

Global patterns of macroinvertebrate biomass in marine intertidal communities

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ABSTRACT: We examine global patterns of benthic macroinvertebrate biomass and its distribution among functional feeding guilds in marine intertidal communities. Variation in ash-free dry biomass was related to physical variables (mean annual air and water temperatures, sediment grain size, intertidal slope, tide range and type, wave height and exposure) by least-squares regression analysis of data for 36 rocky shores and 245 sedimentary shores. Linear combinations of physical variables explain up to 44 % of the variance in total biomass on sedimentary shores and 40 % of the variance in the biomass on rocky shores. Grain size and wave exposure are the best single predictors of total biomass for sedimentary shores and rocky shores, respectively. Biomass estimates peak in temperate regions and are an order of magnitude higher on rocky shores than on sedimentary shores. In fact, macroinvertebrate biomass on temperate rocky shores attains levels 10 to 100 times higher than those documented for other benthic marine environments. Suspension feeders tend to dominate temperate intertidal communities (they typically comprise >30 to 60 % of the macroinvertebrate biomass), reflecting the importance of benthic-pelagic coupling in these ecosystems. Contrary to consumer stress models for rocky shores, there is no compelling evidence for biomass limitation of grazers and carnivores at high wave exposure.

KEY WORDS: Macrofauna · Biomass · Benthos · Intertidal · Rocky shore · Sandy beach

INTRODUCTION

Macroscopic analyses of emergent patterns of organismal abundance, distribution, and diversity over large geographic scales have great potential for testing the generality of underlying mechanisms that structure the natural world (e.g. Currie & Fritz 1993, Brown 1995, Pearson & Carroll 1998, Lawton 1999). To date, such analyses have been used to address questions predominantly in terrestrial ecology. While marine intertidal shores are model systems for ecological research on population and community dynamics, large-scale quantitative analyses of these systems have rarely been attempted (but see Dexter 1992, McLachlan et al. 1993). This is indicated by the paucity of interecosystem comparisons in the marine literature; for example, less than 8 % (47/630) of all field studies published in 'Limnology & Oceanography' and 'Marine Ecology Progress Series' in 1996 made statistical comparisons of 2 or more

ecosystems (A. Ricciardi pers. obs.). Consequently, the generality of numerous accepted paradigms derived from experimental studies of intertidal communities is untested (Underwood & Denley 1984, Foster 1990).

Because intertidal benthic invertebrates are a major link in the energy flow between primary producers and larger consumers such as fish and shorebirds (McDermott 1983, Baird et al. 1985, Reise 1985, DeLancey 1989, Edgar & Shaw 1995), and are of substantial commercial value (FAO 1997), a predictive understanding of spatial variation in macroinvertebrate biomass has both fundamental and applied importance. Attempts to characterize this variation are challenged by the complex suite of physical and biological factors that structure coastal communities (reviewed by Connell 1975, McLachlan 1983, Dayton 1984, Underwood & Denley 1984, Foster et al. 1988, Menge & Farrell 1989, Brown & McLachlan 1990). However, in recent decades, several studies have quantitatively related regional variation in intertidal biomass to physical variables such as sediment grain size, shore slope, water temperature, and exposure to

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waves (e.g. Eleftheriou & Nicholson 1975, McQuaid & Branch 1984, 1985, McLachlan 1990, 1996, Jaramillo & McLachlan 1993, Jaramillo et al. 1993, McLachlan et al. 1993, Bustamante & Branch 1996a). Synoptic surveys of South African rocky shores have shown that macrofaunal biomass increases with increasing wave exposure (McQuaid & Branch 1984, 1985, Bustamante & Branch 1996a). In a study of 23 wave-exposed sandy beaches, McLachlan (1990) found wave height and beach slope to be significant correlates of macrofaunal biomass. A similar analysis of a larger dataset concluded that both the height and periodicity of waves play significant but weak roles in controlling biomass on exposed sandy beaches (McLachlan et al. 1993). The generality of these relationships remains to be tested across a broad range of latitudes and habitat types.

In this paper, we extend the efforts of previous studies by statistically linking intertidal macroinvertebrate biomass to physical variables over a broad range of latitudes, geographic regions, and habitat types, in order to identify important environmental predictors of biomass and to explain patterns of its distribution among major functional feeding guilds. Specifically, we examine the effects of hydrodynamic variables (e.g. grain size, wave exposure, tide range) and climatic variables (mean annual air and water temperature) on the macroinvertebrate biomass of sedimentary and rocky shores worldwide.

METHODS

Estimates of intertidal macroinvertebrate biomass were extracted from marine literature published after 1960, using Aquatic Sciences and Fisheries Abstracts on CD-ROM and references cited by review articles. We added new field data for intertidal sites in the St. Lawrence River estuary (E. Bourget unpubl. data) and Icelandic fjords (A. Ingólfsson, Institute of Biology, University of Iceland, pers. comm.). Data were thus obtained for 36 rocky shores and 245 sedimentary shores (sandy beaches and mudflats) (Table 1). We included estuarine sites with mean annual salinities $>20 \text{ g l}^{-1}$, as preliminary analysis showed no correlation between biomass and salinity above this threshold.

In the various source studies, samples were collected using corers (on sedimentary shores) or by hand from quadrats (on rocky shores) and sieved through screens with apertures ranging from 0.25 to 1.6 (median 1.0) mm. Biomass estimates used in our analysis represent values averaged across the width of the intertidal zone. Data reported as biomass per linear meter of beach (g m^{-1}) were used when information on intertidal width allowed these values to be expressed as g m^{-2} . Because

ash-free dry weight (AFDW) is the most ecologically meaningful measure of biomass (Crisp 1984), we converted all biomass estimates to AFDW using general conversion factors (Ricciardi & Bourget 1998). One-third of the biomass estimates for sedimentary shores, and half of those for rocky shores, are annual means. In addition, we included estimates averaged over days or months within a summer season. Differences associated with the use of annual and summer estimates were tested using a categorical dummy variable (0 = summer, 1 = annual) in all regression models. Whenever possible, biomass estimates were also obtained for individual functional feeding guilds (suspension feeders, deposit feeders, carnivores/scavengers, and herbivorous grazers). Each species was assigned to a guild based on its dominant dietary habit as determined from the literature (e.g. Fauchald & Jumars 1979, Barnes 1986, Brown & McLachlan 1990, Squires 1990).

