

Topographic heterogeneity, hydrodynamics, and benthic community structure: a scale-dependent cascade

Frédéric Guichard*, Edwin Bourget

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

ABSTRACT: The influence of boulder size on flow velocity and rocky shore intertidal macrobenthic diversity and biomass was examined. A 3.6 m radius area around boulders of different size categories (50–75, 75–100, and 200–250 cm) and control sites (no boulders) was divided into six 60° sectors and 4 distance classes away from boulders (0–30, 30–90, 90–180, and 180–360 cm), forming 24 sampling cells for each boulder and control site. Flow velocity patterns near boulders were examined with Marsh-McBirney current meters and plaster cylinders immersed in the center of each sampling cell. Sessile organisms in 4 randomly positioned 10 × 10 cm quadrats from each sampling cell were sampled. The blotted mass of each species collected was determined for each quadrat (n = 1440). Downstream of a large boulder, mean flow velocity was half that upstream. This was also the only orientation where flow velocity never reached >15 cm s⁻¹. Similarly, velocity indices obtained from the erosion of plaster cylinders were significantly lower downstream compared to upstream of boulders, and differences were greater for large boulders. Invertebrate biomass decreased significantly downstream of boulders. This effect increased with boulder size, and was significant for the large boulder category (200–250 cm). Algal biomass was not significantly influenced by boulders, though distribution patterns were analogous to invertebrate biomass. Diversity (*H'*) peaked along the distance gradient around larger boulders, and generally increased with boulder size. The positive correlation between biomass and the velocity index was stronger with increasing boulder size. The correlation between invertebrate biomass and the flow velocity index was not significant at control sites, but 27.4 % of the variation in invertebrate biomass around large boulders could be explained by the velocity index. These results support the hypotheses that (1) hydrodynamics is a vector linking topographic heterogeneity and community structure, and (2) this cascade (topographic heterogeneity → hydrodynamics → community structure) is scale-dependent.

KEY WORDS: Topographic heterogeneity · Spatial scales · Benthos · Hydrodynamics · Community structure

INTRODUCTION

Spatial ecology is a growing field (Levin et al. 1997, Tilman & Kareiva 1997). With the explicit treatment of space in ecological studies, problems related to spatial variability and spatial scales need to be addressed (Wiens 1989, Levin 1992, Schneider 1994). Experiments testing the influence of environmental variables (physical or biological) on community structure seldom include space and spatial scale explicitly as main treat-

ments, with the result that 'pattern-oriented' spatial models (Grimm 1994, Grimm et al. 1996) based on environmental variables are difficult to make. Experiments must be designed to test relationships between spatial variability of physical (e.g. current velocity) and biological (e.g. biomass) variables over gradients of spatial scales. In order to test for the existence of such scaling in intertidal habitats, we examined the influence of scales of topographic heterogeneity on hydrodynamic patterns and their influence on 2 community characteristics (biomass and diversity) in a rocky shore intertidal community.

*E-mail: frederic.guichard@giroq.ulaval.ca

Although stable over ecological temporal scales, topographic heterogeneity influences the abundance and distribution of organisms by creating refuges against harsh physical (e.g. wind blowdown, Boose et al. 1994; desiccation, Garrity 1984; and ice scouring, Bergeron & Bourget 1986) and biotic (e.g. competition and predation, Garrity & Levings 1981, Gosselin & Bourget 1989) conditions. Topographic features can also modify hydrodynamics over very small (Eckman 1979) to regional scales (Wolanski & Hammer 1988), and control juvenile transport (Rankin et al. 1994), recruitment (Johnson 1994), and feeding rates (Fréchette et al. 1989) of benthic organisms. Few studies have investigated the influence of topographic heterogeneity on community structure at the scale of meters. In marine systems, topographic heterogeneity has been shown to modify community characteristics in soft-bottom communities (Cusson & Bourget 1997) and benthic fish recruitment by creating favorable local hydrodynamic conditions (Breitburg et al. 1995).

On subarctic rocky shores, glacially deposited boulders are an important source of topographic heterogeneity (Dionne 1972, Drapeau 1990). In the St. Lawrence system in particular, boulders are relatively spherical, and offer the possibility of testing scale effects by using boulders of increasing size. Since biological interactions are limited in subarctic mid intertidal environments (see below), we used these intertidal boulder fields to test the following hypotheses: (1) surrounding bedrock community characteristics (diversity and biomass) are modified as a function of both position (orientation, distance from boulder) and boulder size (scale); (2) the spatial patterns of community characteristics near boulders are correlated with hydrodynamic patterns. Our results show that (1) boulders locally influenced hydrodynamics and spatial distribution of benthic organisms, and (2) boulder size modulates the strength of these relationships. We also present evidence that hydrodynamics was likely a vector linking topographic heterogeneity to community characteristics.

METHODS

Study area. Sainte-Flavie, along the south shore of the St. Lawrence Estuary, Québec, Canada (Fig. 1) was chosen as our study site. A 3 km long intertidal shore section was selected with the following criteria: (1) it was located along a relatively straight part of the coastline and there were no large scale topographic features nearby to affect the hydrodynamic flow regime, (2) the hydrodynamic regime of the area was under investigation as part of the CHASE project (Coastal Heterogeneity And Scaling Experiments), (3) a rela-

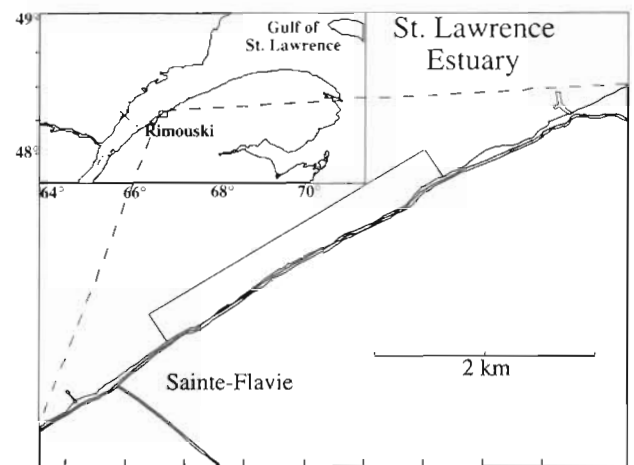


Fig. 1. Study area along the south shore of the St. Lawrence Estuary, Québec, Canada

