 m radius. Each treatment was replicated 4 times; thus, 16 sampling sites were selected (4 replicates per boulder size).

A circle with a radius of 2.25 m was defined around each boulder and control site, and was divided into six 60° sectors (orientations) and three 75 cm distance classes for sampling: this totaled 18 sampling cells per boulder (Fig. 2b). For the control sites, we used the same spacing as for the medium boulder sizes (1.5 m). All faunal and sediment samples were collected between 8 and 24 June 1994 to avoid changes due to seasonal succession.

**Sediment samples.** In each sampling cell, 1 core [6 cm interior diameter (i.d.) and 5 cm long] was collected, using random coordinates (orientation and distance), to examine sediment characteristics in 2 sites randomly chosen out of the 4 sites per size class (boulders and controls) (total = 144 samples: 18 samples per site × 2 replicates × 4 size categories). Within 1 h after collection, samples were deep-frozen (-20°C) to ensure preservation of organic matter.

Sediment grain size was analysed by sieving oven-dried (40°C for 24 h) samples through 2, 1, 0.5, 0.25, 0.125 and 0.062 mm mesh sieves. The resulting material was classified as gravel, sand or mud (including silt and clay) (Rivière 1977) and weighed using a Mettler PE balance ( $\pm 0.0005$  g) to determine the total fraction of each type of material. The % organic matter was determined by loss after combustion (600°C for 8 h) for each sediment core (Kristensen & Andersen 1987).

**Surrogate measurements for relative flow.** Flow around boulders and at control sites was estimated indirectly using weight loss (erosion) of standard plaster (plaster of Paris) cylinders (e.g. Muus 1968, Petticrew & Kalff 1991). Temperature and salinity were approximately constant over all sites, and relative differences in current velocity can be estimated from plaster weight loss. All plaster cylinders were 30 mm in diameter with a height of  $80 \pm 0.05$  mm. A 4 mm diameter stainless steel rod was inserted through a hole along the longitudinal axis of the cylinder. Both ends of the plaster cylinder were protected with epoxy to ensure equal contact with the water from one cylinder to the next. In each sampling cell, 1 cylinder was fixed vertically 1 cm above the substratum by driving the rod into the sediment at the centre of each sampling cell. The cylinders were left for 24 h (2 tidal cycles). Plaster dissolution (weight loss in g per exposure time) was the difference between oven-dried weights ( $\pm 0.0005$  g) before and after installation.

For each treatment size category, 4 series of plaster erosion estimates were carried out. The first 2 series

(18–19 July and 20–21 July) was carried out during neap tides. One site per size category and a control site were randomly selected. The other 2 series (24–25 July and 26–27 July) was carried out during spring tides. One site per size category and a control site were randomly selected from the 3 remaining sites per size category and control sites. The total number of samples for relative flow analyses was 288 (4 series, 18 samples per site, 4 size categories). Different brands of plaster were used for the 2 sets of series because of supply problems. Discrimination between measurements for the site location factor and plaster (brand) type on plaster dissolution was not possible. The 2 sets of measurements (series 1-2 and series 3-4) were analysed separately.

A Marsh-McBirney (Rockville, MD, USA) electromagnetic flowmeter (model 512) with 2 sensors was used to measure current direction and speed over 5 consecutive days (9 tidal cycles) at 1 control site, and over 3 days (5 tidal cycles) at a small boulder site. No data were obtained for the other size boulder sites due to equipment failure. The sensors were placed 15 cm above the sediment surface into the first distance class. Both sensors were placed into different orientation cells after 2 tidal cycles.

**Faunal samples.** In each sampling cell for all treatments and all controls (3 treatments + 1 control × 4 replicates × 18 cells = 576 total), 2 sample cores (6 cm i.d., 5 cm long) were randomly taken to investigate the fauna. Random coordinates of orientation and distance ensures random sampling. The cores were sieved through a 500  $\mu$ m mesh sieve, and the material filtered and residue were both fixed in 4% (v/v) formalin in seawater. After 2 wk, samples were transferred to 70% alcohol. In the laboratory, the macrofauna (>500  $\mu$ m) in each core were sorted under a stereomicroscope, identified to the lowest taxonomic level possible and counted. Samples were weighed (towel-dried weight  $\pm 0.0001$  g, including shells) by taxon. Some hard bottom epibenthic species were observed in some cores and counted as part of the community.

Biological variables obtained from each sample core included (1) species richness (no. of species), (2) total biomass, (3) density (no. ind. core<sup>-1</sup>), (4) diversity estimated using the Shannon diversity index ( $H'_a$ ) ( $\log_2$  base) for density of each taxon per core sample (Legendre & Legendre 1984), and (5) diversity estimated using the Shannon diversity index ( $H'_b$ ) ( $\log_2$  base) calculated using the biomass of each taxon per core sample (Wilhm 1968, Magurran 1989).

**Data analysis.** Split-plot ANOVAs (Montgomery 1991) were used to examine differences among all factors (size, site, distance, orientation, and crossed factors) on sediment characteristics (see Table 1). The % gravel data distribution had to be normalized using

square-root transformations, other % data were normally distributed.