Hydrodynamic and climatic predictor variables were chosen on the basis of published studies suggesting their potential influence on intertidal macroinvertebrate biomass. For sedimentary shores, hydrodynamic variables included mean grain size, mean wave height, maximum tide range, and intertidal slope. In addition, categorical exposure variables (EXP1, EXP2) were used to group sheltered sites receiving very limited wave action (EXP1 = 0, EXP2 = 0), sites fully exposed to waves (EXP1 = 0, EXP2 = 1), and sites of intermediate exposure (EXP1 = 1, EXP2 = 0). These categories were assigned solely on the basis of physical information from the source studies (or atlases) on the degree to which a site was exposed to wave action or prevailing winds; any site that was only partially exposed to prevailing winds was classified as 'intermediate'. Another categorical variable was added to distinguish diurnal and semidiurnal (including mixed) tide types. Air and water temperature variables, the latter already shown to be correlated with benthic production (Tumbiolo & Downing 1994), were also included as potential predictors. Site-specific estimates of mean annual air and water temperatures, as well as maximum tide range and type, were obtained from the source studies or from Gorshkov (1978). Latitudinal trends in intertidal biomass were also examined.

Although rocky shores may be covered by sand and gravel, we did not apply a grain size variable to them. Also, insufficient data were available to determine the relationships of wave height, intertidal slope, and tide type to rocky shore biomass. Thus, a total of 5 predictors (latitude, exposure, tide range, air and water temperature) were tested for rocky shores, while 9 were tested for sedimentary shores. Finally, because sieve mesh size varies among studies and may potentially bias biomass estimates when small organisms domi-

nate intertidal assemblages, we tested this methodological variable in all regression models for sedimentary shores. The complete dataset is available from the Depository of Unpublished Data, CISTI, National Research Council, Ottawa, Canada.

Regression procedures. Relationships between biomass and the predictor variables were modeled by least-squares linear regression (Rawlings 1988) using SAS procedures (SAS Institute Inc. 1988); the error term associated with each predictor variable was assumed to be small compared with that of the biomass variable. Biomass values spanned several orders of magnitude, and were log-transformed because the mean (m)-variance (s^2) relationship of the data ($s^2 =$

$1.74m^{2.01}$; $r^2 = 0.86$) suggested that this was the most appropriate transformation to reduce the influence of large values and stabilize variance (Downing 1979). Mean grain size estimates for sedimentary shores were standardized to their respective phi (ϕ) values (i.e. the negative log base 2 of the grain size in mm). Residual plots were inspected to determine whether transformation of other predictor variables was appropriate. Multiple regressions were generated by a stepwise selection technique with significant levels of 0.15 and 0.10 chosen *a priori* for variable entry and retention, respectively. These regression models included categorical variables (following Hardy 1993) and were generated separately for rocky and sedimentary shore

Table 1. Sources of data used in regression analyses of intertidal macroinvertebrate biomass

Region	No. sites	Latitude range	Source
Arctic/subarctic			
Rocky shores	3	65°N–69°N	Ingólfsson (1996, unpubl. data), Zenkevitch (1963)
Sedimentary shores	4	64°N–73°N	Ellis (1960), Ingólfsson (1996, unpubl. data), Olafsson (1991)
Western Atlantic			
Rocky shores	3	48°N	Archambault & Bourget (1996), Bourget (unpubl. data)
Sedimentary shores	36	35°S–49°N	Sanders et al. (1962), Moore et al. (1968), Hughes & Thomas (1971), Dexter (1972, 1979), Edwards (1973), Croker et al. (1975), Maurer (1977), Holm (1978), Larsen (1979), Maurer & April (1979), Carlo (1980), Swennen et al. (1982), Bourget & Messier (1983), McDermott (1983), Schwinghamer et al. (1986), Defeo et al. (1992), Hubertz et al. (1994), Heck et al. (1995)
Eastern Atlantic			
Rocky shores	11	34°S	McQuaid & Branch (1984, 1985)
Sedimentary shores	87	34°S–59°N	Ushakov (1965), Seed & Lowry (1973), Eleftheriou & Nicholson (1975), Eleftheriou & McIntyre (1976), Hibbert (1976), Withers (1977), Koop & Griffiths (1982), Bally (1983, 1987), McLachlan (1985a, 1996), Tarr et al. (1985), Warwick & Ruswahyuni (1987), Donn & Cockcroft (1989), Dewarumez et al. (1991), Kalejta & Hockey (1991), Wolff et al. (1993), Arias & Drake (1994), McLusky et al. (1994), Sprung (1994), Bachelet et al. (1996)
Mediterranean			
Sedimentary shore	1	43°N	Massé (1972)
Gulf of Mexico			
Sedimentary shores	5	27°N–30°N	Bloom et al. (1972), Shelton & Robertson (1981)
North Sea			
Sedimentary shores	36	51°N–59°N	Gray & Rieger (1971), Beukema (1974), Kay & Knights (1975), Wolff & Wolff (1977), Reise (1985), Möller (1986), McLusky (1987), Eleftheriou & Robertson (1988), Meire et al. (1991), Kristensen (1993), Reise et al. (1994)
Pacific			
Rocky shores	15	33°N–48°N	Glynn (1965), Batzli (1969), Littler (1980), Straughan (1982), Fuji & Nomura (1990), Littler et al. (1991), Iwasaki (1995)
Sedimentary shores	25	44°S–48°N	Pamatmat (1968), Dexter (1972, 1979), Nichols (1977), McLachlan (1990), Jaramillo et al. (1993), McLachlan et al. (1993), Edgar & Shaw (1995), Haynes & Quinn (1995)
Indian Ocean			
Rocky shores	4	30°S–49°S	McLachlan et al. (1981a), Lawrence & McClintock (1987), Fielding et al. (1994)
Sedimentary shores	51	49°S–16°N	McIntyre (1968), Trevallion et al. (1970), Eleftheriou & Jones (1976), Hughes & Gamble (1977), McLachlan (1977a,b, 1985b, 1990), Ansell et al. (1978), Dye et al. (1981), McLachlan et al. (1981b), Woolridge et al. (1981), Broom (1982), Wendt & McLachlan (1985), Kurian & Baba (1987), Warwick & Ruswahyuni (1987), Erfemeijer & Swenner (1990), Edgar & Shaw (1995)

data. As the latter data set included a few sites where macrofauna were absent, biomass values were transformed as $\log_{10}(x + 0.01)$.