tively large number of morainic boulders was stranded on the horizontal intertidal bedrock, so that stringent boulder selection criteria could be applied (see below). The study area shore was a weakly inclined rocky platform, with different sized boulders and some fine sediments. Overall, the shoreline of the Estuary was oriented along the 240°/60° axis relative to magnetic north. The macrobenthic community (31 algal and invertebrate species were identified; Table 1) was dominated by *Mytilus edulis* and/or *Mytilus trossulus*, hereafter referred to as *Mytilus*, indistinguishable by simple morphological examination, and *Fucus* species. *Littorina saxatilis* and *Littorina obtusata* were also very abundant. We did not observe any strong correlation among dominant species at the scale of quadrats. *Mytilus* biomass was weakly correlated with *L. saxatilis* ($r = 0.18$; $p < 0.01$) and with *L. obtusata* ($r = 0.01$; $p < 0.01$), and *Fucus* biomass was correlated with *L. obtusata* ($r = 0.12$; $p < 0.01$). In the mid intertidal of the study area, no known predators or effective competitors of the mussel are known. Semidiurnal tidal range varied from about 2 m (neap tides) to 4.5 m (spring tides). In spring, ice scouring is an important disturbance factor, dislodging most exposed organisms (Archambault & Bourget 1983, Bourget et al. 1985, Bergeron & Bourget 1986).

Boulder selection. Size categories were determined after a preliminary examination of available boulders. Three size categories of rounded boulders were selected, based on the average of the maximum height, minimum diameter, and maximum diameter: (1) 50 to 75 cm, (2) 75 to 100 cm, and (3) 200 to 250 cm. The control site was an area with no boulders (Fig. 2). For each boulder size category and control, 4 experimental replicate sites were randomly selected from 16 pre-marked potential sites in the study area, except for the

large boulder sites, for which only 3 replicate sites corresponded to the criteria (see below). To limit the within- and among-site treatment variability, the following *a priori* criteria were established: (1) each boulder dimension (height, length, width) should not exceed 2× the others, (2) selected boulders must stand on bedrock, and (3) sites must be free of any topographic irregularity (other boulders and crevices) larger than 30 cm within a radius of 5 m, and (4) sites must be free of a sediment layer thicker than 2 cm, and of water (tide pools >2 cm depth) over a minimum of 60% of the total area. The diameter of selected boulders ranged from 53 to 73 cm (small boulders), 85 to 98 cm (medium boulders) and 200 to 250 cm (large boulders). The area around the randomly selected sites was divided into six 60° sectors relative to magnetic north, and 4 classes of distance from boulders (30, 90, 180, 360 cm), to examine the distribution of organisms in the vicinity of boulders, forming 24 sampling cells around each boulder. At each control site we structured the sampling around a medium size circle

(75 cm) and obtained a comparable number of sampling cells (Fig. 2).

Flow measurements. Dissolution of plaster cylinders: We used plaster cylinders anchored in the center of each sampling cell (24 cells per boulder or control site; $n = 360$; Fig. 2) over 24 h (2 full semi-diurnal tidal cycles) to obtain a relative measure of flow velocity. Plaster mass loss was shown to be linearly related to mean water velocity (Muus 1968, Komatsu & Kawai 1992, Thompson & Glenn 1994). Each cylinder was vertically anchored 2 cm above the bottom using a metal rod (4 mm diam.) running through it that was solidly anchored to the intertidal bedrock. Each cylinder (8 cm long × 2.5 cm diam.) was made from plaster of Paris (Lepage™, Brompton, Ontario, Canada). The ends were covered with epoxy to prevent dissolution and maintain a near constant exposed area during the immersion period. The cylinders were dried for 21 d at ambient temperature then weighed before immersion and then dried 21 d and reweighed after retrieval to obtain the dry mass loss (± 0.005 g). All plaster cylin-

Table 1. Species of the macrobenthic community at the study site. Each species is listed with its frequency of occurrence and mean biomass in quadrats, and its total and maximum biomass in all quadrats ($n = 1440$)

Species	Frequency (%)	Mean (\pm SD) biomass (g)	Total biomass (g)	Maximum biomass (g)
<i>Littorina saxatilis</i>	99.58	0.59626 (0.54378)	858.607	8.878
<i>Fucus</i> sp.	88.26	26.49733 (39.80772)	38130.000	324.010
<i>Littorina obtusata</i>	86.04	0.65898 (1.00810)	948.277	14.590
<i>Mytilus edulis</i> (and/or <i>trossulus</i>)	86.04	20.56315 (26.79250)	29611.000	220.140
<i>Macoma balthica</i>	43.54	0.10758 (0.36761)	154.917	9.971
<i>Acmaea testidunalis</i>	23.54	0.03124 (0.11471)	44.978	1.439
<i>Mesodesma arctatum</i>	7.15	0.09310 (1.01557)	134.060	21.131
<i>Mya arenaria</i>	6.39	0.01038 (0.06664)	14.950	1.385
<i>Cistena granulata</i>	5.21	0.01085 (0.06551)	15.622	0.964
<i>Petalonia fascia</i>	3.75	0.03165 (0.34039)	45.582	8.573
<i>Lacuna vincta</i>	3.47	0.00257 (0.02326)	3.706	0.660
<i>Ulva lactuca</i>	1.39	0.01195 (0.17964)	17.214	5.563
<i>Skenea planorbis</i>	0.97	0.00004 (0.00055)	0.058	0.014
<i>Antithamnion</i> sp.	0.76	0.01014 (0.36582)	14.598	13.878
<i>Bunodactis stella</i>	0.76	0.00210 (0.03355)	3.017	0.785
<i>Balanus crenatus</i>	0.69	0.00102 (0.01449)	1.473	0.290
<i>Hiatella arctica</i>	0.69	0.00141 (0.02719)	2.032	0.920
<i>Polysiphonia</i> sp.	0.63	0.00093 (0.02358)	1.342	0.665
<i>Rhodomela confervoides</i>	0.56	0.00097 (0.01714)	1.401	0.425
<i>Scytosiphon lomentaria</i>	0.49	0.00256 (0.05367)	3.687	1.807
<i>Margarites helicinus</i>	0.21	0.00003 (0.00101)	0.043	0.038
<i>Enteromorpha</i> sp.	0.14	0.00047 (0.01477)	0.680	0.544
<i>Hydrobia minuta</i>	0.14	0.00001 (0.00025)	0.013	0.008
<i>Acrosiphonia arcta</i>	0.07	0.00027 (0.01023)	0.388	0.388
<i>Aeolidia papillosa</i>	0.07	0.00115 (0.04380)	1.662	1.662
<i>Halosaccion ramentaceum</i>	0.07	0.00001 (0.00037)	0.014	0.014
<i>Desmarestia aculeata</i>	0.07	0.00071 (0.02699)	1.024	1.024
<i>Elachista fucicola</i>	0.07	0.00002 (0.00063)	0.024	0.024
<i>Littorina littorea</i>	0.07	0.00024 (0.00922)	0.350	0.350
<i>Porphyra</i> sp.	0.07	0.00009 (0.00343)	0.130	0.130
<i>Semibalanus balanoides</i>	0.07	0.00036 (0.01368)	0.519	0.519