Split-plot ANOVA with 1 nested element (series within location), was used to test the effects of site location, measurement series, size, distance, orientation, and crossed factors on plaster dissolution (see Table 1).

Finally, a split-plot ANOVA, with 1 nested element (site replicate within size), was used to test effects of all factors (size, site, distance, orientation, and crossed factors) on  $H'_a$ ,  $H'_b$ , total biomass, and species richness in the community (see Table 2). For both types of diversity, and for richness, square-root transformations were used to normalize the data. A reciprocal transformation was used to normalize total biomass data.

Normality was verified using the Shapiro-Wilk's test (Zar 1984). Homoscedasticity was confirmed by graphical examination of the residuals (Scherrer 1984, Montgomery 1991). Least-square means multiple comparisons tests were carried out to determine differences (LS means; SAS Institute Inc. 1988). These comparisons were done at a corrected level of significance,  $\alpha/df$ , where  $df$  is the degree of freedom of the tested factor and  $\alpha = 0.05$ . Thus, the maximum error rate under any complete or partial null hypothesis was less than  $\alpha$ .

A stepwise multiple regression was used to examine the relationships between biological dependent variables ( $H'_a$ ,  $H'_b$ , species richness, and total biomass) and sedimentary variables (% of organic matter, sand,

mud, and gravel). A stepwise multiple regression was also used to describe the relationships between biological dependent variables and plaster dissolution as a surrogate measure for current velocity. The Aitchison's transformation (Aitchison 1982) was applied to the different % of sediment fractions (mud, sand, and gravel) to facilitate their use for the multiple regression. This transformation accounts for the structural dependency among the percentages of different fractions, since any variation in % of 1 component (e.g. sand) affects the relative values of the other fractions (e.g. % of mud and gravel). All data were analysed using GLM and REG procedures with SAS software (SAS Institute Inc. 1988). A significance threshold of 0.05 was adopted for all statistical tests.

Mean individual weight (total weight/no. ind.) was used as a condition index for the dominant taxa. Kruskal-Wallis nonparametric analysis of variance was used to test for differences with boulder size, followed by multiple comparisons (Zar 1984).

## RESULTS

### The benthic community at Baie des Milles Vaches

A total of 24 taxa were identified and the assemblage was characteristic of a *Macoma balthica* Boreo-Atlantic community (Desrosiers et al. 1984), dominated by the pelecypods *M. balthica* and *Mya arenaria*, the gastropod *Hydrobia minuta*, and the polychaete *Nereis virens*. Other taxa observed included Polychaeta (6 taxa), Sipunculida (1), Gastropoda (4), Pelecypoda (1), Crustacea (5), Oligochaeta (1), and Nemerta (1).

### Sediments

All sediment fractions (except gravel) showed significant differences for 1 or more treatment levels (size, distance, and orientation) (see Table 1). The highest % sand was observed at control sites (Fig. 3a). Sand percent values significantly decreased for boulder sites compared to the control. The proportion of sand increased with increasing distance classes (Fig. 3b), while the opposite trend was observed for mud (Fig. 3d). The proportion of mud was significantly higher in the presence of boulders than at control sites, and values were highest near small and large boulders (Fig. 3c). The proportion of sand in relation to orientation class varied according to boulder size (Fig. 4). Small and medium size boulders showed significant differences in % sand among sectors. For instance, % sand was highest in near opposite sectors

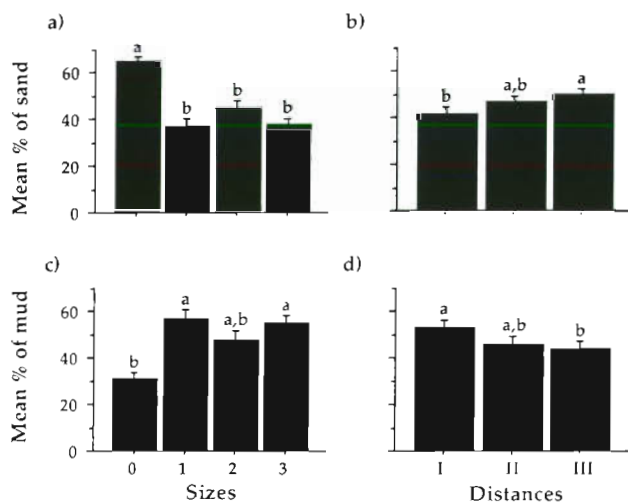


Fig. 3. Mean proportion (%) of sand and mud for each (a, c) boulder size (0: control, 1: 0.5–1.0 m, 2: 1.25–1.75 m, 3: 2.0–2.5 m) and (b, d) distance class (I: 0–0.75 m, II: 0.75–1.5 m, III: 1.5–2.25 m). Bars having different letters above them differ significantly (LS means multiple comparisons; SAS 1988). All classes of orientation are combined. Error bars are SE