Statistical treatment of zero values. The constant scaling parameter b in the $\log_{10}(x + b)$ transformation is generally chosen to represent the lowest detectable non-zero value. However, because the detection limit varies among the source studies used in our analysis, we cannot select a representative scaling parameter that will correct for the numerous zero values obtained for functional feeding guilds in our sedimentary shore data. The number of zeroes obtained were 19 (out of 83 estimates) for suspension feeders, 8 (of 83 estimates) for carnivores, 14 (of 83 estimates) for deposit feeders, and 50 (of 81 estimates) for grazers. Preliminary regression analysis showed that the choice of scaling parameter in logarithmic transformation influenced the coefficient of determination (R^2) for models involving functional feeding guilds. Preliminary analyses using the fourth-root transformation (Downing 1979) showed similar strong biases from zero values and failed to achieve the criterion for normality. In fact, there is no known transformation that will correct for the presence of zeroes (McArdle et al. 1990); thus zero values obtained for each functional feeding guild in sedimentary shore data were omitted *a priori* from regression analysis. Even after exclusion of zeroes, biomass estimates for each functional feeding guild

spanned 3 to 5 orders of magnitude and included numerous small values, i.e. $<1 \text{ g m}^{-2}$ (Table 2).

We used discriminant function analysis to examine the presence or absence (zero biomass) of individual feeding guilds on sedimentary shores in relation to physical environmental factors. We first used a step-wise discriminant analysis to select predictor variables that best distinguished sites with and without the particular feeding guild, and then ran all significant predictors in a second analysis to produce linear discriminant functions (SAS Institute Inc. 1988). The ability of the discriminant functions to correctly classify the presence or absence of a particular feeding guild was assessed by an F -test on the Wilks' lambda statistic. The number of correctly classified sites for both categories are presented.

RESULTS

Macroinvertebrate biomass estimates for sedimentary shores do not vary linearly with latitude, but peak values ($<380 \text{ g m}^{-2}$) occur in north and south temperate

Table 2. Ranges and median values for variables used in regression analyses

	Range (min–max)	Median	N
Rocky shores			
Total biomass (g m^{-2})	7.34 – 1143.9	79.1	36
Suspension feeders (g m^{-2})	0.3 – 1089	35.72	24
Carnivores (g m^{-2})	0.02 – 33.6	3.6	21
Deposit feeders (g m^{-2}) ^a	0.003 – 4.7	0.9	19
Grazers (g m^{-2})	0.31 – 97.8	22.9	23
Air temperature ($^{\circ}\text{C}$)	0.3 – 21.2	15.8	36
Water temperature ($^{\circ}\text{C}$)	4 – 22.7	16.0	36
Tide range (m)	0.98 – 4.8	1.75	36
Sedimentary shores			
Total biomass (g m^{-2})	0 – 380.4	3.7	245
Suspension feeders (g m^{-2}) ^a	0.004 – 339.8	1.37	64
Carnivores (g m^{-2}) ^a	0.02 – 16.29	0.14	75
Deposit feeders (g m^{-2}) ^a	0.001 – 29.51	1.21	69
Grazers (g m^{-2}) ^a	0.001 – 9.7	0.18	31
Air temperature ($^{\circ}\text{C}$)	–14.9 – 27.8	11.9	245
Water temperature ($^{\circ}\text{C}$)	1.0 – 29.0	12.1	245
Tide range (m)	0.1 – 15.0	2.7	239
Wave height (m)	0.3 – 3.2	1.3	53
Slope (%)	0.1 – 20.0	3.6	105
Sediment grain size (ϕ)	–1.23 – 7.5	2.25	212

^aExcluding zero values

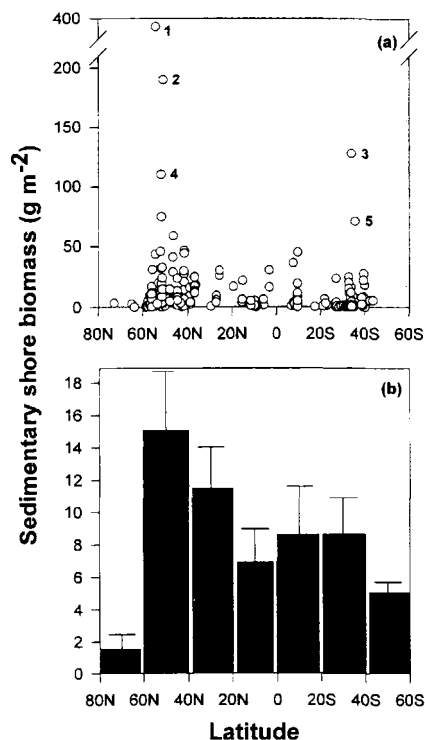


Fig. 1. Latitudinal distribution of biomass (ash-free dry weight) estimates for macroinvertebrates on sedimentary shores. (a) Scatterplot of data: 1, Konigshafen (Germany); 2, Hamble Spit (England); 3, Maitland River (South Africa); 4, Oosterschelde (Netherlands); 5, Barker Inlet (Australia). (b) Mean biomass (\pm SE) for 20° latitudinal intervals. Interval size was chosen to include a minimum of at least 3 data points per interval

regions (Fig. 1). The highest estimates of any intertidal system (500 to 1150 g m⁻²) are found on temperate rocky shores. Macroinvertebrate biomass in temperate regions is 14 times higher on rocky shores than on sedimentary shores, owing to dense populations of suspension feeders and grazers (Fig. 2) that account for an average 55% and 35% of the total biomass, respectively. On temperate sedimentary shores, by contrast, suspension feeders typically comprise about 35%, deposit feeders ~30%, carnivores ~30%, and grazers 5% of the macroinvertebrate biomass.

Effects of individual physical variables on intertidal biomass

Rocky shores

There are some marked differences in the effects of physical factors on rocky and sedimentary shore fauna. On rocky shores, total macroinvertebrate biomass is correlated weakly with mean annual water temperature (Fig. 3) and strongly with wave exposure (Fig. 4). Mean annual water temperature has positive effects on carnivores ($r^2_{\text{adj}} = 0.14$, $p = 0.050$) and grazers ($r^2_{\text{adj}} = 0.12$, $p = 0.059$). Wave exposure has a strong influence only on suspension-feeder biomass (Fig. 5). Total biomass is also correlated negatively with tide range ($r^2_{\text{adj}} = 0.08$, $p = 0.049$); large tide ranges are associated with reduced biomass estimates for carnivores ($r^2_{\text{adj}} = 0.16$, $p = 0.039$) and grazers ($r^2_{\text{adj}} = 0.11$, $p = 0.066$), but have no apparent effect on suspension feeders and deposit feeders.