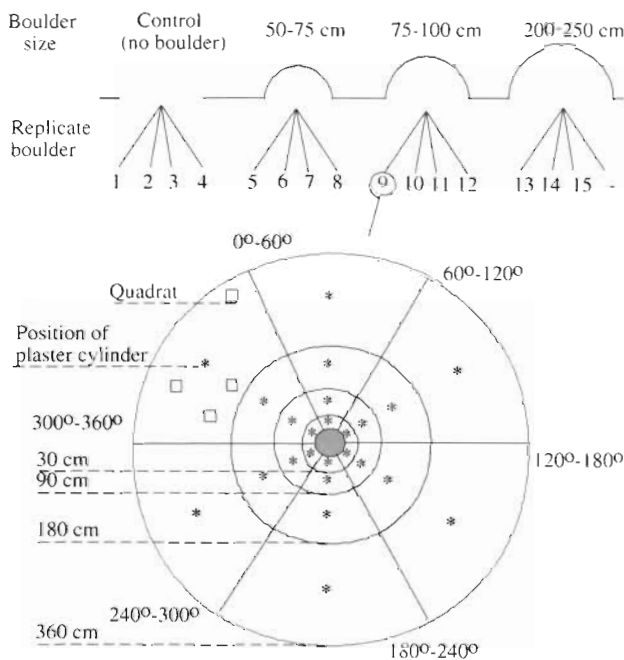


Fig. 2. Schematic representation of the sampling design. Orientations are relative to magnetic north

ders were immersed on 18 August 1994. Dry mass loss (initial – end weight in g) was used as a relative index of mean water velocity.

Current velocity measurements: Current velocities were also measured around one randomly selected site for each size category, simultaneously using 2 Marsh-McBirney electromagnetic current meters, linked to a EMOBS (self-contained ocean data acquisition system; Dalhousie University, Nova Scotia, Canada). The 2 current meters were placed 10 cm above the substratum. During each 12 h mooring period, both current meters were placed at the site on opposite sides (0°/180° or 90°/270° relative to magnetic north) and at a defined distance from the boulder (50 or 150 cm). The 4 positions [2 orientation axes (u_x and u_y) and 2 distances] around each site were investigated within a 48 h period (4 tidal cycles). Each site was investigated at 2 randomly selected dates, a first time between 2 and 16 August 1994, and a second time between 17 and 24 August 1994. The datalogger was programmed to record the average of 60 velocity measurements (60 u_x and 60 u_y) measured over 1 min by each probe, at 10 min intervals, when water depth was greater than 50 cm.

Community characteristics. Benthic community sampling at each experimental site was carried out between 17 July and 8 August 1994. The sampling period was kept short to minimize biases from temporal changes in community structure. At each cell of each boulder and control site, four 10 × 10 cm quadrats

were randomly chosen ($n = 1440$) from random polar coordinates. All organisms (invertebrates and algae) were taken from each quadrat, except for encrusting species, which could not be collected effectively, and the % cover was estimated visually by one observer. Samples were kept frozen at –18°C until analysis. They were then sieved using 1 mm mesh sieves and all sessile or sedentary individuals were sorted and identified to species level, or the lowest taxonomic unit possible. The blotted mass of all species in each quadrat was weighed using a Mettler 360 balance (± 0.005 g). A Shannon diversity index (H'), based on biomass (Frontier & Pichod-Viale 1993), was computed for each quadrat. An evenness index was computed as H'/H'_{\max} , where H'_{\max} is the diversity index computed for an evenly distributed biomass among species in each quadrat.

Some potentially influential environmental variables were also measured. The covariables in each quadrat were small-scale topographic heterogeneity (rugosity, see below), height above the zero tidal level, % cover of soft substratum, and % water cover (pools). Since small-scale topography (1 to 10 cm) has been shown to influence rocky shore benthic communities, especially in regions exposed to ice scouring (Chabot & Bourget 1988, Bourget et al. 1994, Archambault & Bourget 1996), substratum heterogeneity within quadrats was determined using a woodworker's profiler (1 mm resolution). This instrument consists of 150 metal rods (1 mm diam., 10 cm high) tightly aligned over 15 cm, capable of moving vertically and individually, thus allowing the profiler to retain the contour of any surface along a 15 cm long transect. Profiles along two 10 cm perpendicular transects were obtained for each quadrat. The profiles were immediately traced on paper in the field, then digitized in the laboratory (72 dpi resolution). For every quadrat transect, heterogeneity indices were computed at 10 spatial resolutions, from 1 to 50 mm, using the box-counting method (Hastings & Sugihara 1993). For each quadrat, we took as a scale-specific index of heterogeneity the mean number of boxes (N) needed to cover profiles at each resolution (box size), as computed by a box-counting algorithm. Similar single scale indices of heterogeneity have previously been used in ecological studies (McCormick 1994). The fractal dimension (D), computed as the slope of the regression line ($n = 12$) of $\log(N)$ against $\log(1/S)$, where S is the box size, was also used as an index of substratum heterogeneity, which varied from 1 (straight line) to 1.12 in our samples.