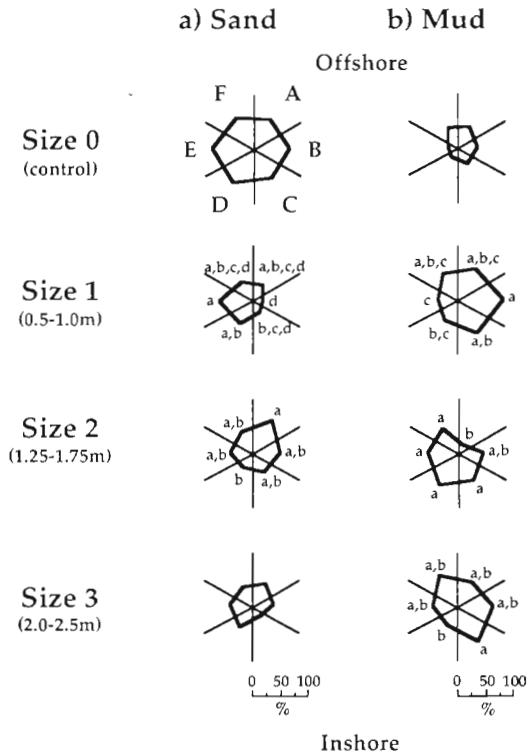


Fig. 4. Circular graphs of mean percentages of (a) sand and (b) mud for each orientation class and size of boulders, all distances combined (results of LS means multiple comparisons are shown when differences in orientation were significant). Sectors are identified in the top left control graph

in the small and medium size boulders (Fig. 4). For all boulder sizes, there were significant effects of orientation on % mud (Fig. 4). In general, the proportion of organic matter followed the distribution of the mud fraction; trends associated with boulder size and distance were not significant. There were significant differences with orientation of % organic matter between the smaller boulders and the control sites.

**Plaster dissolution**

There were no significant effects of location on plaster dissolution (in g per 24 h). There was a significant effect of boulder size on plaster dissolution (Table 1a). Highest plaster dissolution values were observed at the control sites. Dissolution values decreased with increasing boulder size (Fig. 5a). Orientation had no influence on dissolution (Table 1a), though values were slightly higher along the B-E axis than along the A-D axis.

Flood and ebb currents were not symmetrical at control sites (Fig. 5b). The mean current velocity was  $13 \text{ cm s}^{-1}$  at control sites on windless days. Mean current velocity decreased to  $6 \text{ cm s}^{-1}$  at the closest distance class at small boulder sites.

**Diversity**

$H'_a$  decreased significantly with increasing boulder size (Table 2a, Fig. 6a) while it increased significantly with increasing distance (Table 2a, Fig. 6i). The latter trend was more pronounced for smaller boulders (Fig. 6e). The interaction Orientation  $\times$  Size influenced  $H'_a$  significantly (Fig. 7a).  $H'_a$  was highest in the A and D sectors for small boulders while it was highest in the A and E sectors for large boulders. No significant treatment effects were observed on  $H'_b$  (based on biomass) (Table 2b).

**Biomass**

Highest total biomass was observed at control sites (Fig. 6d), and the ANOVA did not detect a trend among boulder sizes. The interaction Orientation  $\times$  Size significantly influenced total biomass (Table 2c). For small boulders the highest total biomass was observed for orientation E and the lowest in sectors A and B (Fig. 7b) No significant differences were observed among the other treatments.

**Species richness**

There were significant differences in richness among the boulder sizes and controls (Table 2b). Val-

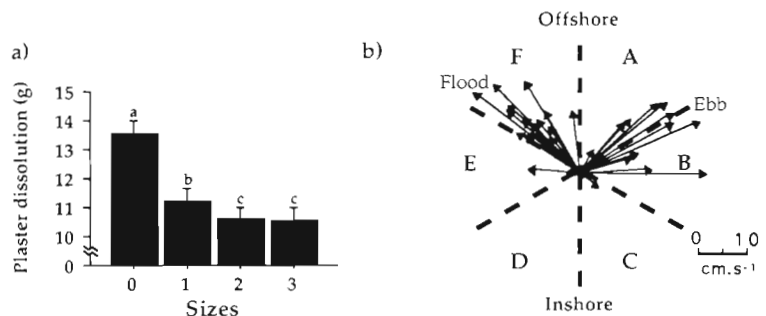


Fig. 5. (a) Mean plaster dissolution (in g per 24 h) for each boulder size, all series of measurement, distances, and orientations combined. Bars having different letters above them differ significantly (LS means multiple comparisons). Error bars are SE. (b) Vector diagram of flood and ebb currents during a representative tidal cycle at 1 randomly chosen control site on 1 windless day

Table 1. Summary of ANOVAs showing the effect of size, site (location for plaster dissolution), series of measurement (for plaster dissolution only), distance, orientation, and crossed factors on (a) rate of erosion, (b) % organic matter, (c) % mud, (d) % sand, (e) % gravel. Proportion (%) of the gravel fraction was square-root transformed to normalize the data. \*p < 0.05, \*\*p < 0.01, \*\*\*p < 0.001