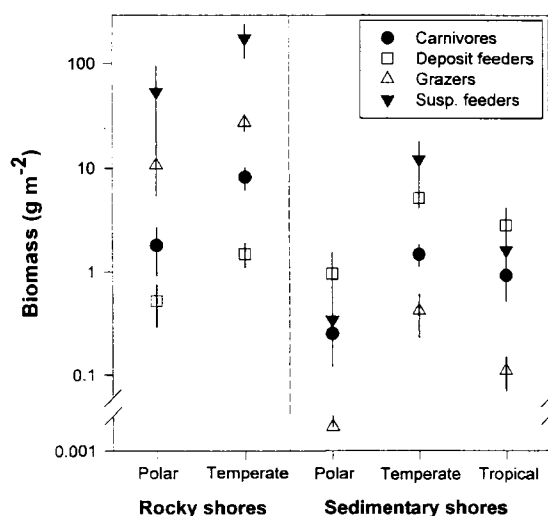


Fig. 2. Distribution of biomass among functional feeding guilds on polar (>60°N), temperate (25° to 60°N, S), and tropical (0 to 25°N, S) shores. Standard error bars are shown. Note break in vertical logarithmic axis

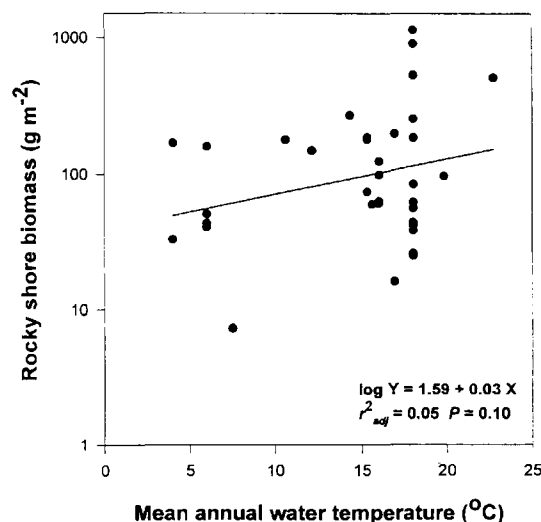


Fig. 3. Relationship between mean annual water temperature and macroinvertebrate biomass on rocky shores

Sedimentary shores

On sedimentary shores, total macroinvertebrate biomass does not vary significantly with mean annual air and water temperature variables. Nevertheless, water temperature has a negative effect on the biomass of grazers ($r^2_{\text{adj}} = 0.17$, $p = 0.011$), suspension feeders ($r^2_{\text{adj}} = 0.06$, $p = 0.028$), and carnivores ($r^2_{\text{adj}} = 0.08$, $p = 0.009$), but has no detectable effect on deposit-feeder biomass, which normally accounts for a third of the total biomass. Total biomass increases with wave height at exposed sites, but varies inversely with wave exposure for sedimentary shores in general (Fig. 6)

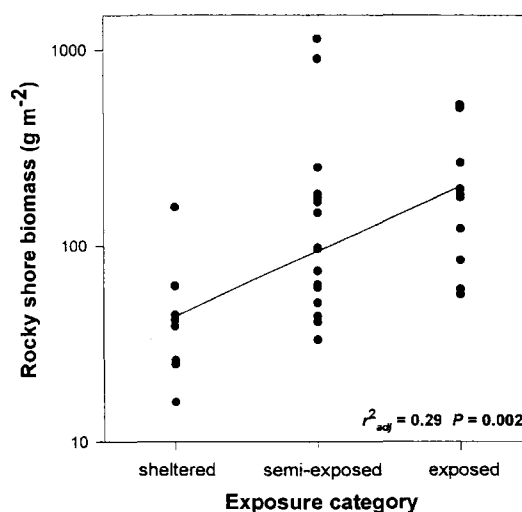


Fig. 4. Relationship between the degree of wave exposure and macroinvertebrate biomass on rocky shores

because of the high abundances of deposit feeders and carnivores at sheltered sites (Fig. 7). Total biomass is highest on flat beaches (Fig. 6), again reflecting a high abundance of deposit feeders. Grazer biomass follows an opposite pattern by increasing with beach slope (Fig. 8).

Tide range has a weak negative influence on suspension-feeder biomass ($r^2_{\text{adj}} = 0.07$, $p = 0.02$) and a positive influence on deposit-feeder biomass ($r^2_{\text{adj}} = 0.13$, $p = 0.002$). These effects are most pronounced at sheltered sites ($r^2_{\text{adj}} = 0.25$, $p = 0.001$ for suspension feeders; $r^2_{\text{adj}} = 0.19$, $p = 0.004$ for deposit feeders). Tide range has a positive effect on carnivore biomass only on exposed shores ($r^2_{\text{adj}} = 0.10$, $p = 0.046$), while tide type has no detectable effect on any functional feeding guild.

The effect of grain size is greater than that of any other variable. The relationship between total biomass and mean grain size is curvilinear (Fig. 6), with biomass reaching peak levels on mudflats ($>5 \phi$ units) and fine-grained sandy beaches (2 to 3 ϕ units), and minimal levels on unstable coarse sands ($<1 \phi$ units). Deposit-feeder biomass increases with decreasing grain size (i.e. increasing ϕ values; $r^2_{\text{adj}} = 0.33$, $p < 0.0001$), while no significant trends are found for the

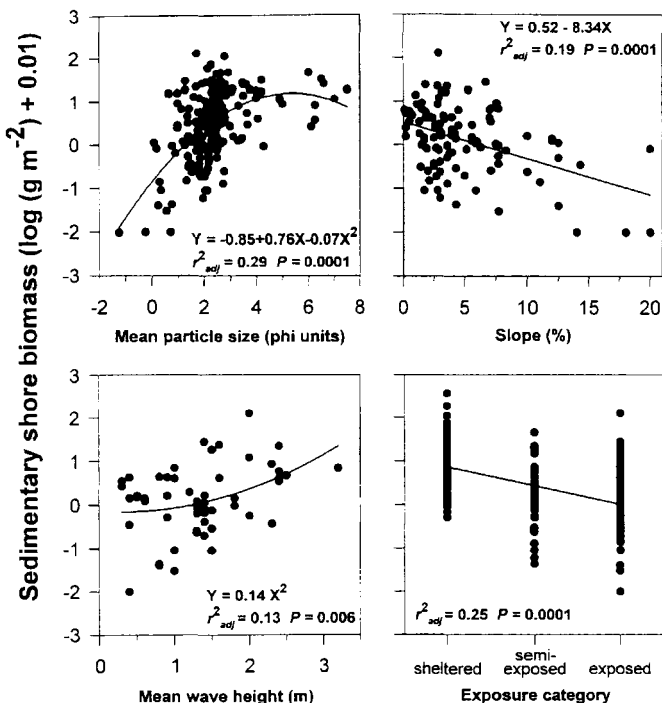


Fig. 6. Relationships between macroinvertebrate biomass and physical variables on sedimentary shores