Analysis. The null hypotheses that there was no effect of boulder size, orientation and distance on dry mass loss of plaster cylinders, the biomass of each dominant species, invertebrate biomass, algal biomass,

diversity (H'), evenness (H'/H'_{\max}), and the proportion of species other than *Mytilus* and *Fucus* sp., were tested by a mixed factorial ANOVA model, using an SAS statistical package (SAS 1988). Normality and homoscedasticity were examined on residuals. Square-root transformation was applied to invertebrate biomass to achieve these postulates. Replicate sampling design allowed us to discriminate between treatment effects and random variability. For the latter we computed among-boulder variability [boulder (boulder size)], within boulder (i.e. among sampling cells) variability [orientation \times distance \times boulder (boulder size) or orientation \times boulder (boulder size) + distance \times boulder (boulder size), depending on the model], and within-sampling-cell variability (error term). The within- and among-boulder random variability (random factors) were not interpreted. Covariables were not included in the ANOVA model since they violated at least 1 of 3 conditions: (1) significant, and (2) linear effect on the dependent variable, and (3) no interaction with main treatments. We used a stepwise multivariate regression model using JMP statistical software (SAS 1994) to determine variation of invertebrate biomass, algal biomass and H' explained by covariates. The presence of autocorrelated spatial structure was visually investigated from semivariograms computed for each control site, where the 96 quadrats were positioned in a cartesian coordinates system before the computation of omnidirectional semivariograms with Variowin geostatistical software (Pannatier 1996). We did not observe any consistent increase of the semivariance as a function of the spatial lag (i.e. autocorrelation). Autocorrelation would have violated assumptions of independence of samples (Fortin et al. 1989, Dutilleul 1993). Correlation between biological and hydrodynamic (velocity index) variables was tested using Pearson correlation coefficients between velocity index values and mean biomass or diversity in each sampling cell. In order to test for the scale-dependent relationship between flow velocity and biological variables, correlation coefficients were computed for each boulder size category and significant differences among coefficients were tested using a z-transformation (Sokal & Rohlf 1981).

RESULTS

Flow patterns

Current velocity at 10 cm above the substratum and at water depth greater than 50 cm ranged from <1 to 50 cm s^{-1} with an average velocity of 6 cm s^{-1} . Mean orientation at the control site was $68^\circ \pm 51^\circ$ relative to magnetic north, i.e. approximately eastward and par-

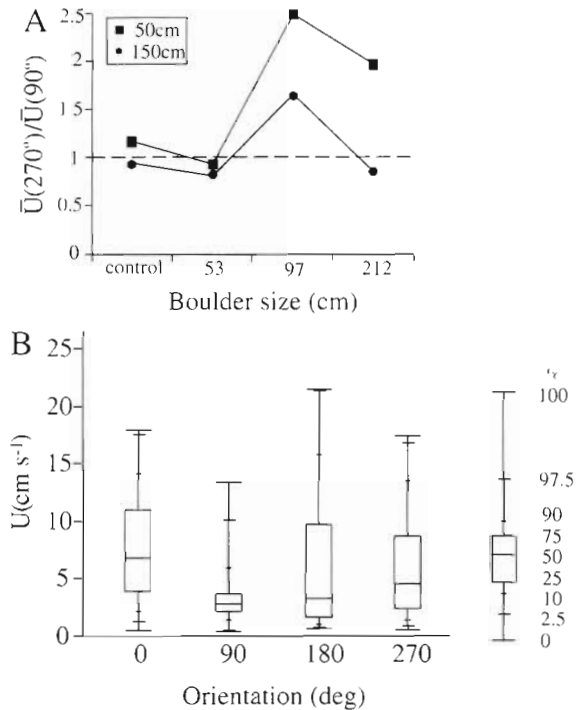


Fig. 3. Current meter data represented as (A) ratio of upstream to downstream mean velocity, and (B) quantile box plot (see legend on the right) obtained for 4 orientations at 50 cm distance from a large boulder

allel to the shore. Both flow orientation and velocity remained relatively unchanged within one semi-diurnal tidal cycle. Thus, we did not observe a flow reversal or velocity decrease near the time of high tide. These data are in agreement with long time series current measurements at the scale of the study area (Guichard unpubl. data).

There were well-defined flow velocity patterns around boulders. Near the boulders (50 cm from the edge), the ratios of mean velocity upstream to mean velocity downstream (see 'Methods') increased with boulder size (near 1 at control and small boulder sites, to 1.97 around the large boulders) (Fig. 3A). The high ratio value near the medium boulder could have been caused by unsuspected local characteristics of the flow, since even at 150 cm from the boulder, the ratio was still relatively high (Fig. 3A). This relation between boulder size and velocity ratio (Fig. 3A) holds for velocity values averaged over 24 h; no pattern was detected for values averaged over shorter time intervals. Similarly, orientation significantly influenced the flow velocity index (Table 2, Fig. 4A). Plaster cylinders at 90° and 150° (downstream side) were significantly less eroded than cylinders at 30° and 210° (opposite directions). This effect was detected graphically only around large boulders (Fig. 4B).

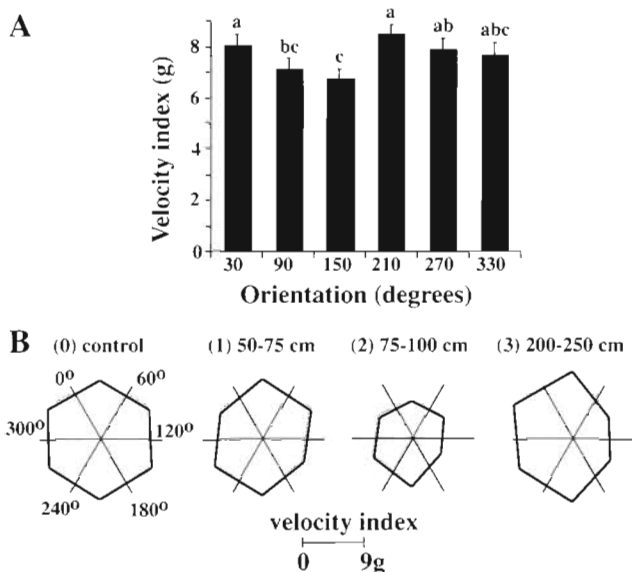


Fig. 4. Mean velocity index for 6 equal orientation sectors around boulders. (A) All boulder size categories combined. Statistically different orientation categories are indicated by different letters (+ SE). (B) Velocity index for each boulder size category