Source of variation	df	MS	F-value	p
<b>(a) Plaster dissolution</b>				
Location	1	2772.9	8.7867	0.0975
Series (Location)	2	315.58	291.51	0.0001***
Size	3	133.78	123.58	0.0001***
Distance	2	0.5537	0.5114	0.6004
Orientation	5	2.3434	2.1647	0.0592
Distance × Orientation	10	1.3168	1.2164	0.2818
Size × Distance	6	0.9836	0.9086	0.4896
Size × Orientation	15	0.5966	0.5511	0.9087
Size × Distance × Orientation	30	0.6891	0.6366	0.9296
Error	212	1.0826		
Corrected total	286			
<b>(b) % organic matter</b>				
Size	3	2.6660	5.4360	0.0678
Site (Size)	4	0.4904	6.8671	0.0001***
Distance	2	0.1797	2.5167	0.0882
Orientation	5	0.1340	1.8770	0.1098
Distance × Orientation	10	0.0531	0.7434	0.6813
Size × Distance	6	0.1336	1.8705	0.0986
Size × Orientation	15	0.2017	2.8248	0.0018**
Size × Distance × Orientation	30	0.0544	0.7615	0.7982
Error	68	0.0714		
Corrected total	143			
<b>(c) % mud</b>				
Size	3	4959.9	9.6754	0.0264*
Site (Size)	4	512.63	1.6488	0.1721
Distance	2	984.03	3.1650	0.0485*
Orientation	5	1571.3	4.8930	0.0007***
Distance × Orientation	10	193.75	0.6232	0.7889
Size × Distance	6	214.14	0.6887	0.6594
Size × Orientation	15	996.99	3.2067	0.0005***
Size × Distance × Orientation	30	255.64	0.8222	0.7189
Error	68	310.91		
Corrected total	143			
<b>(d) % sand</b>				
Size	3	6193.8	40.331	0.0019**
Site (Size)	4	153.58	0.6471	0.6308
Distance	2	775.36	3.2671	0.0442*
Orientation	5	882.46	3.7183	0.0049**
Distance × Orientation	10	132.66	0.5590	0.8413
Size × Distance	6	146.17	0.6159	0.7168
Size × Orientation	15	670.87	2.8268	0.0018**
Size × Distance × Orientation	30	189.51	0.7985	0.7488
Error	68	237.32		
Corrected total	143			
<b>(e) % gravel</b>				
Size	3	3.7928	0.7717	0.5672
Site (Size)	4	4.9151	2.7296	0.0361*
Distance	2	0.8513	0.4727	0.6253
Orientation	5	2.3483	1.3041	0.2726
Distance × Orientation	10	2.0318	1.1284	0.3546
Size × Distance	6	0.4899	0.2721	0.9482
Size × Orientation	15	2.5328	1.4066	0.1697
Size × Distance × Orientation	30	1.2676	0.7039	0.8552
Error	68	1.8007		
Corrected total	143			

Table 2. Summary of ANOVAs showing the effect of size, site, distance, orientation, and crossed factors on (a) faunal diversity ( $H'_a$ : based on density), (b) faunal diversity ( $H'_b$ : based on biomass), (c) total faunal biomass, and (d) species richness. Both types of diversity and richness data were square-root transformed. Reciprocal transformations were applied to total biomass. \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$

Source of variation	df	MS	F-value	p
<b>(a) Diversity (<math>H'_a</math>)</b>				
Size	3	1.5307	6.2314	0.0085**
Site (Size)	12	0.2456	11.9112	0.0001***
Distance	2	0.0755	3.6589	0.0275*
Orientation	5	0.0109	0.5307	0.7529
Distance $\times$ Orientation	10	0.0097	0.4712	0.9073
Size $\times$ Distance	6	0.0186	0.9019	0.4945
Size $\times$ Orientation	15	0.0582	2.8200	0.0005***
Size $\times$ Distance $\times$ Orientation	30	0.2261	1.0966	0.3428
Site $\times$ Distance $\times$ Orientation (Size)	204	0.0206	1.1760	0.1033
Error	287	0.0175		
Corrected total	574			
<b>(b) Diversity (<math>H'_b</math>)</b>				
Size	3	0.1398	0.5766	0.6413
Site (Size)	12	0.2425	3.3574	0.0002***
Distance	2	0.2131	2.9501	0.0546
Orientation	5	0.1324	1.8328	0.1079
Distance $\times$ Orientation	10	0.0903	1.2498	0.2613
Size $\times$ Distance	6	0.1064	1.4733	0.1889
Size $\times$ Orientation	15	0.0497	0.6882	0.7947
Size $\times$ Distance $\times$ Orientation	30	0.0718	0.9938	0.4816
Site $\times$ Distance $\times$ Orientation (Size)	204	0.0723	1.3890	0.0052**
Error	287	0.0520		
Corrected total	574			
<b>(c) Total biomass</b>				
Size	3	0.9085	3.2339	0.0607
Site (Size)	12	0.2810	9.1407	0.0001***
Distance	2	0.0376	1.2248	0.2960
Orientation	5	0.0446	1.4512	0.2075
Distance $\times$ Orientation	10	0.0115	0.3736	0.9570
Size $\times$ Distance	6	0.0426	1.3859	0.2218
Size $\times$ Orientation	15	0.0631	2.0548	0.0134*
Size $\times$ Distance $\times$ Orientation	30	0.0136	0.4433	0.9951
Site $\times$ Distance $\times$ Orientation (Size)	204	0.0308	1.5900	0.0001***
Error	287	0.0193		
Corrected total	574			
<b>(d) Species richness</b>				
Size	3	4.7101	4.2368	0.0294*
Site (Size)	12	1.1118	12.5817	0.0001***
Distance	2	0.5374	6.0817	0.0027**
Orientation	5	0.0395	0.4472	0.8151
Distance $\times$ Orientation	10	0.0528	0.5971	0.8153
Size $\times$ Distance	6	0.1508	1.7065	0.1210
Size $\times$ Orientation	15	0.1025	1.1600	0.3057
Size $\times$ Distance $\times$ Orientation	30	0.1150	1.3018	0.1467
Site $\times$ Distance $\times$ Orientation (Size)	204	0.0884	1.0718	0.2935
Error	287	0.0825		
Corrected total	574			