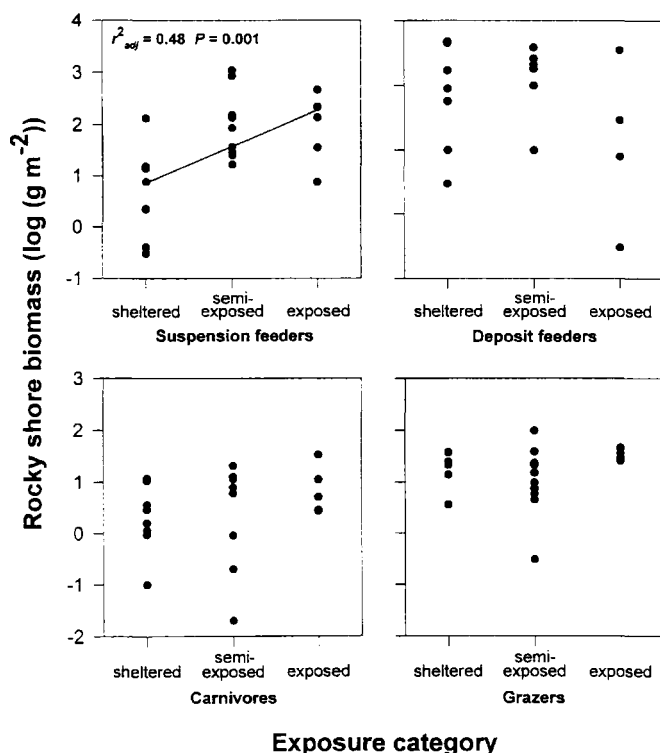


Fig. 5. Patterns of biomass for different functional feeding guilds in relation to categories of wave exposure on rocky shores. Note that some rocky shores lack deposit feeders or grazers; thus sample sizes vary

other functional feeding guilds. Sieve mesh size was not a significant correlate of total biomass nor of any guild except for deposit feeders ($r^2_{\text{adj}} = 0.24$, $p = 0.0001$); but even this correlation became insignificant when the effect of covariance with grain size was partialled out.

Linear discriminant functions successfully classified 60 to 80 % of shores in which the biomass of the respective functional feeding guild was estimated to be zero (Table 3). The best functions were obtained for carnivores, using tide variables, grain size, and intertidal slope as predictors. Grain size was a significant predictor for every guild except grazers.

Multiple regression models

Multiple regressions explain up to 44 % and 40 % of the variance of total macroinvertebrate biomass on sedimentary and rocky shores, respectively (Tables 4 & 5). Stepwise regression rejected collinear combinations of variables, often resulting in models composed of only 2 or 3 predictors; thus, independent variables that were significant in simple regressions were sometimes rejected as redundant predictors in multiple regressions. Tables 4 & 5 list the best multiple regression models obtained for sedimentary and rocky shores. For sedimentary shore data, grain size accounts

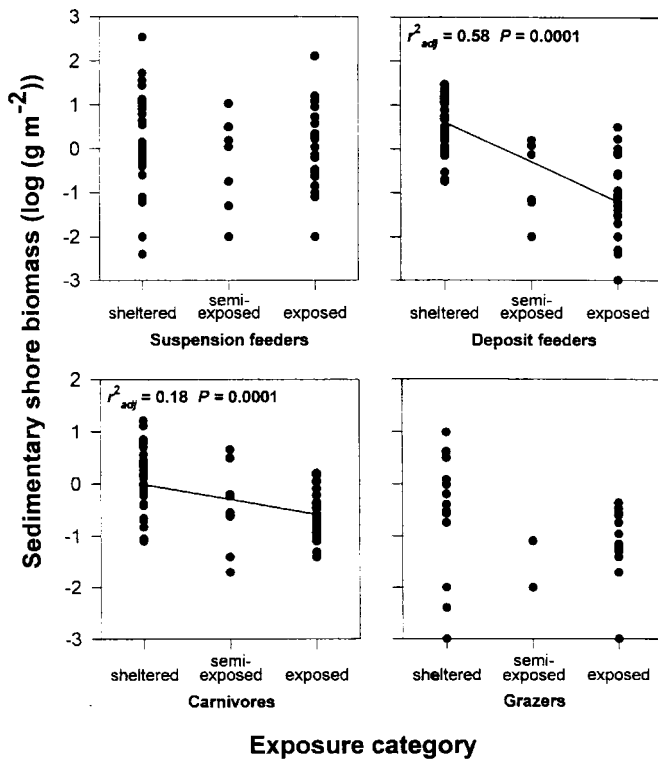


Fig. 7. Patterns of biomass for different functional feeding guilds in relation to categories of wave exposure on sedimentary shores

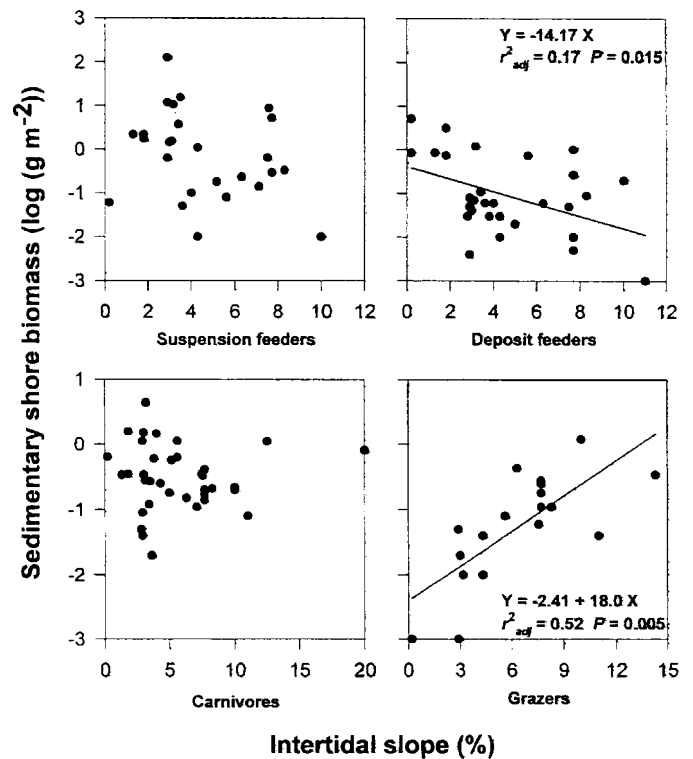


Fig. 8. Patterns of biomass for different functional feeding guilds in relation to tide range on sedimentary shores

for about a third of the variance in total biomass—more than that explained by exposure, wave height, and tide variables combined. For rocky shore data, a combination of water temperature and wave exposure variables explains a significant fraction of the variance in total biomass.