Table 2. Analysis of variance showing the effect of boulder size (Bsize), orientation (Ort), distance (Dst), among-[B(Bsize)] and within-boulder variability [Ort × B(Bsize) and Dst × B(Bsize)], on velocity index (initial – end mass of plaster cylinders). *Significant at 5% and ***0.1% levels

Source of variation	df	MS	F	p
Bsize	3	152.2675	1.5862	0.2486
B(Bsize)	11	95.8618	10.5968	0.0001***
Ort	5	28.1546	3.1510	0.0143*
Dst	3	1.3704	0.2357	0.8708
Ort × Dst	15	7.1816	1.2607	0.2326
Bsize × Ort	15	11.4832	1.2852	0.2430
Bsize × Dst	9	3.2384	0.5571	0.8215
Bsize × Ort × Dst	45	5.1864	0.9105	0.6347
Ort × B(Bsize)	55	8.9340	1.5683	0.0159*
Dst × B(Bsize)	33	5.8130	1.0204	0.4463
Error	165	5.6965		
Corrected total	359			

Current velocity above 10 cm s^{-1} occurred less than 3% of the time on the downstream side, 50 cm from a large boulder. The velocity was at least this high 20% of the time for every other orientation (Fig. 3B).

Community characteristics

There was a significant interaction effect of boulder size and distance from boulders on diversity H' . Invertebrate biomass was significantly influenced by the

Table 3. Analysis of variance showing the effect of boulder size (Bsize), orientation (Ort), distance (Dst), among-[B(Bsize)] and within [B × Ort × Dst(Bsize)] boulder variability, on invertebrate biomass (g), algal biomass (g) and diversity (H'). Squared-root transformation was applied to invertebrate biomass to achieve normality and homoscedasticity. Significant at **1% and *** 0.1% levels

Source of variation	df	MS	F	p
Invertebrate biomass				
Bsize	3	116.6878	0.7226	0.5592
B(Bsize)	11	161.4806	20.4511	0.0001***
Ort	5	8.5087	1.0776	0.3732
Dst	3	7.2462	0.9177	0.4329
Ort × Dst	15	7.0592	0.8940	0.5715
Bsize × Ort	15	17.6795	2.2391	0.0058**
Bsize × Dst	9	6.6014	0.8360	0.5835
Bsize × Ort × Dst	45	8.4313	1.0678	0.3663
B × Ort × Dst(Bsize)	253	7.8959	1.5395	0.0001***
Error	1080	5.1290		
Corrected total	1439			
Algal biomass				
Bsize	3	83975.6283	3.0907	0.0718
B(Bsize)	11	27169.0219	18.5805	0.0001***
Ort	5	3288.2969	2.2488	0.0501
Dst	3	1191.1174	0.8146	0.4868
Ort × Dst	15	2366.0455	1.6181	0.0692
Bsize × Ort	15	2240.2021	1.5320	0.1369
Bsize × Dst	9	689.8247	0.4718	0.9984
Bsize × Ort × Dst	45	879.2227	0.6013	0.8729
B × Ort × Dst(Bsize)	253	1462.3215	1.2837	0.0045**
Error	1080	1139.1335		
Corrected total	1439			
Diversity (H')				
Bsize	3	0.8146	1.6271	0.2396
B(Bsize)	11	0.5007	2.5964	0.0038**
Ort	5	0.2273	1.1786	0.3201
Dst	3	0.2965	1.5378	0.2052
Ort × Dst	15	0.10434	0.5413	0.9157
Bsize × Ort	15	0.1554	0.8061	0.6706
Bsize × Dst	9	0.6234	3.2332	0.0010**
Bsize × Ort × Dst	45	0.2499	1.2961	0.1116
B × Ort × Dst(Bsize)	253	0.1928	1.2659	0.0069**
Error	1080	0.1523		
Corrected total	1439			

interaction between boulder size and orientation around boulders (Table 3). Boulder size, orientation, and the interaction between orientation and distance also showed a trend toward influencing algal biomass (but $0.05 < p < 0.1$). There was significant variability among and within boulders for H' , invertebrate biomass and algal biomass.

Influence of boulder size

There was a trend toward decreasing mean algal and invertebrate biomass, and increasing mean diver-

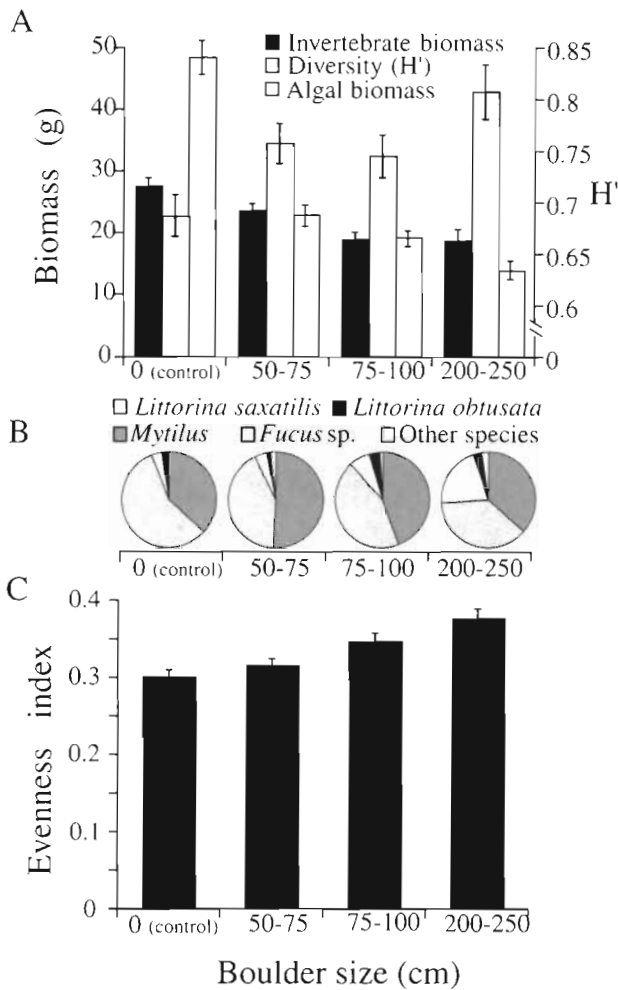


Fig. 5. Influence of boulder size (A) on mean invertebrate biomass, algal biomass, and H' , (B) on mean proportion of dominant species, and (C) on evenness index ($H'/H'_{max} + SE$)

sity with increasing boulder size (Fig. 5A). In general, the proportion of *Fucus* sp. and *Mytilus* biomass in the community decreased with boulder size, while other species biomass increased from 6% at control sites to 26% around large boulders (but $p > 0.05$; Fig. 5B). The evenness (H'/H'_{max}) of biomass increased with boulder size (but $p > 0.05$; Fig. 5C). Boulder size together with mean height above the zero level were good predictors of mean algal biomass within a given perimeter (< 3.6 m) (Fig. 6).