ues were highest at control sites, and decreased with increasing boulder size (Fig. 6c). As for  $H'_a$ , richness significantly increased with distance from boulders (Table 2b, Fig. 6k) with the lowest richness values observed close to boulders.

### Species composition

The biomass and density distribution of taxa among boulder sizes indicated a change in species dominance (Fig. 8). For example, the relative biomass of *Mya are-*

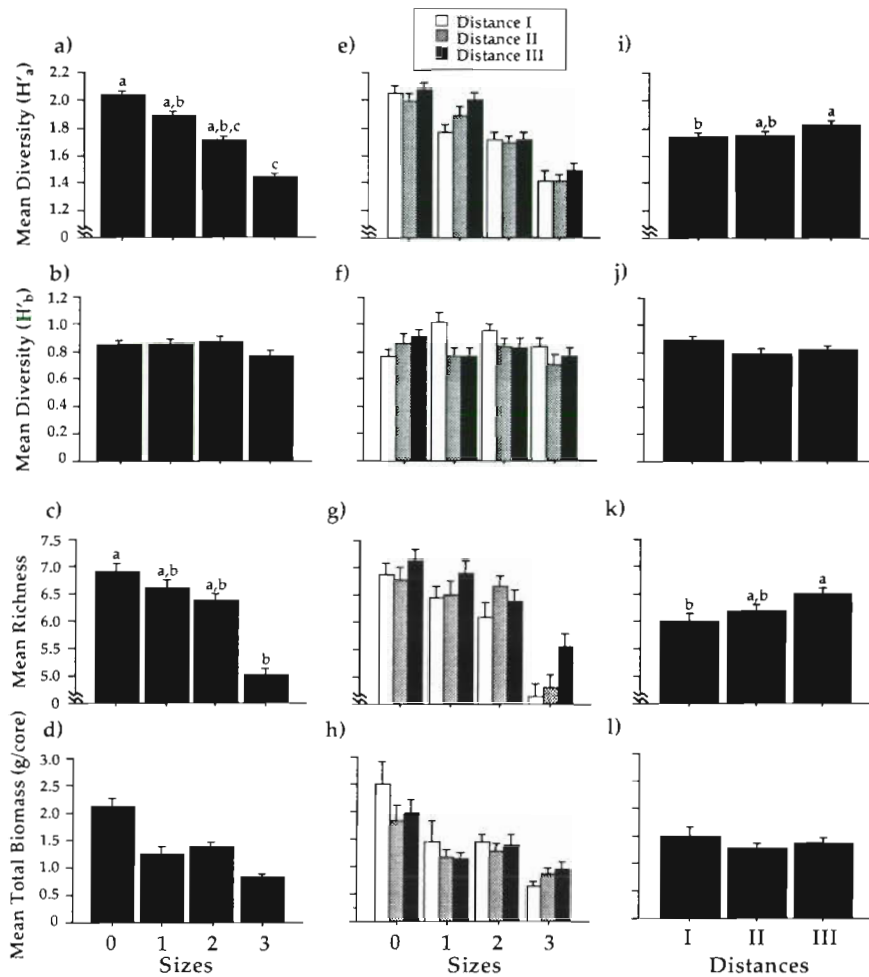


Fig. 6. Variations of mean (a) diversity based on density,  $H'_a$ , (b) diversity based on biomass,  $H'_b$ , (c) species richness, and (d) biomass for each boulder size. Variations of mean (e)  $H'_a$ , (f)  $H'_b$ , (g) species richness, and (h) biomass for each size by distance class. Variations of mean (i)  $H'_a$ , (j)  $H'_b$ , (k) species richness, and (l) biomass for each distance class. Dissimilar letters above bars are shown when values differ significantly (LS means multiple comparisons). All classes of orientation are combined. Error bars are SE

*narica* decreased with boulder size, while that of *Macoma balthica* increased along the same gradient. *Hydrobia minuta* was the dominant species in terms of density in all boulder sizes. The relative abundance of *H. minuta* increased with boulder size, while the density of *Oligochaeta* decreased along the size gradient.