Methodological variables are insignificant in this analysis. Sieve mesh size was consistently rejected as a

predictor in all stepwise models in which grain size is tested. The categorical variable distinguishing annual and summer mean biomass estimates was rejected as a predictor in all sedimentary and rocky shore models.

Multiple regression models also highlight the disparate influences of various physical factors on sedimentary and rocky shore functional feeding guilds. Variation in deposit-feeder biomass on sedimentary

Table 3. Discriminant functions (D1, D2) that classify sedimentary shores with and without functional feeding guilds on the basis of site characteristics. Coefficients for each predictor variable are shown as table entries. The feeding guild is predicted to be absent (i.e. biomass = 0) if $D1 > D2$, and present (biomass > 0) if $D1 < D2$. The number of sites classified correctly by each function is presented

	Suspension feeders		Deposit feeders		Grazers		Carnivores	
	D1	D2	D1	D2	D1	D2	D1	D2
Constant	-4.770	-6.583	-0.427	-6.621	-2.089	-1.125	-14.405	-8.200
Grain size ($-\log_2 \text{mm}$)	1.935	5.791	1.804	5.367	-	-	-6.092	-0.552
Grain size ($-\log_2 \text{mm}$) ²	-0.215	-0.790	-0.249	-0.670	-	-	-	-
Intertidal slope (%)	-	-	-	-	-	-	-16.208	-9.168
Tide range (m)	-	-	-	-	1.602	1.176	3.088	2.424
Tide type	-	-	-	-	-	-	17.571	6.379
Air temperature (°C)	0.411	0.265	0.400	0.286	-	-	-	-
Correct classifications	11/18	49/57	9/15	55/59	24/30	25/48	5/8	33/33
Wilks' lambda	0.654		0.683		0.932		0.490	
p	0.0001		0.0001		0.0001		0.0001	

Table 4. Best multiple regression models for predicting sedimentary shore macroinvertebrate biomass [\log_{10} (g AFDW m^{-2})] for the entire community (Total) and principal functional feeding guilds. Regression coefficients for each predictor variable are shown as table entries. Numbers in parentheses are standard errors (SE) for the coefficients. -: not tested; ns: tested but not significant; ^ap < 0.10, *p < 0.05, **p < 0.01, ***p < 0.001

	Total	Suspension feeders	Deposit feeders	Grazers	Carnivores
Intercept	ns	1.36 (0.44)***	ns	-2.41 (0.30)***	ns
Grain size ($-\log_2 mm$)	0.68 (0.11)***	ns	0.19 (0.11) ^a	ns	ns
Grain size ($-\log_2 mm$) ²	-0.07 (0.01)***	ns	ns	ns	ns
Intertidal slope (%)	-	-	-	18.0 (4.1)***	-
Exposure (EXP1)	-0.54 (0.11)***	ns	-1.20 (0.34)***	ns	-0.37 (0.21) ^a
Exposure (EXP2)	-0.46 (0.11)***	ns	-1.52 (0.22)***	ns	-0.52 (0.14)***
Tide range (m)	-0.09 (0.02)***	-0.22 (0.09)*	0.16 (0.07)*	ns	ns
Tide type	-0.92 (0.25)***	ns	ns	ns	ns
Water temperature (°C)	ns	-0.5 (0.02)*	ns	ns	-0.02 (0.01) ^a
R ² _{adj}	0.444	0.173	0.671	0.517	0.210
p	<0.0001	0.0075	<0.0001	0.0005	0.0002
SE of estimate	0.578	0.913	0.669	0.545	0.543
N	204	54	58	18	75

shores is well predicted by a combination of wave exposure, grain size and tide range ($R^2_{adj} = 0.67$, $p = 0.0001$), while no significant models can be derived for deposit feeders on rocky shores. Wave exposure explains 44 % of the variation in suspension feeder biomass on rocky shores, but has no general predictive value for suspension feeders on sedimentary shores. Conversely, wave exposure does not predict carnivore biomass on rocky shores, but is correlated negatively with carnivore biomass on sedimentary shores (Figs. 5 & 7). The average amount of variation in functional feeding guild biomass explained by multiple regression models is 39 % for sedimentary shores and 24 % for rocky shores.

DISCUSSION

Latitudinal patterns of intertidal biomass

Maximal biomass values on temperate shores (Fig. 1) may be the net result of limiting factors in polar and tropical regions, including the relatively high abundance and diversity of mobile predators in the tropics (Bertness et al. 1981, Menge & Lubchenco 1981, Lubchenco et al. 1984, Garrity et al. 1986) and freezing temperatures and ice disturbance at high latitudes (Bourget et al. 1985, Bergeron & Bourget 1986, Pugh & Davenport 1997). However, during ice-free seasons, even arctic shores can support biomass levels that are at least as great as those of tropical shores (Fig. 1; Ellis 1960, Zenkevitch 1963). Tropical shores (reviewed by Alongi 1990) are also subject to intense climatic disturbance, severe desiccation stress, variable salinity regimes, hypoxic waters, and intensely heated sands (exceeding 50°C; Dexter 1979).

Furthermore, primary planktonic production appears to be transferred to higher trophic levels less efficiently at warmer latitudes (Petersen & Curtis 1980). Less phytoplankton production may reach tropical benthos because it is continuous and in phase with zooplankton production (Levinton 1982, Banse & English 1994). By contrast, phytoplankton production in temperate regions is highly seasonal and a larger amount may escape pelagic herbivores and thus become available for benthic consumption, particularly by suspension feeders (Fig. 2). The biomass of temperate shore communities is also enhanced by inputs of organic detritus from kelp beds, particularly in winter when phytoplankton production is low (Duggins et al. 1989, Bustamante & Branch 1996b).