Influence of orientation

The negative effect of boulder size on invertebrate biomass was significant at all orientations except between 240° and 360° (Fig. 7B). Invertebrate biomass values were significantly lower on the downstream

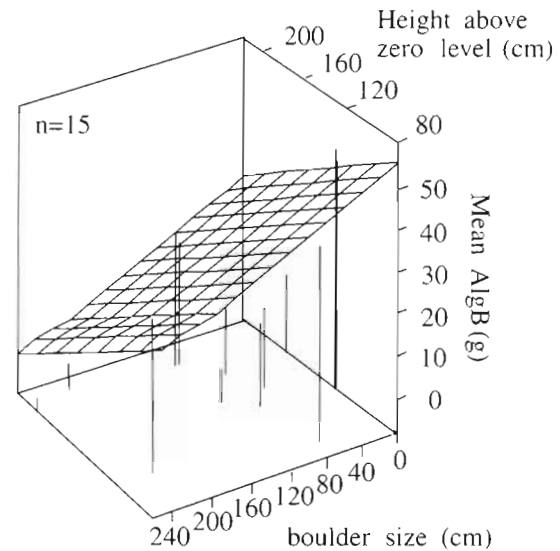


Fig. 6. Relationship between algal biomass (Mean AlgB), boulder size and height above zero tidal level (mean algal biomass = $72.56 - 0.11(\text{boulder size}) - 0.21(\text{height})$; $R^2 = 0.48$; $p < 0.05$) of all boulders and control sites. Algal biomass values were averaged for each boulder and control site before the regression analysis was performed

side compared to the upstream side of large boulders (Fig. 7A) and invertebrate biomass on the downstream side of boulders decreased with boulder size. Fig. 7B also shows that *Mytilus* was responsible for invertebrate biomass decrease as a function of boulder size. A similar pattern was observed for algal biomass, almost exclusively composed of *Fucus* sp. (Fig. 7A). H' was not significantly influenced by orientation.

Influence of distance from boulders

While there was a trend toward increasing diversity as a function of boulder size (Fig. 5A), the diversity peak was generally displaced along the distance gradient with increasing boulder size (Fig. 8). A similar trend was observed for the evenness index (Fig. 8).

Influence of covariables

Multiple stepwise regression carried out for covariable effects (% cover of soft substratum, % water cover, height above zero tidal level, substratum heterogeneity at 1 cm resolution) on biological variables (H' , invertebrate biomass, algal biomass) showed that all covariables together could explain 25.4% of the invertebrate biomass variability, 9.5% of algal biomass variability and 3.7% of H' variability. For invertebrate biomass, % cover of soft substratum was the most influ-

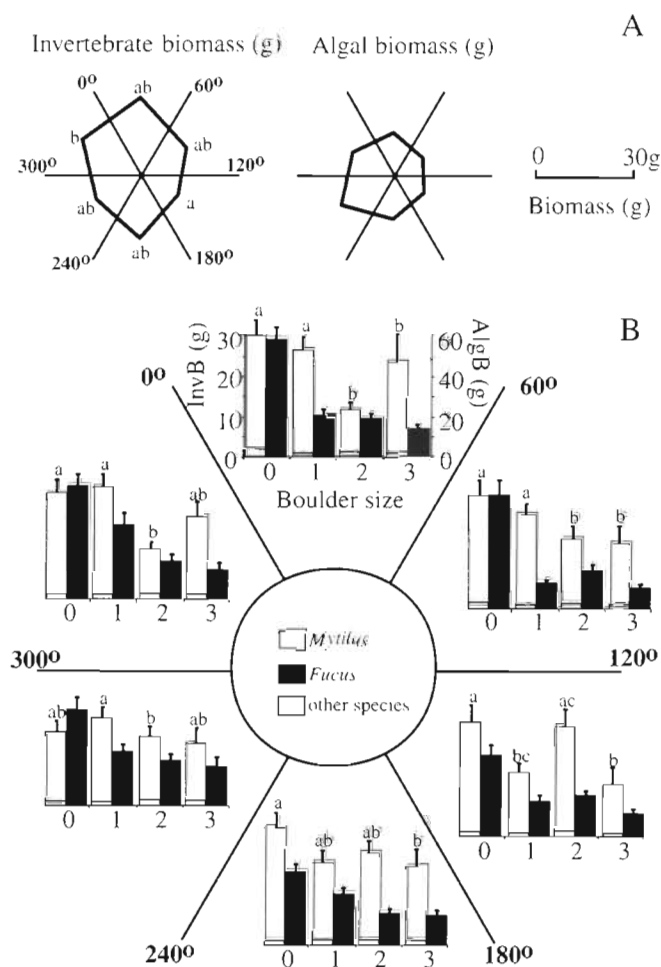


Fig. 7 Mean invertebrate biomass (InvB) and algal biomass (AlgB) for the 6 orientation categories (A) around large boulders and (B) as a function of boulder size categories (invertebrate biomass, first series; algal biomass, second series; +SE), with each bar represented as the sum of dominant and other species. Orientation categories (A) or boulder size categories (B) with significantly different invertebrate biomass values are indicated by different letters

ential covariable ($R^2 = 0.137$, $p < 0.0001$), and height above zero tidal level alone explained 6.15% of algal biomass variability.

Relationship between flow velocity index and biological variables

There was no direct effect of boulder size on velocity index (Table 2), but boulder size positively influenced the correlation between velocity index and the biomass values for invertebrates and algae (Fig. 9A). For example, r values between velocity index and invertebrate biomass were significantly larger around large

boulders than at control sites (chi-square test of homogeneity of coefficients, $p < 0.001$; pairwise comparisons of z -transformed coefficients; Fig. 9A). Near large boulders, the variance and maximum invertebrate biomass increased with increasing velocity, and the following regression model best described this relationship between invertebrate biomass and velocity index: $\text{invertebrate biomass} = 0.18(\text{velocity index})^2 - 0.51(\text{velocity index}) + 7.37$ ($R^2 = 0.274$; $p < 0.001$) (Fig. 9B). No significant correlation coefficient between velocity index and H' was observed though there was a trend toward larger negative correlations with increasing boulder size.