Mean individual weight of *Macoma balthica*, *Polydora ciliata*, and *Mya arenaria* significantly decreased with boulder size, while that of *Hydrobia minuta* increased along the same gradient (Fig 9). No significant trend was observed for *Nereis virens*, *Littorina saxatilis* and *Mytilus edulis*.

#### Influence of physical variables on community characteristics

A multiple stepwise regression using sediment characteristics (normalized: % of organic matter, mud, sand, and gravel) as independent variables and community characteristics ( $H'_a$  and  $H'_b$ , species richness, total biomass) as response variables was carried out to

test the influence of sediment characteristics on community characteristics (Table 3a). Overall, sediment characteristics explained 27% of total biomass variance. For the 2 diversity indices,  $H'_a$  and  $H'_b$ , and species richness, the resulting models were significant, but only explained a small proportion of the variance (8, 3, and 7%, respectively).

Similarly, the stepwise regression using plaster dissolution as independent variables (2 sets of 2 series of measures) and community characteristics as the response variables showed that plaster dissolution explained up to 35% of the variance of  $H'_a$ , 30% for species richness, and 25% for total biomass.  $H'_b$  was not retained by the model (Table 3b)

#### DISCUSSION

Ours results show that boulder size (as topographical heterogeneity on a scale of meters) affects sediment characteristics (grain size and organic matter), hydrodynamic flow around boulders, and community char-



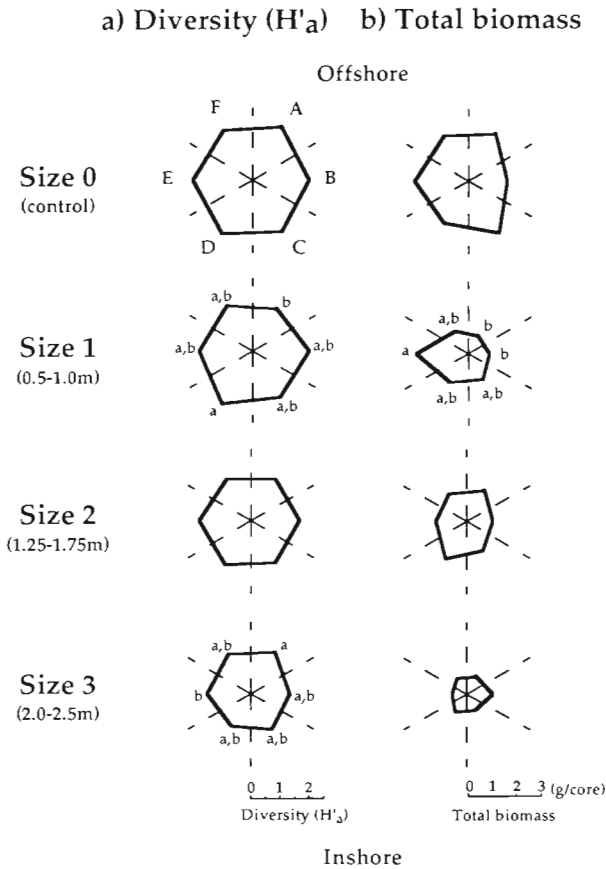


Fig. 7. Circular graphs of mean (a) diversity ( $H'_a$ ), and (b) total biomass for each orientation classes and size of boulders, all distances combined (results of LS means multiple comparisons are shown when differences in orientation are significant). Sectors are identified in the top left control graph

acteristics (diversity, richness and biomass). These parameters varied as a function of distance, orientation and boulder size.

**Effects of topographical heterogeneity in soft-bottom**

In the vicinity of intertidal boulders,  $H'_a$  and species richness decrease with boulder size, and increase with distance from boulders. Similar results associated with reef structures (Davis et al. 1982, Ambrose & Anderson 1990, Posey & Ambrose 1994) were interpreted as resulting from fish predation. The distance classes used in those studies (>5 m) were very different from those used in our study (0.75 m). In our study, there were no noticeable traces of predation by intertidal fish, shorebirds, or crabs. Physical variables such as sediment composition or flow rate are probably the main ones influencing the local distribution of the community characteristics.

**Influence of flow**

Plaster dissolution, hence flow intensity, decreased with increasing boulder size (Fig 5a). Protruding bodies such as boulders break the boundary-layer over flat substrata, reduce the flow rate on the lee side, and enhance the flow on lateral sides (Paola et al. 1986, Breitbart et al. 1995). For bi-directional currents, these structures create a low flow rate zone both upstream and downstream. However, the non-symmetrical direction of flood and ebb tidal currents and their variability in direction and intensity of flow at control sites (Fig. 5b) implies additional flow pattern complexity around boulders. This complex flow perturbation was expressed as reduced flow in the vicinity of boulders and by the lack of any trend in orientation on the flow index.

Our regression results indicate that hydrodynamic flow was more important than sediment characteristics in explaining variations in  $H'_a$  and species richness (Table 3). There were large differences in the variability of community characteristics between the 2 plaster dissolution groups, but we have no way of knowing if this was due to the brands of plaster or the different tidal periods (Table 3b).