Influence of temperature and tide variables

In the multiple regression model for rocky shores (Table 5), mean annual water temperature is a significant predictor of the total macroinvertebrate biomass, and the best single predictor of grazer biomass. Some low biomass values associated with mean annual water temperatures <10°C (Fig. 3) may represent, at least in part, disturbance due to ice scour (e.g. at St. Lawrence River estuary sites; Bergeron & Bourget 1986). The inverse correlation between carnivore biomass and tide range ($r^2_{adj} = 0.16$, $p = 0.039$) may reflect the environmental stress that a wide intertidal zone places on predators which cannot easily escape to a subtidal refuge.

On sedimentary shores, by contrast, water temperature has a negative effect on the biomass of grazers, suspension feeders, and carnivores. For grazers, the best multiple regression model obtained was based

Table 5. Best multiple regression models for predicting rocky shore macroinvertebrate biomass [\log_{10} (g AFDW m^{-2})] for the entire community (Total) and principal functional feeding guilds (no significant models were obtained for deposit feeders). Regression coefficients for each predictor variable are shown as table entries. Numbers in parentheses are standard errors (SE) for the coefficients. ns: tested but not significant; * $p < 0.10$, ** $p < 0.05$, *** $p < 0.001$

	Total	Suspension feeders	Grazers	Carnivores
Intercept	1.21 (0.19)***	0.64 (0.25)*	0.66 (0.29)*	1.25 (0.40)**
Exposure (EXP1)	0.62 (0.16)***	1.39 (0.34)***	ns	ns
Exposure (EXP2)	0.61 (0.17)**	1.35 (0.39)**	ns	ns
Tide range (m)	ns	ns	ns	-0.36 (0.16)*
Tide type	ns	ns	ns	ns
Water temperature (°C)	ns	ns	0.04 (0.02) ^a	ns
Water temperature (°C) ²	0.001 (0.001)*	ns	ns	ns
R ² _{adj}	0.400	0.435	0.119	0.163
p	0.0004	0.001	0.0596	0.0395
SE of estimate	0.374	0.715	0.532	0.742
N	36	24	23	21

exclusively on intertidal slope (Table 4). The next best model was based solely on a negative correlation with mean annual water temperature ($r^2_{adj} = 0.18$, $p = 0.011$). Deposit-feeder biomass appears unrelated to both mean annual temperature variables. In multiple regression models, tide range has opposing effects on suspension feeders and deposit feeders. When the data are stratified according to degree of wave exposure, tide range shows significant effects only at sheltered sites, where it is correlated negatively with suspension-feeder biomass ($r^2_{adj} = 0.25$, $p = 0.001$) and positively with deposit-feeder biomass ($r^2_{adj} = 0.19$, $p = 0.004$); these trends support the generalization that tidal currents are the major supplier of nutrients, food, and larvae to sheltered marine habitats but can also raise concentrations of suspended solids and flocculant material high enough to inhibit active suspension feeders (Leonard et al. 1998).

Influence of sedimentary shore morphology: grain size and intertidal slope

The negative relationship between slope and biomass occurs over a wide range of beach types and tidal regimes (Fig. 6) and can be explained by 2 factors, wave energy and shore stability. The slope of a sedimentary shore determines how much wave energy is dissipated on intertidal sands. Reflective beaches have steep faces and coarse sands, and reflect wave energy back to sea. Dissipative beaches have flat slopes and fine-grained sands, and are subject to heavy wave action whose energy is dissipated over the intertidal zone (Brown & McLachlan 1990). Macroinvertebrate biomass tends to be higher on dissipative beaches (McLachlan 1990, McLachlan et al. 1993), whose swash climates allow greater retention of organic par-

ticles for suspension feeders and deposit feeders (Talbot & Bate 1989).

The second important factor, shore stability, is the capacity of a shore to resist morphological variation due to wave or tidal disturbance. Coarse-grain beaches tend to be too unstable to support dense macroinvertebrate populations (Eleftheriou & Nicholson 1975, Dexter 1976, 1988, McLachlan 1985b, Allan & Moore 1987, Jaramillo & McLachlan 1993). Overall, intertidal biomass is greatest on rocky shores (generally, -11 to -6 ϕ units, depending on the proportions of sand, gravel, and boulders), but declines precipitously to nearly negligible values on gravel beaches (-1 to 1 ϕ units), and then increases with progressively smaller grain sizes toward compact fine sands and mudflats (Fig. 6). Discriminant function analysis predicts the absence of suspension feeders, deposit feeders, and carnivores on shores with large grain sizes (<1 ϕ units), and intertidal slope is the major threshold factor for grazers (Table 3). Therefore, human activities that reduce the stability of sedimentary shores, such as beach sand harvesting (which causes intertidal recession; Carter et al. 1992) and the disposal of mine tailings (which increases sediment size and beach slope; McLachlan 1996), may cause substantial reductions in the biomass and trophic composition of resident macrofauna.

Influence of wave exposure

Because there is no widely used method of measuring spatial variation in wave exposure, our synthesis of literature data required that we use a simple discrete variable to compare sites. Thus, our classification is somewhat subjective and does not distinguish between exposed sites with different wave fetches. Nevertheless, a few strong patterns emerge. Total biomass

is higher on exposed (rather than on sheltered) rocky shores, due mostly to dense populations of suspension-feeding mussels, barnacles, and ascidians (Figs. 4 & 5). The opposite trend is observed for sedimentary shores (Fig. 6), supporting the broad generality of regional observations in Scotland, South Africa, and Chile (Eleftheriou & Nicholson 1975, Eleftheriou & McIntyre 1976, McQuaid & Branch 1984, 1985, Jaramillo & McLachlan 1993, Bustamante et al. 1995, Bustamante & Branch 1996a). Macroinvertebrate biomass on sheltered rocky shores, where macroalgal standing stocks may be large, tends to be dominated by grazers (Dayton 1971, McQuaid & Branch 1984, 1985, Bustamante & Branch 1996a, Ingólfsson 1996, unpubl. data). On sheltered sedimentary shores, a rich microflora is often present (Broom 1982, McLachlan 1983, Reise 1985, Schwinghamer et al. 1986, Kristensen 1993) and deposit feeders and carnivores/scavengers reach their maximum biomass (Fig. 7).