DISCUSSION

Our results support the hypothesis that topographic heterogeneity in the form of boulders affects local hydrodynamics and spatial variations in community characteristics. We have shown that flow velocity and spatial patterns of biomass around boulders were correlated (Fig. 9). Moreover, boulder size influenced (1) flow velocity patterns, (2) invertebrate biomass and diversity patterns, and (3) the relationship between flow velocity and invertebrate biomass.

Topographic scales and hydrodynamics

In marine habitats, the influence of topographic heterogeneity on hydrodynamics has been studied at small scales (e.g. mm and cm) (Eckman 1983, Butman 1987, Abelson et al. 1993, Worcester 1995, Harvey & Bourget 1997; see Nowell & Jumars 1984 for a review) and at large scales (km) (Genin et al. 1986, Wolanski & Hammer 1988, Alvarez et al. 1994). However, to our knowledge hydrodynamic patterns induced by a gradient of topographic scales, at or near the metre scale have not been studied extensively. Ferrier et al. (1996) examined flow patterns around an 8 m reef and showed the importance of bottom friction in shallow water. Flow velocity has also been examined around boulders in an oyster reef habitat where downstream velocity reduction was observed around boulders 30 to 75 cm in diameter (Breitburg et al. 1995).

The effect of protruding boulders on hydrodynamics can be compared to cylinders placed perpendicular to the flow. There has been much research on this phenomenon, both theoretical and empirical. The flow structure in relation to the Reynolds number (Re) has previously been investigated. Re is a non dimensional characteristic of flow (Tritton 1988) defined as $Re = DU/\mu$, where D is equal to the diameter of the cylinder, U is the mean ambient flow velocity, and μ is the kine-

matic viscosity. Re values reflect flow velocity and turbulence patterns around cylindrical objects. At Re between 4 and 40, 2 eddies are formed behind cylinders and do not move downstream. At Re = 40, the wake of the cylinder becomes unsteady and eddies are formed alternatively on one side and then on the other side of the cylinder (Kármán vortex street), so that only 1 eddy is present at a given time. Instability grows with Re in the wake of cylinders, leading to a turbulent wake once $Re > 400$. Near $Re = 10^5$, another threshold is observed and the entire boundary layer becomes turbulent. This results in a narrower wake and a turbulent separation of flow from the walls of cylinders (Vogel 1984, Denny 1988, Tritton 1988). In our study, the boulders can be roughly compared to cylinders perpendicular to the flow; given an ambient water velocity of 5.25 cm s^{-1} , a kinematic viscosity of $0.01 \text{ cm}^2 \text{ s}^{-1}$, and mean boulder sizes of 64 cm (small), 93 cm (medium) and 221 cm (large), then Re values are 3.3×10^4 , 4.88×10^4 and 1.16×10^5 respectively. Thus, large boulders (200 to 250 cm of diameter) were the only boulder sizes producing a completely turbulent hydrodynamic regime according to Re values. Only around large boulders were both velocity indices and current meter values consistently reduced on the downstream side, in agreement with this interpretation. These observations suggest the existence of a boulder size threshold (boulders of 190 cm diameter) above which hydrodynamic flow changes drastically. The irregular boulder shape and the roughness of both boulder surface and the surrounding substratum prevent us from establishing a precise relationship between classical fluid mechanics theory and hydrodynamic patterns around boulders (Vogel 1984, Lighthill 1986, Granger 1995, Ferrier et al. 1996). Here we use the non dimensional Reynolds number as a rough index to understand how scaling-up topographic heterogeneity may influence hydrodynamics, especially when this scaling-up causes Re to vary around threshold values.

Flow velocity and community characteristics

Two processes related to flow could explain biomass changes: (1) a direct effect of flow on the adhesion of individuals (Butman 1986, Denny 1988, Abelson 1994); and (2) an indirect effect of flow on food availability, that depends on food flux and feeding rate (Jumars & Nowell 1984, Nowell & Jumars 1984). We found that invertebrate biomass was positively correlated with

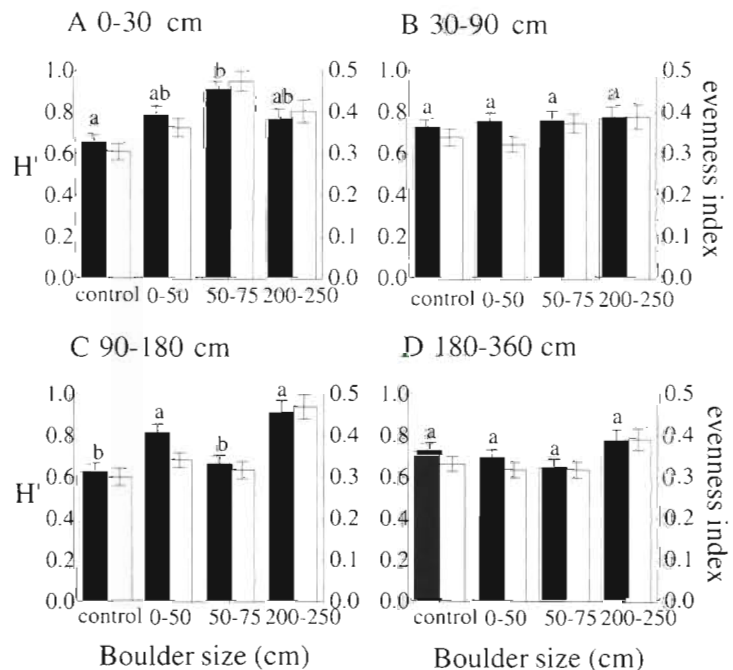


Fig. 8. Mean diversity (H') and evenness for the 4 boulder size categories, at (A) 0–30 cm, (B) 30–90 cm, (C) 90–180 cm, and (D) 180–360 cm from the edge of boulders. Boulder size categories with significantly different H' values are indicated by different letters. Evenness was not significantly influenced by treatments (\pm SE)

velocity index. Both velocity index and invertebrate biomass decreased downstream of large boulders, and the relationship between invertebrate biomass and velocity index showed a significant increase in invertebrate biomass in the middle of the overall velocity index range (Fig. 9B). Moreover, velocity on the downstream side of large boulders was always $<15 \text{ cm s}^{-1}$, and was usually $<10 \text{ cm s}^{-1}$. At other orientations, velocity was $>10 \text{ cm s}^{-1}$ at least 20% of the time, and often reached 15 cm s^{-1} (Fig. 3B). Some processes causing biomass changes (e.g. recruitment, growth, mortality) of dominant invertebrate species were positively affected by velocity over 10 cm s^{-1} . Although invertebrate biomass was significantly influenced by our treatments, Figs. 5B & 7B show that changes in *Mytilus* biomass were responsible for the observed significant patterns. The similarity between diversity and evenness patterns is further evidence that significant patterns of diversity are due to changes in the biomass of dominant species.