Reduced flow rate may influence the quantity of food particles available to filter feeders by decreasing horizontal seston flux (see Muschenheim 1987, Grizzle & Morin 1989, Irlandi & Peterson 1991). Although we did not measure food characteristics, the decrease in aver-

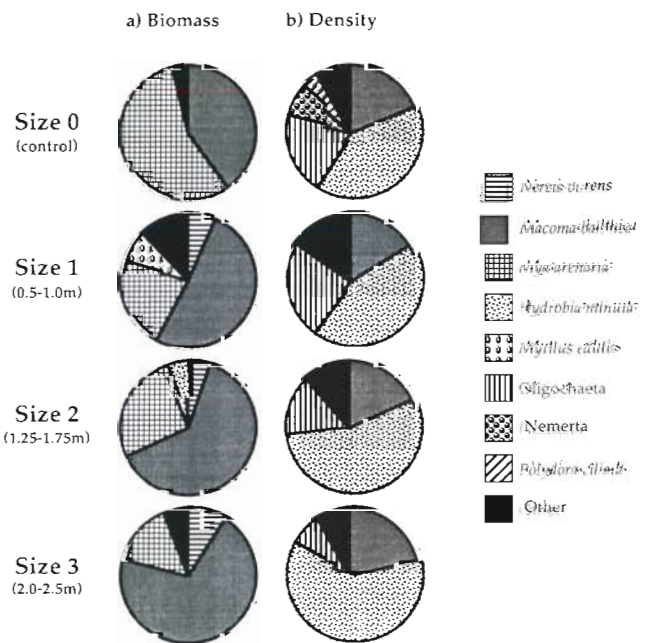


Fig. 8. Relative abundance of dominant taxa near boulders expressed as a percentage of (a) biomass and (b) density

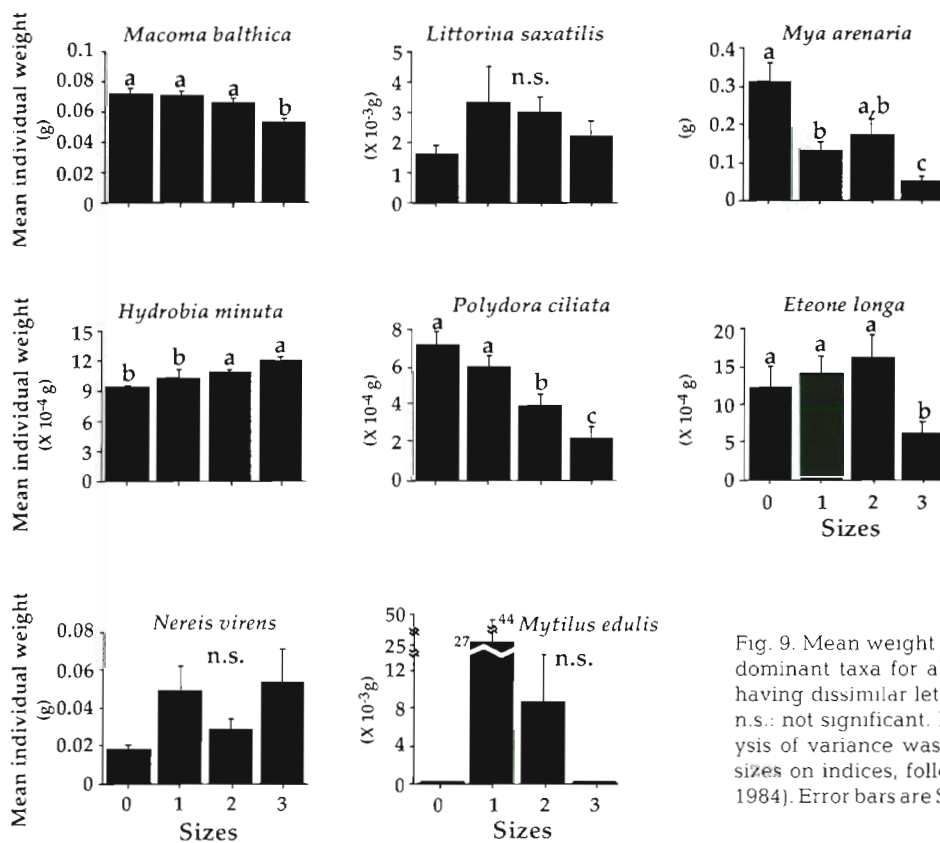


Fig. 9. Mean weight per individual (biomass per ind.) for dominant taxa for all cores for each boulder size. Bars having dissimilar letters above them differ significantly. n.s.: not significant. Kruskal-Wallis nonparametric analysis of variance was used to test the effects of boulder sizes on indices, followed by multiple comparisons (Zar 1984). Error bars are SE. Ordinate scales vary with species

age individual weight of *Mya arenaria* and *Polydora ciliata* (suspension feeders; Fauchald & Jumars 1979, Taghon et al. 1980) with boulders size may indicate less suitable habitat due to reduced flow rate, hence food, near boulders (Emerson 1990). However, a reduced flow near boulders could also enhance the abundance of other species. For example, the increase in density of *Hydrobia minuta* at boulder sites may be associated with increased passive dispersal (Newell 1962) or deposition of pellic materials (Newell 1965) along with higher deposition rates in areas of reduced flow.