Increased exposure to wave action results in increased food availability and feeding time for suspension feeders (Fréchette & Bourget 1985), which demonstrate higher growth potential on exposed versus sheltered rocky shores (Bertness et al. 1991, Dahlhoff & Menge 1996). Indeed, mussel beds on exposed rocky shores have been shown to be as productive as rainforests (Leigh et al. 1987). As a result of the extraordinary abundance and growth of sessile suspension feeders, macroinvertebrate biomass on temperate rocky shores (Table 2) reaches peak values that are 10 to 100 times higher than those recorded in subtidal (non-Antarctic), continental slope, and deep-sea benthic environments (Zenkevitch 1963, Alongi 1990, Brey & Gerdes 1997).

Field experiments have shown mobile predators and grazers to be less efficient at foraging on exposed rocky shores (Lubchenco & Menge 1978, Menge 1978, Peterson 1979, Burrows & Hughes 1989), unless they have access to refugia provided by surface heterogeneity (Gosselin & Bourget 1989). Thus, environmental stress models of community structure (Menge & Sutherland 1987, Menge & Olson 1990) predict that mobile consumers (carnivores/scavengers and grazers) will be limited by high wave exposure. However, our data show no evidence of carnivore and grazer biomass limitation on exposed rocky shores (Fig. 5). Conversely, carnivore biomass is reduced on exposed sedimentary shores (Fig. 7), due possibly to a greater susceptibility to wave stress.

Why do suspension feeders dominate rocky shores?

To address the question of why suspension feeders tend to dominate the world's rocky shores, we must

consider the sources of food available to the various functional feeding guilds. Suspension feeders exploit diverse particulate food resources (phytoplankton, detritus, bacteria, dissolved organic matter) produced in a 3-dimensional pelagic environment and replenished by wave action and tidal currents that flow over attached and sedentary animals (Fréchette & Bourget 1985, Gili & Coma 1998). By contrast, except for periodic strandings of macroalgal debris (McLachlan 1985b, Bustamante & Branch 1996b), the food of grazers is produced in relatively limited 2-dimensional space *in situ*. Accordingly, a study of South African rocky shores by Bustamante et al. (1995) found that suspension-feeder biomass was correlated with nearshore primary planktonic production while the biomass of grazers was correlated with intertidal benthic algal production. Broad access to diverse food sources, combined with relatively low energetic cost of food capture for sessile organisms, suggests that the success of benthic suspension feeders is related, at least in part, to optimal foraging (Riisgård & Larsen 1995, Gili & Coma 1998).

The somatic growth of suspension feeders on rocky shores has been shown to be limited by nearshore phytoplankton concentration (Bertness et al. 1991, Fréchette & Grant 1991, Dahlhoff & Menge 1996, Loo & Rosenberg 1996) and the influx of kelp-derived organic matter (Duggins et al. 1989). Similarly, high inputs of particulate organic matter (e.g. from surf diatom blooms, or advection from upwelling zones) are correlated with high suspension-feeder biomass on sandy beaches (McLachlan 1983). As suspension feeders are dominant components of intertidal systems and often support a rich associated fauna (Fielding et al. 1994, Seed 1996, McKindsey & Bourget unpubl.), nearshore primary production may be a useful predictor of intertidal biomass over large geographic scales if data of sufficient spatial resolution are available (Bustamante et al. 1995, Menge et al. 1997).

CONCLUSIONS

Our analysis identifies several patterns along latitudinal, hydrodynamic, and climatic gradients. While the heterogeneity of our data obviously reduces precision in the regression models, highly significant trends observed for grain size, wave height, exposure, shore slope, tide and temperature variables demonstrate the strong influence of these physical factors on intertidal macroinvertebrate biomass. Wave exposure appears to be a factor of universal importance in limiting intertidal biomass; this is not surprising given that exposure combined with wave energy determines sedimentary shore profiles and stability, affects sediment charac-

teristics (texture, organic content, oxygen content of interstitial water), delivers food resources and larvae, and can mediate biological interactions (predation, competition, commensalism) (Fréchette & Bourget 1985, Menge & Farrell 1989, Talbot & Bate 1989, Brown & McLachlan 1990).

Community composition and abundance on intertidal rocky shores is traditionally viewed as the outcome of biological interactions, modified by environmental stressors (Dayton 1971, Paine 1974, Connell 1975, Peterson 1979, Menge & Farrell 1989, and others). Although the scarcity of published biomass estimates for rocky shores limits statistical power, the significant amount of variance explained by our models supports the broad validity of the concept of the rocky shore as an environment in which secondary production is strongly influenced by climatic and hydrodynamic factors. Conversely, exposed sedimentary shores are assumed to be physically controlled systems where biological interactions have negligible influence on community structure (McLachlan et al. 1983, Brown & McLachlan 1990, Dexter 1992). The generality of this paradigm has been challenged (Defeo et al. 1997), and the large residual variance for sedimentary shores in our models may partly reflect the importance of predation in regulating macroinvertebrate biomass (Baird et al. 1985, Möller 1986).

The substantial contribution to intertidal biomass by suspension feeders suggests that further precision in our empirical models would likely be obtained by accounting for spatial differences in nearshore primary productivity. Factors that influence the delivery of organic matter and nutrients to intertidal shores (e.g. wave energy and periodicity; coastal upwelling) may also prove to be important predictors of biomass (Bosman et al. 1987, Leigh et al. 1987). However, any major improvements in precision will require additional comparable data which are not presently available in the literature. The relative paucity of community biomass data for rocky shores is surprising given the popularity of these environments for ecological experimentation. More data are required, particularly for tropical rocky shores, to make further generalizations about organismal abundance in intertidal systems. Therefore, we strongly encourage researchers to make raw data broadly accessible, e.g. by placing them on Internet websites. This practice would help pave the way for statistical syntheses to identify other global trends and test the generality of theories in marine ecology.

Acknowledgements. We are grateful to A. Ingólfsson for sharing unpublished data on Icelandic shores, and P. Archambault for information on St. Lawrence River estuary sites. We also thank L. E. Johnson, H. M. Reiswig, and C. McKindsey for

thoughtful comments on the manuscript. This work was funded by a postdoctoral fellowship to A.R. from the Natural Sciences and Engineering Research Council of Canada.

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*Editorial responsibility: Otto Kinne (Editor),
Oldendorf/Luhe, Germany*

*Submitted: December 28, 1998; Accepted: April 9, 1999
Proofs received from author(s): July 29, 1999*