Flow velocity affects the structure of the boundary layer which influences invertebrate growth (Nowell & Jumars 1984). For example, Fréchette et al. (1989) showed that, over an established mussel bed, an increase in flow velocity amplifies turbulence in the boundary layer due to the roughness of the mussel bed, preventing food depletion. Butman et al. (1994)

modeled the relationship between flow speed and filtration rate in a mussel bed and showed that the depletion of phytoplankton was much faster at a flow velocity of 5 cm s^{-1} than at 15 cm s^{-1} . These results agree with ours, which showed that around large boulders, invertebrate biomass values were lower on the downstream side of boulders, where flow velocity was $<15 \text{ cm s}^{-1}$. It is possible that maximum flow velocity over the substratum limited the feeding rate of mussels downstream of large boulders, and influenced biomass levels. However, other biological processes (recruitment, emigration and mortality) affecting biomass may have been influenced by flow velocity (Gosling 1992). For instance, the relationship between flow velocity and invertebrate (mainly mussel) biomass around large boulders could also be related to the flux of larvae over the substratum or to the movement of young settlers on the substratum.

Topographic scale and community characteristics

Spatial variability in community characteristics may be explained by different environmental and biological variables according to spatial and temporal scales (Wiens 1989, Barry & Dayton 1991, Allen & Hoekstra 1992, Levin 1992, Pinel-Alloul 1995). Topographic heterogeneity has been shown to have a complex non-linear effect on benthic communities, particularly at the large scale (Archambault & Bourget 1996), but few authors have examined the influence of heterogeneity on benthic communities at meter scales. Breitburg et al. (1995) showed that the diameter (30 to 75 cm) of boulders increased the area of the flow wake in which fish larvae were capable of maintaining their position or swimming. Cusson & Bourget (1997) showed that in a soft-bottom benthic community, boulder size had a negative effect on species richness, diversity and biomass (boulders $<225 \text{ cm}$). In the present study, boulder size decreased mussel and *Fucus* sp. mean biomass and, thus, dominance, enhancing mean diversity and evenness. Changes in hydrodynamics as a function of boulder size could account for this effect, but the relationship between boulder size and the spatial structure of the benthic communities is complex. Indeed, the effect of boulder size on invertebrate biomass depended on the orientation, and there was a significant decrease in invertebrate biomass downstream of boulders as a function of boulder size. The interaction between boulder size and orientation could not be shown to account for the increase in H' as a function of boulder size. However, boulders created areas of reduced flow velocity on the downstream side which corresponded to lower abundance of dominant species (i.e. *Mytilus* and *Fucus* sp.), possibly favoring recruit-

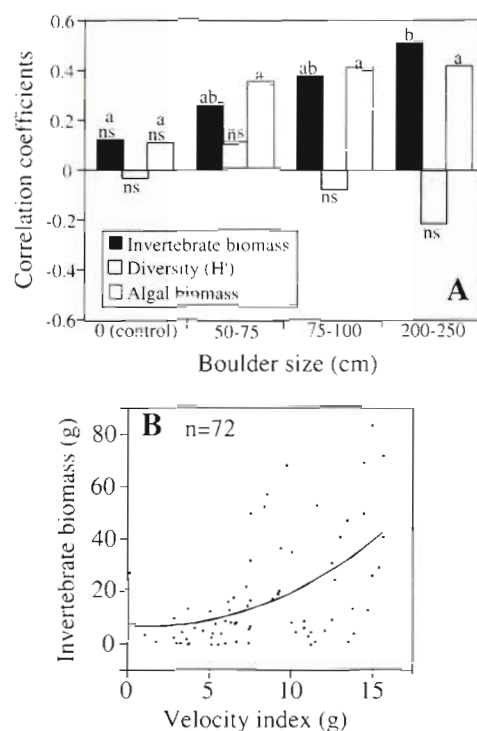


Fig. 9. Relationship between velocity index and biological variables as a function of boulder size. (A) Correlation coefficients between velocity index and biological variables (invertebrate biomass, algal biomass, H'), as a function of boulder size. Coefficients differing significantly from one another are indicated by different letters (ns = non significant coefficient). (B) Quadratic regression model (invertebrate biomass = $0.18(\text{velocity index})^2 - 0.51(\text{velocity index}) + 7.37$; $R^2 = 0.274$; $p < 0.001$) showing the influence of velocity index on invertebrate biomass

ment or development of other species. The patterns become more pronounced with greater boulder size, and may account for consistent and significant biological patterns around large boulders, and the observed decrease of invertebrate biomass and increase of diversity with boulder size. Indeed, the topographic gradient (height above zero tidal level) and heterogeneity (boulder size) can be used to predict the spatial pattern of mean algal biomass (Fig. 6).

Conclusion

Understanding and modeling how spatial scales affect or modulate the response of organisms to heterogeneity in their environment is becoming a central problem in ecological research. In marine habitats, small-scale topography has been shown to influence the settlement process via hydrodynamics (Harvey et al. 1995, Grégoire et al. 1996, Lemire & Bourget 1996). We examined the relationships between biomass,

hydrodynamics, and boulder size. Our results showed that topographic features such as boulders locally modify the patterns of flow velocity, biomass, and diversity. We also highlighted the influence of boulder size (topographic scale) on these patterns. Finally, we have shown that the strength of the relationship between biomass and an index of flow velocity increased with boulder size, confirming a scale-dependent cascade of influences linking topography, hydrodynamics and biomass.

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