### Sediment disturbance

We observed a higher proportion of mud (clay and silt) in the immediate vicinity of boulders regardless of boulder size. These differences in sediment characteristics may be attributed to increased passive deposition and retention of fine-grain particles at low flow rates (Eckman et al. 1981, Jumars & Nowell 1984). Community characteristics such as  $H'_a$ , richness, and biomass are known to be related to grain size (Rhoads & Young 1970, Gray 1974, Rhoads 1974, but see Snelgrove & Butman 1994). No persistent sediment patterns in rela-

tion to orientation were detected among boulder sizes. Moreover, no consistent pattern of  $H'_a$  was observed among Orientation  $\times$  Size treatments, and no direct relationship with sediment characteristics was detected. This was reflected in the small percentage of  $H'_a$ ,  $H'_b$ , and richness variability explained by sediment composition. Organisms may be less sensitive to small changes in sediment quality observed within sites on the scale considered in this study. This is consistent with Butman's (1987) comment that the relationship between intertidal species and sediment composition might become more apparent when the distance between samples is large (>5 m to 800 m).

$H'_b$  was not influenced by any treatment. Wilhm (1968) suggested that an estimate of diversity based on biomass, as opposed to density, would be more closely related to energy distribution among macroinvertebrate species. We assume that the high biomass dominance of *Mya arenaria* contributed to the lack of difference in  $H'_b$  among boulder sizes.

Sediment composition explained a greater portion of variability in community biomass (Table 3). However, no evident relationship between biomass and sediment characteristics was observed with orientation at different scales. For orientation E of small boulder size, faunal biomass had a high value (see Fig. 7); this is

Table 3. Results of multiple regression analyses. Intercepts (a) and independent variables of (a) % organic matter (OM), % mud (M), % sand (S), and % gravel (G); (b) plaster dissolution of first 2 series of measures (PD 1, at neap tide) and last 2 series of measures (PD 2, at spring tide)

(a) Variable	a	OM	M	S	G	p	R <sup>2</sup>
Diversity ( $H'_a$ )	1.25	-	-	0.08	-	0.0006	0.08
Diversity ( $H'_b$ )	0.92	-	-	-	0.05	0.0340	0.03
Species richness	2.61	0.18	-	-	-	0.0018	0.07
Total biomass	0.53	0.09	-	-0.14	-	0.0483	0.27
(b) Variable	a	Plaster dissolution			p	R <sup>2</sup>	
<b>PD1</b>							
Diversity ( $H'_a$ )	0.82		0.12		0.0005		0.08
Diversity ( $H'_b$ )	-		-		-		-
Species richness	3.03		0.4		0.0025		0.06
Total biomass	1.33		-0.1		0.0001		0.25
<b>PD2</b>							
Diversity ( $H'_a$ )	-1.08		0.19		0.0001		0.35
Diversity ( $H'_b$ )	-		-		-		-
Species richness	-3.35		0.65		0.0001		0.30
Total biomass	1.13		-0.04		0.0001		0.15

likely associated with the high percentage of sand in the same sector (Fig. 4).

### Habitat complexity

Studies from freshwater streams have highlighted the importance of topographic heterogeneity, such as boulders, for the distribution and abundance of organisms. For example, boulders enhance habitat complexity by modifying local currents and increase the abundance of aquatic insects and moss in stream benthos (Hynes 1970, McAuliffe 1983, Hildrew & Giller 1992). The presence of hard substrate (e.g. stabilized sediment, gravel, boulders) in soft-bottom environments permits the coexistence of both rocky-substrate and soft-bottom species. This source of habitat complexity, combining various scales of topographic heterogeneity, may affect abundance of organisms by offering refuges or additional microhabitats (Woodin 1978) and in turn should increase richness and diversity over large scales (e.g. the whole bay). On a scale of meters, our results showed that species composition was similar irrespective of the scale of topographic heterogeneity (boulder sizes). However, the relative abundance (density and biomass) of dominant species varied near boulders, which influenced estimates of diversity, richness, and community biomass in the vicinity of boulders.

The change in flow rate and sediment composition around isolated boulders and the subsequent effect on

community characteristics increased with boulder size. Therefore, in a complex assemblage of boulders, which occurs more commonly than do isolated boulders, we hypothesize that the influence of flow regime on sediment characteristics must be greater and the effect on infauna more pronounced than in the vicinity of a single boulder.

In summary, topographic heterogeneity in the form of boulder size on a scale of meters influenced community diversity, richness, and biomass significantly by modifying sediment characteristics and hydrodynamic flow. Because the flow and sediment characteristics are interrelated, further work needs to be carried out to partition the relative contribution of these 2 factors in the vicinity of boulders. There is also need to examine the precise effect of topographic heterogeneity on food supply and larval recruitment in soft-bottom benthic organisms.

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